Primate Ecology:
Studies of feeding and ranging behaviour in lemurs, monkeys and apes

Edited by

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Preface

After reading its title, the ecologist with little experience of primate field research may be surprised at the contents of this book. All the 17 field studies which it includes are concerned with the ecology or behaviour of particular social groups of primates rather than of whole populations. None of them touches on population dynamics in any depth and only two investigate energetic aspects of feeding behaviour. Instead, they describe behavioural aspects of ecology: activity patterning, food selection and ranging behaviour.

Differences between ecological research on primates and research on other vertebrates have developed for two reasons. First, interest in primate ecology has been stimulated by investigation of the adaptive significance of social systems. Early attempts to investigate their functional aspects of social behaviour relied on correlations between particular kinds of social system and gross ecological variables such as habitat or diet type (e.g. Crook and Gartlan, 1966). Subsequent critiques (Struhsaker, 1969; Clutton-Brock, 1974a; S. A. Altmann, 1974; Wilson, 1975) pointed out that social behaviour varies widely between species allocated to the same ecological category and challenged the view that interspecific differences were closely related to ecological variation at this level. This, in turn, led to the development of detailed research in those aspects of primate ecology most likely to reveal the adaptive significance of differences in social behaviour: food selection, the availability and dispersion of supplies, ranging behaviour, variation in grouping patterns and antipredator behaviour.

A second, and perhaps more important, reason for the divergence between primate studies and those of most other vertebrates, is the difference in accessibility of ecological information. Most primates cannot be trapped with ease; it is often both impracticable and undesirable to consider killing adequate samples of animals; and the majority of species have relatively long lifespans. Difficulties are enhanced by the fact that only small numbers of individuals can usually be sampled since unhabituated animals can rarely be observed consistently. Consequently, it is seldom possible to collect the kind of information required for detailed research on population dynamics. In contrast, because individual animals can usually be recognized and their behaviour followed (if intermittently) over considerable time periods, it is often possible to examine a range of questions not accessible to most studies of other vertebrates. For example, it is frequently feasible to assess interindividual variation in food selection, to describe sequences of food choice and to measure ranging patterns. While it is important that future studies should investigate more traditional ecological questions, the main contribution to vertebrate ecology that primate studies can provide may lie primarily in those areas of behavioural ecology to which the observation conditions are best suited.

Between 1972 and 1974, a regular discussion group of primate field workers developed in England. We met for one-day workshop sessions on particular aspects of primate ecology or social organization—on food selection, on ranging behaviour, on social structure and on grouping patterns. Our primary interest lay in the functional significance of interspecific and intraspecific variation in aspects of behaviour and ecology. Attempts to construct or test generalizations about variation at either level required comparison of the results of different studies, and a regular complaint at our meetings was the lack of comparability between studies. Though many of us had completed similar work on different species, our interests varied and it was usually impossible to make as wide a range of comparisons as the data could have allowed. At one of these meetings, the idea arose of producing a symposium on primate ecology, and it was agreed that we should draw up an outline of the topics which an ideal chapter should cover and invite selected workers in the field to write similar chapters on different species. We did this, and the final list of topics included feeding heights and sites, activity patterns, food selection (by part and species), home range size and utilization, day range length and group size. For all these measures, we wished to compare the ways in which they varied between populations, between times of day, between sex/age categories and between species. Each author was invited to prepare a chapter which covered as many of these topics as possible. Though none of the 17 field study chapters has covered the whole range of topics, the book allows comparison of most topics across a considerable range of species.

As in previous studies, accurate comparisons are complicated by methodological differences between studies. Sampling methods, sample distributions, study duration and analytical techniques all vary widely and past experience shows that such variation can sometimes produce major discrepancies between estimates (see Appendix I). At first, it seemed possible that these differences would obscure important relationships and might invalidate quantitative comparisons. Two points are relevant to this problem. First, methodological variation is more likely to affect absolute values than relative ones, so that even where the former cannot be compared, it may still be possible to compare intraspecific trends. Second, the evidence shows that where firm predictions can be made about relationships between different aspects of feeding and ranging behaviour at an interspecific level, significant associations can be demonstrated in most cases where a reasonably large sample of species can be used (see Milton and May, 1976; Clutton-Brock and Harvey, in press). We believe that this justifies attempts at broad comparisons, though results must be interpreted with great care (see Chapter 19).

An alternative view, expressed both at our meeting and elsewhere, is that comparisons should not be made until measuring techniques have been standardized. Not only does the empirical evidence indicate that this is an unduly pessimistic opinion but there is another reason why this position is impracticable. Although a greater degree of standardization will probably emerge in future studies, differences in observation conditions and in the focus and duration of field studies will always be sufficient to prevent full standardization of recording techniques. Consequently, quantitative comparisons between species will always be limited to aspects of behaviour and ecology where differences are sufficiently robust to override the effects of varying methodology.

The first 17 chapters are arranged in the taxonomic order of the species concerned. The final two chapters survey some of the generalizations emerging from comparison of inter- and intraspecific differences in feeding and ranging behaviour. The aim of these is to suggest areas of particular interest where research can be usefully developed rather than to provide definitive answers concerning interrelationships between behaviour and ecology.

King's College, Cambridge T. H. CLUTTON-BROCK
May 1977

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1

Feeding Behaviour of *Lemur catta* and *Lemur fulvus*

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1. INTRODUCTION

In this paper I will describe the diet and foraging behaviour of *Lemur catta* and *Lemur fulvus* (Figs 1 and 2). These species were studied between September 1969 and November 1970, and filmed during July and August 1974. The focus of the study was to compare the behaviour and ecology

FIG. 1. *Lemur catta*.

FIG. 2. *Lemur fulvus rufus* (female).

of sympatric and allopatric populations of the two species (Sussman, 1972, 1974).

Populations of *L. fulvus* are found in all forested regions of Madagascar except the south. The subspecies that I studied, *L. f. rufus*, is located in the west and south-west and inhabits the wet deciduous forests in these areas. *L. catta* is located in the south-west and south and inhabits a variety of forest types, including very dry bush and scrub forests. Much of the activity of *L. catta* takes place on the ground, whereas *L. fulvus* rarely comes to the ground. The two species coexist in the south-west between 20°44′ and 23°92′ south latitude.

The study was carried out in three forests: Antserananomby and Tongobato in the south-west and Berenty in the south. At Antserananomby, *L. fulvus* and *L. catta* are sympatric. *L. fulvus* is found alone at Tongobato, and *L. catta* is found alone at Berenty. The location of the study areas is shown in Fig. 3, and the age and sex composition of the groups censused at the three forests is given in Tables I and II. Groups of *L. catta* on the average are approximately twice as large as those of *L. fulvus*. The two species are similar in general morphology, size and weight.

2. STUDY AREAS

2.1. Antserananomby

Antserananomby is 12 km north of the Mangoky river (see Fig. 3). The major portion of my study in this forest was conducted within an area of 10 ha, which coincides approximately with the home range of one group of *Lemur catta* and 12 groups of *Lemur fulvus* (Fig. 4). Approximately 7·5 ha of this area contain a closed canopy dominated by *Tamarindus indica*. This closed canopy is part of a gallery forest which borders the Bengily river, a tributary of the Mangoky river. During the three months of observation at Antserananomby, the river was dry. Along the dry river bed bordering the gallery forest, there are sandy regions which are probably covered with water when the rainfall is extremely heavy. In these areas (approximately 1·5 ha of the total 10 ha) there are many small trees and bushes, as well as species of large trees which are also found in the continuous canopy. However, the large trees are spread out in the sandy area and do not form a continuous canopy.

To the north and north-west of the river the soil becomes drier, there is an increase in altitude, and a brush and scrub vegetation replaces the closed canopy. Farther to the north-west, there are hills which are also

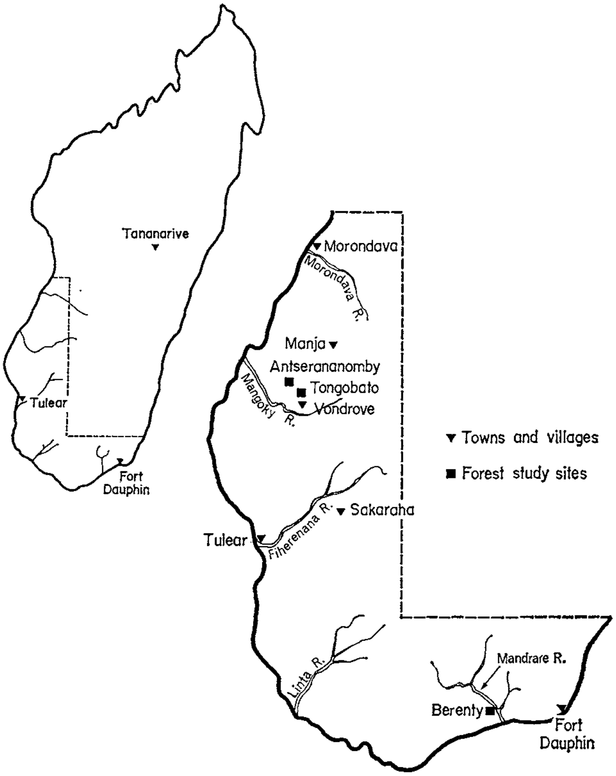

FIG. 3. Study sites.

covered with primary brush and scrub vegetation. One-and-a-half hectares of this dry vegetation are contained within the 10-ha study area.

The continuous canopy portion of the forest is formed by a *Tamarindus indica* consociation. There is a scattered, discontinuous layer made up mainly of *Acacia* and *Terminalia*, and more rarely occurring tall trees. The distribution of these trees along paths within the closed canopy (Fig. 5) is shown in Table III. The number of *Acacia* and *Terminalia* is higher along the edges of the canopy than in the middle of the forest and is highest on the 1·5 ha of the sandy region bordering the closed canopy forest. The subordinate tree layer is made up of smaller trees (e.g. *Flacourtia ramontchi*, *Poupartia caffra* and *Tisomia* sp.) and saplings of the taller trees. Throughout the forest there are many lianas. The ground layer is sparse with a few herbaceous species such as *Achyranthes aspera*, *Mimilopsis* sp. and *Commicarpus commersonii*. Epiphytes and ferns are rare.

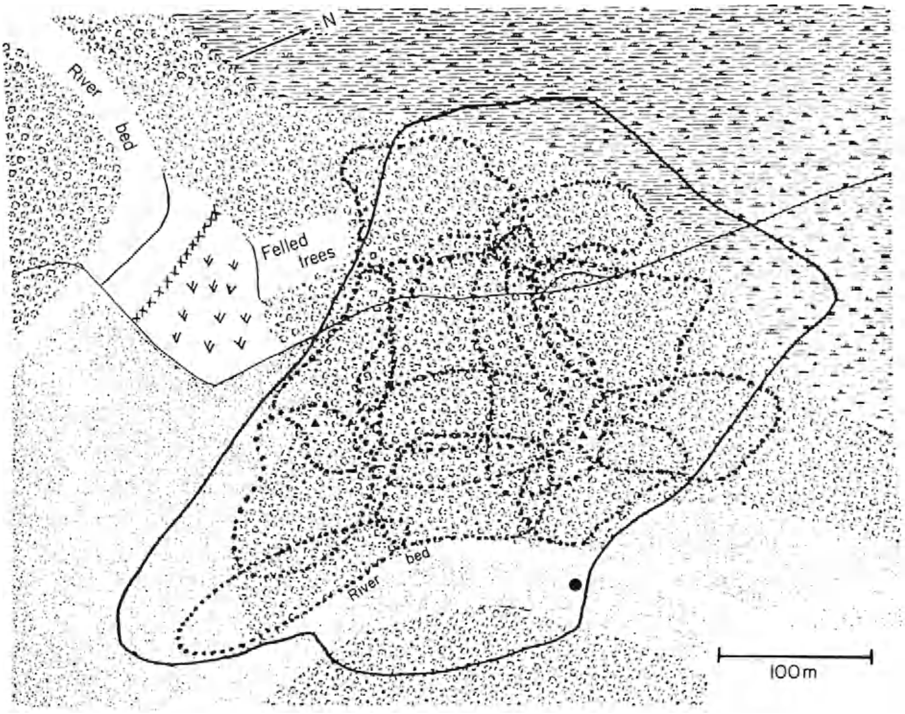

FIG. 4. Antserananomby. Home ranges of *Lemur fulvus* and *Lemur catta*. (▲, *Ficus soroceoides* trees; ●, *Ficus cocculifolia* tree.)

▨	Primary closed canopy forest	ᐯ ᐯ	Cultivated field
▤	Brush and scrub	——	*Lemur catta*
░	Sand	•••••	*Lemur fulvus rufus*

The annual cycle of leaf growth is very uniform. The leaves begin to form at the first rains of the hot season (in November). However, fruiting and flowering of various plant species is variable throughout the year, and there are also some evergreen plant species in the forest. Although a detailed study of the phenology of the forest was not possible, the study areas in all three forests were constantly surveyed to determine when the trees and species utilized by the animals were in fruit and flower. This was possible because of the small areas involved.

The brush and scrub forest reaches only the height of the subordinate tree layer of the continuous canopy. There is no dominant tree species but only an association made up of many co-dominant species. The

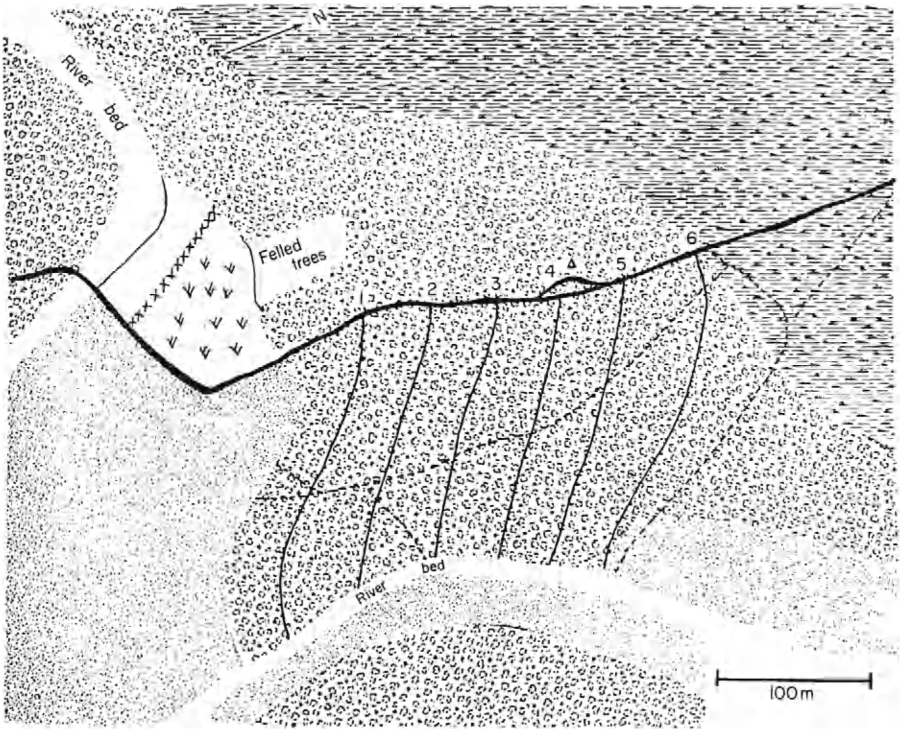

FIG. 5. Antserananomby. Vegetation and transects.

most frequent of these small trees are *Alchornea* sp., *Mimosa delicatrala* and *Protorhus perrieri*.

Western Madagascar is characterized by a marked dry season (austral winter) lasting from April to October or November. In this region, there is about 700 mm of rain but hardly a tenth of this falls during the dry season. Most of my observations at Antserananomby were made between 10th July and 20th September 1970. The temperature during this period varied little. The average daily maximum was 32·1° C in July and 35·5° in August and September. The average minimum temperature was 11·8° C in July, 13·9° in August, and 15·5° in September. The humidity did not vary greatly throughout this period. There was no rainfall.

I counted and made observations on 12 groups of *L. fulvus* (112 animals) in this forest. Intensive observations were made on one group of 19 *L. catta*. The ranges of two other groups of *L. catta* bordered the 10-ha study area, but these two groups were not routinely followed and observations were made on them only when they happened to be seen within this area. There were many groups of *Propithecus verreauxi* and we estimated their population to be approximately 40 to 50 individuals.

The following nocturnal species of lemur are found at Antserananomby: *Lepilemur mustelinus*, *Phaner furcifer*, *Cheirogaleus medius* and *Microcebus murinus*.

Besides lemurs, the mammals in the forest were domesticated dogs and zebu (*Bos indicus*), at least two species of tenrec (*Tenrec ecaudatus* and *Echinops telfairi*), large fruit bats (*Pteropus rufus*), at least one species

TABLE I

Composition of groups of Lemur fulvus rufus

Name of group	Adult		Juvenile		Infant	Total	Adult sex ratio M : F
	Male	Female	Male	Female			
Antserananomby							
AF-1	4	6	1	1	0	12	1 : 1·50
AF-2	4	5	1	0	0	10	1 : 1·25
AF-3	4	3	0	1	0	8	1·33 : 1
AF-4	2	5	2	1	0	10	1 : 2·50
AF-5	4	6	0	2	0	12	1 : 1·50
AF-6	3	2	0	0	0	5	1·50 : 1
AF-7	3	4	1	1	0	9	1 : 1·33
AF-8	2	2	0	0	0	4	1 : 1·00
AF-9	2	2	1	0	0	5	1 : 1·00
AF-10	4	5	2	0	0	11	1 : 1·25
AF-11	5	7	1	2	0	15	1 : 1·40
AF-12	4	4	1	0	0	9	1 : 1·00
Totals	41	51	10	8	0	110	41 : 51 = 1 : 1·24
Means	3·42	4·25	0·83	0·66	0	9·17	
Tongobato							
TF-1	5	8	0	0	4	17	1 : 1·60
TF-2	2	3	1	0	1	7	1 : 1·50
TF-3	4	5	0	1	2	12	1 : 1·25
TF-4	3	4	0	0	1	8	1 : 1·33
TF-5	3	2	0	1	1	7	1·50 : 1
Totals	17	22	1	2	9	51	17 : 22 = 1 : 1·29
Means	3·40	4·40	0·20	0·40	1·80	10·20	
Overall totals	58	73	11	10	9	161	58 : 73 = 1 : 1·26
Overall means	3·41	4·29	0·64	0·59	0·53	9·47	

TABLE II

Composition of groups of Lemur catta

Name of group	Adult Male	 Female	Juvenile	Infant	Total	Adult sex ratio M : F
Antserananomby						
AC-1	7	8	4	0	19	1 : 1·14
Berenty						
BC-1	4	5	2	4	15	1 : 1·25
BC-2	7	6	3	4	20	1·17 : 1
Totals	11	11	5	8	35	11 : 11 = 1 : 1·00
Means	5·50	5·50	2·50	4·00	17·50	
Overall totals	18	19	9	8	54	18 : 19 = 1 : 1·05
Overall means	6·00	6·30	3·00	2·70	18·00	

of small bat and the wild pig (*Potomochoerus larvatus*). Possible predators on the lemurs were the viverrid, *Cryptoprocta ferox*, and the hawk, *Gymnogenys radiata*. Snakes, lizards and chameleons were plentiful.

2.2. Tongobato

The forest of Tongobato is located in the same general area as Antserananomby (Fig. 3). It is near the village of Vondrove, 2 km north of the Mangoky river and 10 km south of Antserananomby. The forests of Antserananomby and Tongobato were probably once part of a continuous forest range. Tongobato is a canopy forest which, unlike Antserananomby, does not grade into brush and scrub, but is surrounded by cultivated fields and degraded vegetation. It consists of a continuous canopy of *Tamarindus indica* with a few areas, where the canopy is broken, in which there are stands of small trees, mainly *Flacourtia ramontchi*. This forest is essentially the same as the continuous canopy portion at Antserananomby in both structure and species of plant. The area I studied here was approximately 8 ha.

The average daily maximum temperatures during the study period in this forest were similar to those recorded during the period of study at Antserananomby. They were 36·1° C in December 1969, 36·2° in March 1970, and 35·3° in April 1970. The evening temperatures at Tongobato were higher than those at Antserananomby. The average minimum daily temperature was 18·9° C in December, 19·9° in March, and 16·3° in April. The study was conducted at Tongobato just before the peak of the rainy season and following the rainy season, after the roads were passable. The total rainfall in December was 160 mm in 14 days. In March and April, the rainfall was 0 and 3·5 mm respectively.

Three groups of *Lemur fulvus* were studied. *Lemur catta* is not found at Tongobato. *Propithecus verreauxi* is common in this forest. Both *Lepilemur mustelinus* and *Phaner furcifer* were sighted, but no attempt was made to census the population of the nocturnal species. Many of the mammals, birds and reptiles that are found at Antserananomby are also found here.

2.3. Berenty

The forest at Berenty borders the Mandrare river in the south of Madagascar (Fig. 3) and has been described in detail by Jolly (1966). The structure of the vegetation at Berenty differs only slightly from that at Antserananomby and Tongobato. The gallery forest is dominated by a continuous canopy of *Tamarindus indica.* However, there are many species of large trees which are not found in the other two forests (e.g. *Albizzia polyphylla*, *Celtis bifida* and *Pithecelobium dulce*). The main structural difference between Berenty and the other forests is the relative absence of an emergent layer. Thus the total height of the forest at Berenty is less than that at Antserananomby and Tonbogato.

My study concentrated on about 9 ha of this forest. The average daily maximum temperature during this period was 34·7° C and the average daily minimum temperature was 19·3°. Thus, the temperatures at night were higher than those at Antserananomby. At Berenty the sun rose at about 5.00h and set at about 18.30h. These were similar to the times of sunrise and sunset at Tongobato, but the days were shorter during the period of my study at Antserananomby (the sun rose at 6.00h and set at about 18.00h). The total rainfall during

TABLE III

Number (and %) of large trees of the most frequently occurring species at Antserananomby along six transects shown in Fig. 5

Species	Transect 1	2	3	4	5	6	Total
Tamarindus indica	16 (19)	39 (55)	34 (72)	19 (46)	23 (52)	53 (55)	184 (48)
Acacia rovumae	40 (47)	16 (22)	10 (21)	9 (22)	19 (43)	35 (36)	129 (33)
Terminalia mantaly	24 (28)	4 (4)	1 (2)	11 (27)	1 (2)	7 (7)	48 (12)
Ficus soroceoides	3 (3)	1 (1)	—	—	—	—	4 (1)
Acacia sp.	2 (2)	12 (17)	2 (4)	2 (5)	1 (2)	2 (2)	21 (5)
Total	85	72	47	41	44	97	386

November was 27·8 mm. However, the rainfall at Berenty was the lowest recorded in the last ten years (Charles-Dominique and Hladik, 1971).

The 9 ha in which I studied included the home ranges of two groups of *Lemur catta*, although this was only part of the total home range of one of the groups. There are no *Lemur fulvus* in southern Madagascar. The nocturnal lemurs found in Berenty are *Lepilemur mustelinus*, *Microcebus murinus* and *Cheirogaleus medius*. Many of the same genera of mammals, birds and reptiles that are in western Madagascar are also found in the gallery forests of the south.

3. SAMPLING METHODS

3.1. General Methodology

Data were collected simultaneously on both the activity of the animals and the forest strata at which this activity took place. Counts were made at five-minute intervals of the numbers of individuals engaged in each of six activities and the level of the forest in which the activity was performed. The following activities were recorded: feeding—the animal actually in the process of ingesting or picking a food item; grooming—mutual and self grooming were distinguished for certain analyses; resting—no body displacement, or feeding, grooming, sunning, etc.; moving—movement of an individual, including individual foraging; travel—movement of the group; and other—e.g., sunning, play, fighting. These data were collected only after the animals under observation were reasonably habituated to the observer. Each observation of an animal constituted an individual activity record (IAR) collected in a given five-minute time sample. Because of the focus of the study and the difficulty in keeping continuous contact with an individual animal, no attempt was made to follow individual animals nor to collect statistical data on specific age or sex classes. Statistical analyses of the data were complicated by the fact that some of the activity records were not independent of each other. The methods used for the statistical analyses are reported in Sussman *et al.* (in press).

To determine levels of the forest, I used Richards' (1957) categories of forest stratification as a model and assigned numbers of one to five to the forest layers. Level 1 is the ground layer of the forest; it includes the herb and grass vegetation. Level 2 is the shrub layer, from one to three metres above the ground. This layer is usually found in patches throughout the continuous canopy forest, but is much more dense and is the dominant layer in brush and scrub regions. Level 3 of the forest consists of small trees, the lower branches of larger trees, and saplings of the larger species of trees. This layer is about three to seven metres high. Level 4 is the continuous or closed canopy layer. It is about five to 15 metres high. The dominant tree of the closed canopy, at all three forests, is the kily (*Tamarindus indica*). Level 5 of the forest is the emergent layer and consists of the crowns of those trees which rise above the closed canopy. It is usually over 15 metres high.

All three forests in which I made intensive studies were primary forests and the tree layers were quite distinct. In most cases, the particular level in which an animal was observed could be distinguished easily. If I could not determine the forest level unambiguously, I did not record it.

Observations recorded in this manner may be biased because animals that are active in certain levels of the forest may be more difficult to see than those active at other levels. (This is discussed in detail in Aldrich-Blake, 1970b and Clutton-Brock, 1975a.) I attempted to minimize this problem by following a relatively small number of animals (usually from five to ten) throughout a period of continuous observation, keeping track of all the animals. For *Lemur fulvus* this usually included the whole group, which was small and, for the most part, moved together. It was more difficult to do this when observing *Lemur catta*, for which it was often necessary to follow and observe subgroups of the larger group. The larger group would disperse, especially during foraging and feeding, and during afternoon rest periods.

Day ranges were mapped by following a group from one night resting site in the morning to the time it settled in another night resting site in the evening. The location of the group was plotted throughout the day on a prepared map of the forest and the amount of time the group spent in each location was recorded. Home ranges include the sum of all of the day ranges. The data on home ranges are limited, however, and probably do not represent total home ranges of the groups, since the study in each area was limited to a few months.

3.2. Data Collection on Feeding Behaviour

The number of animals feeding and the level of the forest in which they were feeding was recorded during the collection of five-minute activity records. The plant and the part being eaten were recorded directly on the data sheet. Plant specimens were collected whenever possible and were later identified by Armand Rakotozafy of the Laboratoire Botanique of ORSTOM, Tananarive. All data on the feeding behaviour and diet of the two species are from direct observation only.

The following quantitative data on feeding behaviour and diet were obtained: (a) the mean proportion of time[a] *Lemur catta* and *Lemur fulvus* spent feeding for each of the 25 half-hour time periods (from 6.00 to 18.25h); (b) the mean proportion of time each species spent feeding at each level of the forest; (c) the number of plant species which *L. catta* and *L. fulvus* were observed eating; (d) the proportion of time the animals were observed feeding on various species of plants; (e) the proportion of time *L. catta* and *L. fulvus* were observed feeding on fruits, leaves, bark, etc. Data were also collected on the location of animals within the forest and group foraging patterns. All the data were collected and compared for *L. catta* and *L. fulvus* at all three forests.

4. FEEDING BEHAVIOUR

4.1. Feeding Techniques

Both species use essentially the same postures while feeding in the trees. The behaviour of *Lemur catta* during feeding has been described by Jolly (1966). Both species frequently feed in the finest branches on the tops and edges of tall trees. They move out to the fine net of tiny branches and then hang on with three extremities while reaching a leaf or branch and pulling it toward them. They then pull the edible part to their mouth and pick it off the twig with a jerk of the head. *L. catta* also feed this way on the tops of bushes or trees in the subordinate layer of the forest. While feeding on fruits, both species tilt their heads back while chewing. Most large fruits are held in the hands, squirrel fashion, and chewed. However, the fruits of some trees were too large for the animals to hold. For example, the fruit of *Ficus cocculifolia* ("adabo") was eaten from one tree by *L. catta* at Antserananomby (see below). *L. catta* fed on this tree by pushing the large, apple-sized fruit against the branch and then taking one or two large bites. In many cases, as many as three or four of these fruit would drop to the ground before the animal was successful in supporting one long enough to get a bite. *L. catta* would not feed on the fruit which dropped to the ground while there were still animals in the tree feeding. Often, in the morning, there were zebu (hump-backed cattle) resting under the tree. When the cattle were there, they would wait for a fruit to drop and finish it with one bite. *L. catta* would eat the adabo fruit which had dropped to the

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[a] In this paper, "proportion of time" is used to refer to the proportion of IARs for the specific activity, level of the forest, or component of the diet.

FIG. 6. *Lemur fulvus* feeding on sap of *Terminalia* tree.

ground only when there were no other *L. catta* in the tree above and when there were no zebu resting under the tree.

Lemur catta often feeds on the ground, either on fallen fruit or on herbs or small bushes. Herbs or branches of bushes are brought to the mouth by one or two of the animal's hands, while he stands bipedally or tripedally. Large fallen fruit are also brought to the mouth with one or both hands, while small fruit are usually picked up with the mouth from a quadrupedal standing or a sitting position.

Both species feed on sap from large trees. The animals usually lick the sap directly from the bark (Fig. 6). However, it is also possible that they use their tooth comb to scrape the sap off the bark.

4.2. Feeding Heights and Feeding Sites

Lemur fulvus is very specific in its choice of vertical habitat. Over 95% of all its activity takes place in the top layers of the forest (levels 3, 4 and 5). The animals spent 45% (Tongobato) and 60% (Antseranaromby) of their feeding time in the continuous canopy of the forest and over 85% in the upper three forest levels (Table IV). *Lemur catta* was active at all levels of the forest. It spent more time on the ground than in any one of the other four levels (36% at Berenty and 30% at Antserananomby), and most of the group travel took place on the ground. *L. fulvus* spent less than 2% of the time on the ground. *L. catta* frequently fed in all of the available levels of the forest. Over 65% of its feeding was done in levels 1, 2 and 3, and less than 20% in level 4.

Groups of *L. fulvus* fed in relatively few trees throughout the day. *L. catta* foraged, the group moving from one feeding site to another, and frequently from one area to another. Within a period of seven to ten days the group visited most of its total range. This constant surveillance of the home range allowed the animals to discover plants which were in flower and fruit within a short time. Even after finding a particular producing tree or stand of trees, the group would not feed at the site exclusively but would continue to move constantly throughout the day. In most instances, movement between food species was not related to any noticeable depletion of the food available. Over half of the species eaten by *L. catta* at a particular forest were often utilized within the course of one day. However, the group would frequently begin and end their day by foraging in a particularly favourable site.

Groups of *L. fulvus* moved very little throughout the day (day ranges were about 125–150 m) and had home ranges between about 0·75 and 1·0 ha. They fed, for the most part, in the evenly distributed species of trees within their home range but often more than one group

TABLE IV

Mean percentage of animals observed at each level for each activity and regardless of activity

			Level		
Activity	1	2	3	4	5
Lemur fulvus rufus at Antserananomby					
Feeding	0·00	2·58	15·60	59·66	22·16
Grooming	0·00	0·54	9·34	78·24	11·88
Resting	0·00	1·20	14·05	79·60	5·15
Moving	2·61	0·60	18·14	66·16	12·48
Travel	0·00	0·00	2·60	87·84	9·56
Other	0·00	8·33	5·95	54·70	31·02
All activities	0·44	2·21	10·95	71·03	15·38
Lemur fulvus rufus at Tongobato					
Feeding	2·17	11·40	5·01	44·66	36·76
Grooming	0·00	0·60	9·93	79·99	9·49
Resting	0·34	0·83	8·03	79·91	10·89
Moving	6·02	1·27	4·14	78·64	9·93
Travel	0·95	3·69	5·92	82·94	6·50
Other	0·00	5·00	15·00	56·18	23·82
All activities	1·58	3·80	8·00	70·39	16·23
Lemur catta at Antserananomby					
Feeding	27·58	12·78	25·23	19·01	15·40
Grooming	4·37	15·90	20·42	46·00	13·31
Resting	9·54	16·74	25·62	35·02	13·08
Moving	44·73	5·88	21·62	17·58	10·20
Travel	64·70	1·81	13·47	17·46	2·57
Other	28·70	5·02	27·31	22·50	16·47
All activities	29·93	9·69	22·28	26·26	11·84
Lemur catta at Berenty					
Feeding	30·84	15·10	41·56	12·32	0·18
Grooming	10·16	23·35	27·97	38·38	0·14
Resting	14·01	26·14	28·18	31·68	0·00
Moving	55·32	13·51	15·82	15·35	0·00
Travel	70·93	6·44	5·48	17·15	0·00
Other	35·71	17·27	20·61	26·41	0·00
All activities	36·16	16·97	23·27	23·55	0·05

would share more rarely occurring species of trees which happened to be in flower or fruit at the time. The day ranges of *L. catta* were usually between 900 and 1000 m. Although *L. catta* slept each night in the continuous canopy, at Antserananomby it spent 58% of the day outside of the closed canopy area, even though this represented only 30% of the total area of its range. Home ranges were 8·8 ha for the group at Antserananomby and 6·0 ha for that at Berenty. However, in a more arid region of Berenty, Budnitz and Dainis (1975) studied a group with a home range of 23 ha.

4.3. Diurnal Activity Patterns and Percentage of Time Spent Feeding

Lemur catta and *Lemur fulvus* are active at different times of the day. The two species do not feed, rest, move or travel during the same hours of the day. Nor do they spend the same proportion of time in each of the noted activities. Figure 7 represents the mean percentage of animals engaged in each of the six activities during periods of several hours.

The most striking differences between the two species are seen in the data from Antserananomby. At this forest, *L. fulvus* rested throughout the afternoon, whereas *L. catta* rested for only a short time at midday (during the third period). *L. fulvus* rested longer in the middle of the day than *L. catta*. Sixty per cent or more of the *L. fulvus* rested between 10.00 and 16.00h (6 hours) at Antserananomby, and between 9.30 and 15.00h (5·5 hours) at Tongobato. In *L. catta*, 60% or more of the animals rested from 12.00 to 14.30h (2·5 hours) at Antserananomby and from 10.30 to 12.30h (2 hours) at Berenty. *L. fulvus* rested more than *L. catta* in all of the forests. The activity to rest ratios at the three forests are as follows:

Lemur fulvus

Tongobato:	$50/50 = 1{\cdot}00$
Antserananomby:	$44/56 = 0{\cdot}79$

Lemur catta

Antserananomby:	$59/41 = 1{\cdot}44$
Berenty:	$61/39 = 1{\cdot}56$

The feeding schedules of *L. catta* and *L. fulvus* are illustrated in Fig. 8. The feeding activity of both species can be described by a bimodal curve. However, *L. fulvus* fed very early in the morning and late in the afternoon and travelled little to obtain its food. *L. catta* began to feed

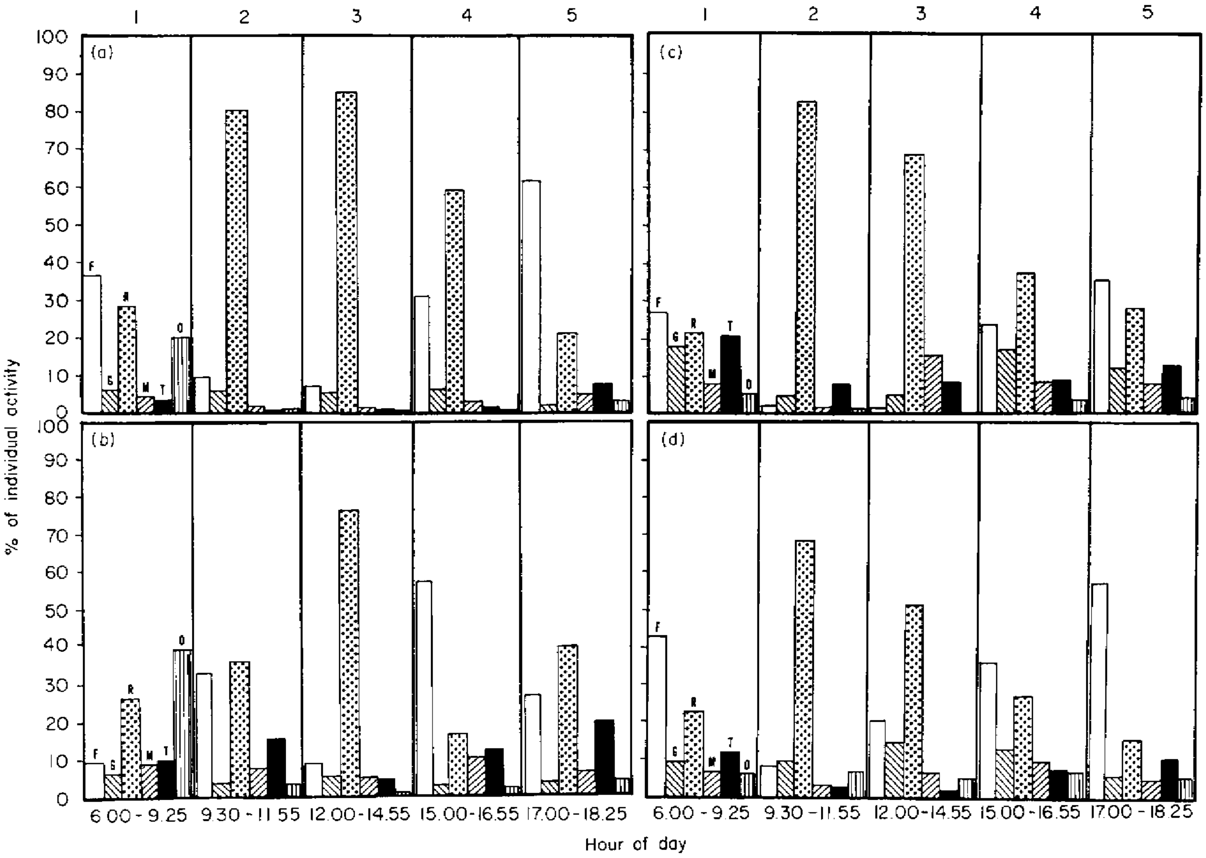

FIG. 7. Mean percentage of individual activity records for each of six activities during five periods of the day. (a) *Lemur fulvus* at Antserananomby; (b) *Lemur catta* at Antserananomby; (c) *L. fulvus* at Tongobato; (d) *L. catta* at Berenty.

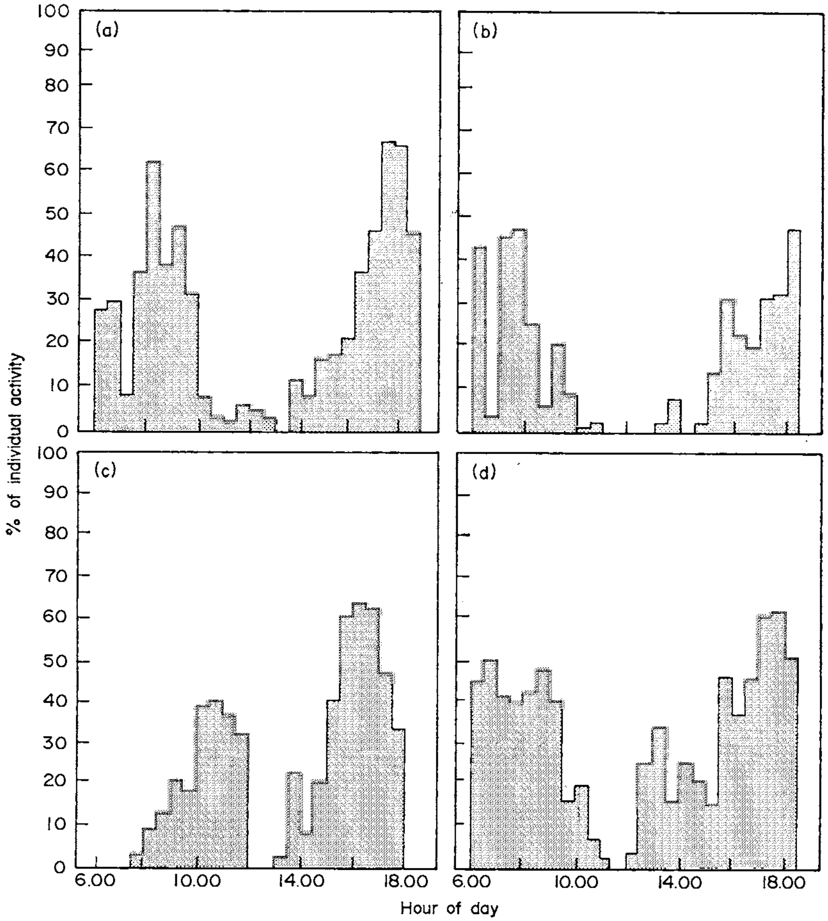

FIG. 8. Percentage of individual activity records for feeding during each half-hour from 6.00 to 18.25h. (a) *Lemur fulvus* at Antserananomby; (b) *L. fulvus* at Tongobato; (c) *Lemur catta* at Antserananomby; (d) *L. catta* at Berenty.

later in the morning and stopped earlier in the evening than *L. fulvus*. Groups of *L. catta* travelled greater distances to obtain food, foraging throughout the afternoon. At Antserananomby, *L. catta* spent an average of 25% of the time—from 6.00 to 18.25h—feeding in relation to the other five activities recorded, and at Berenty 31% (Table V). At Antserananomby, *L. fulvus* spent an average of 26% of the time feeding (Table V). At Tongobato, *L. fulvus* was observed feeding an average of only 16% of the time. The data from Tongobato, however, may not be as reliable as data collected at the other forests. At Tongobato the animals were difficult to find and observe in the morning and afternoon when they were most active. They were also hard to approach because of the frequent hunting in this forest.

TABLE V

Mean percentage of individual activity records for each activity each half-hour

Species and forest	Feeding	Grooming	Activity Resting	Moving	Travel	Other
Lemur fulvus rufus						
Tongobato	16·59	11·30	49·73	7·77	12·21	2·41
Antserananomby	26·22	5·25	56·58	3·09	2·47	6·40
Lemur catta						
Antserananomby	24·94	4·67	41·42	7·45	11·34	10·19
Berenty	31·12	10·97	38·63	6·30	6·91	6·07

At Berenty, *L. catta* began to feed earlier in the morning and its peak of resting was earlier than at Antserananomby. It also began to feed earlier in the afternoon and stretched out its afternoon feeding activity over a longer period of time. These differences, which are most likely related to the early sunrise and high early morning temperatures at Berenty, make the activity pattern of *L. catta* at this forest appear similar to that of *L. fulvus*. Even though the temperature and time of sunrise at Tongobato were more similar to those at Berenty than they were to those at Antserananomby, the pattern of behaviour of *L. fulvus* was similar in both the forests in which it was studied. Seasonal differences (in this case, time of sunrise and sunset and time of the maximum temperature during the day) seem to affect the daily activity cycle of *L. catta* more than that of *L. fulvus*.

A statistical analysis was performed on the feeding and resting activities of *L. catta* and *L. fulvus* at Antserananomby for each five-minute observation period. The results of the analysis are shown in Figs 9 and 10 (see Sussman *et al.*, in press, for further discussion). Statistical analyses comparing data from different forests were difficult to interpret because of the differing forest conditions.

4.4. Species Composition of the Diet

Differences in the diets of the two species can be correlated with differences in the use of vertical and horizontal space by the two species.

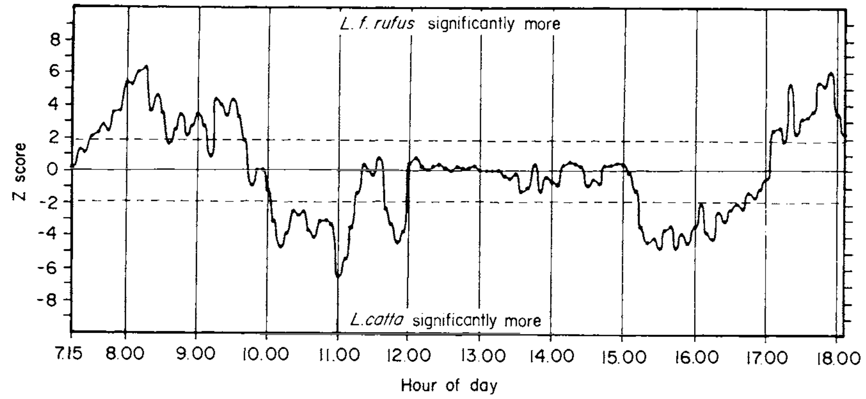

FIG. 9. Z scores for the feeding activity of *Lemur fulvus* and *Lemur catta* at Antserananomby, computed for each five-minute observation period.

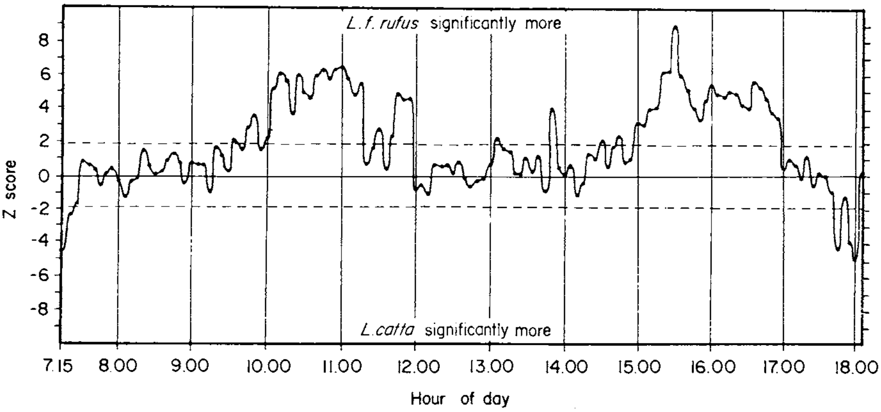

FIG. 10. Z scores for the resting activity of *Lemur fulvus* and *Lemur catta* at Antserananomby, computed for each five-minute observation period.

The more restricted use of space by *Lemur fulvus* is related to a less varied diet than that of *Lemur catta*. The plants which *L. fulvus* was observed eating during the study are listed in Table VI. I recorded *L. fulvus* eating only eight plant species at Tongobato and 11 at Antserananomby. There was a total of 13 different plant species eaten by *L. fulvus* in the two forests. *L. catta*, on the other hand, had a much more varied diet. At both Antserananomby and Berenty, *L. catta* was observed to feed on 24 different plant species (Table VI). There was a

TABLE VI

Plant species eaten by Lemur fulvus rufus *and* Lemur catta

Plant species eaten by *Lemur fulvus rufus* at Tongobato	Plant species eaten by *Lemur catta* at Antseranano mby	Plant species eaten by *Lemur catta* at Berenty
Acacia rovumae Olia*	*Acacia rovumae* Olia	*Acalypha* sp.‡
Acacia sp.*	*Acacia* sp.	*Achyranthes aspera* L.‡
Alchornea sp.	*Acalypha* sp.†	Aizoaceae
Flacourtia ramontchi L'Her.*	*Achyranthes aspera* L.†	*Albizzia polyphylla* L.
Lawsonia alba Lam.	*Adenia* sp.	*Annona* sp.
Tamarindus indica L.*	*Alchornea* sp.	*Azima tetracantha* Lam.
Terminalia mantaly H. Perr.*	*Commicarpus commersonii* (Baill.) Cavaco	*Boerhaavia diffusa* L.
Vitex beravensis Vatke*	*Ficus cocculifolia* Bak.	*Cardiaspermum halicacabum* L.
	Ficus soroceoides Bak.	*Cassia* sp.
Plant species eaten by *Lemur fulvus rufus* at Antserananomby	*Ficus* sp.	*Celtis philippensis* Blanco
	Flacourtia ramontchi L'Her.	*Cissampelos* sp.
	Grevia sp.	*Combretum* sp.
Acacia rovumae Olia*	*Mimilopsis* sp.	*Crateva excelsa* Boj.
Acacia sp.*	*Paederia* sp.	*Ehretia* sp.
Ficus soroceoides Bak.	*Paederia* sp.	*Mangifera indica* L.
Flacourtia ramontchi L'Her.*	Papilionaceae	*Melia azedarach* L.
Papilionaceae	*Poupartia caffra* H. Perr.	*Opuntia vulgaris* Mill.
Quisivianthe papinae Baill.	*Quisivianthe papinae* Baill.	*Phyllanthus* sp.
Rinorea greveana Baill.	*Tamarindus indica* L.†	*Pithecelobium dulce* Benth.
Tamarindus indica L.*	*Terminolia mantaly* H. Perr.	*Rinorea greveana* Baill.
Terminalia mantaly H. Perr.*	*Vitex beravensis* Vatke	*Tamarindus indica* L.‡
Tisomia sp.	Three species unidentified (small trees)	*Zehneria* sp.
Vitex beravensis Vatke*		*Zizyphus jujuba* Mill.
		One species unidentified (vine)

* Plant species eaten by *Lemur fulvus rufus* at both Tongobato and Antserananomby.
† Plants eaten by *Lemur catta* at both Antserananomby and Berenty.
‡ Plants eaten by *Lemur catta* at both Berenty and Antserananomby.

total of 45 plant species eaten by *L. catta* in the two forests. *L. catta* ate only three of the same species of plants at both forests. *L. fulvus* was observed to feed on only two plants which were not used by *L. catta* (*Lawsonia alba* and *Tisomia* sp.).

Many of the plant species eaten by *L. catta* at Antserananomby were found in portions of the forest which were not utilized by *L. fulvus*. There were 12 species of plants at Antserananomby on which *L. catta* was observed to feed which were not used by *L. fulvus*. Of these 12 species, three were ground plants (*Commicarpus commersonii*, *Achyranthes aspera*, *Mimilopsis* sp.), three were vines on small trees, and four were species found on the periphery or outside of the closed canopy forest. Two of the latter were eaten by *L. fulvus* at other forests in our survey. *L. fulvus* was observed to feed on only one species of vine (*Papilionaceae*) which grew mainly on the kily trees.

The diets of *L. fulvus* and *L. catta* do not differ solely in the species of plants eaten, but also in the frequencies at which these plants are utilized. Since each forest was studied at a different time of year, intraspecific variation in the diet may be due to seasonal conditions as well as to differences in the forests. *L. fulvus* appears specialized in its choice of diet. During the period of observations at Tongobato, three species of plants constituted more than 80% of the diet of *L. fulvus* (Table VII) (*Flacourtia ramontchi*, *Tamarindus indica* and *Terminalia mantaly*).[a] *Tamarindus indica* accounted for almost 50% of the diet.

TABLE VII

The number and percentage of individual activity records (IARs) for feeding on identified species of plants

Plant Species	No. of IARs	% of IARs
Lemur fulvus rufus at Antserananomby		
Tamarindus indica L.	1802	75·68
Leaves	1793	75·30
Fruit	9	0·38
Acacia sp.	156	6·55
Ficus soroceoides Bak.	141	5·92
Acacia rovumae Olia	74	3·10
Terminalia mantaly H. Perr.	21	0·88
Quisivianthe papinae Baill.	18	0·75
Other	169	7·06
Total	2381	99·94

(*continued*)

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[a] In this paper, percentage of diet refers to the percentage of individual activity records for feeding on identified species of plants or on various parts of these plants (Table VII).

TABLE VII (*continued*)

Plant Species	No. of IARs	% of IARs
Lemur fulvus rufus at Tongobato		
Tamarindus indica L.	276	48·85
Leaves	237	41·95
Flowers	26	4·60
Fruit	10	1·77
Bark	3	0·53
Terminalia mantaly H. Perr.	127	22·47
Flacourtia ramontchi L'Her.	69	12·21
Acacia rovumae Olia	38	6·72
Vitex beravensis Vatke	18	3·18
Other	37	6·54
Total	565	99·97
Lemur catta at Antserananomby		
Tamarindus indica L.	374	24·36
Fruit	183	11·92
Leaves	174	11·33
Flowers	17	1·11
Small trees:	320	20·84
Alchornea sp.		
Flacourtia ramontchi L'Her.		
Grevia sp.		
Poupartia caffra H. Perr.		
Ground plants (all species)	225	14·65
Ficus soroceoides Bak.	194	12·63
Vines (all species)	140	9·12
Quisivianthe papinae Baill.	94	6·12
Vitex beravensis Vatke	82	5·34
Ficus cocculifolia Bak.	40	2·60
Acacia rovumae Olia	18	1·17
Other	48	3·12
Total	1535	99·95
Lemur catta at Berenty		
Tamarindus indica L.	519	22·97
Leaves	274	12·13
Fruit	225	9·96
Bark	20	0·88
Rinorea greveana H. Bn.	474	20·98
Pithecelobium dulce Benth	433	19·16
Phyllanthus sp.	137	6·06
Melia azedarach L.	132	5·84
Ehretia sp.	130	5·74
Ground plants (all species)	124	5·48
Opuntia vulgaris Mill	84	3·71
Annona sp.	38	1·68
Vines (all species)	27	1·19
Other	161	7·10
Total	2259	99·91

L. fulvus fed on the leaves, pods, stems and bark of this tree, but at Tongobato the leaves of the kily tree alone made up 42% of the total diet. The animals feed on both mature and young leaves of this species. The fruit of the kily was not in season during the time of my observations at either Tongobato or Antserananomby. At Antserananomby, *Acacia* sp., *Ficus soroceoides* and *Tamarindus indica* accounted for over 85% of the diet of *L. fulvus*, and over 75% of its diet consisted of mostly mature kily leaves. Therefore, at both Tongobato and Antserananomby, a few species of plants made up a large proportion of the diet, and kily leaves were the main staple. The amount of time spent feeding on various species of plants other than kily in these two forests was probably directly related to the distribution and seasonality of these plants within the small home range of any particular group and within a particular forest.

The diet of *L. catta* is more varied than that of *L. fulvus*. At Antserananomby, the following species made up over 70% of the diet (Table VII):

Achyranthes aspera
Alchornea sp.
Ficus soroceoides
Flacourtia ramontchi
Mimilopsis sp.
Grevia sp.
Poupartia caffra
Tamarindus indica

The kily tree provided 24% of the diet of *L. catta* in this forest. However, less than half of this (11%) was leaves. Kily pods made up 12% of the diet and ground plants (*Achyranthes aspera* and *Mimilopsis* sp.) 15%.

The diets of *L. catta* at Berenty and Antserananomby consisted of different plant species, but since the foraging patterns in the two forests were very similar, the diets also were very similar in variety of species consumed. At Berenty the following species accounted for over 80% of the observed plants eaten:

Achyranthes aspera
Boerhaavia diffusa
Cassia sp.
Melia azedarach
Phyllanthus sp.
Pithecelobium dulce
Rinorea greveana
Tamarindus indica

The kily tree provided *L. catta* with 23% of its diet. Kily leaves were eaten in 12% of the observations and kily pods in 10%. The fruit of two other trees (*Rinorea greveana* and *Pithecelobium dulce*) together accounted for 40% of the diet. Thus, the species composition of the diet of *L. catta* differed in the two forests. This is likely to be due to the fact that (a) the species composition of the forests differed and (b) the two forests were studied at different times of the year and species of plants in fruit and flower were not the same. However, the foraging pattern of *L. catta* (constant surveillance of the home range, covering the total home range within seven to ten days, and feeding at all levels of the forest) was similar in both forests. This pattern probably guarantees a certain amount of variety in the diet of *L. catta* and a more or less consistent pattern to the diet, given the amount of area covered and the distribution and abundance of plants within this area. In more arid regions, the pattern of foraging probably remains similar, but the size of the home range, as well as the amount of time spent foraging, may increase (see Budnitz and Dainis, 1975).

4.5. Parts of Plants Eaten

Both *Lemur catta* and *Lemur fulvus* eat the fruit, leaves, flowers and sometimes the bark and sap of various species of trees and plants. The amount of time that they spend feeding on the various parts of the plants depends upon the fruiting or blossoming season of the plants. For example, at Antserananomby both *L. catta* and *L. fulvus* ate more leaves than fruit. *L. catta* was observed eating leaves 44% of the time and *L. fulvus* for 89% of the time (Table VIII). During the major portion of my study in this forest (July through September), only two species of plants began to fruit (*Ficus soroceoides* and *Ficus cocculifolia*). *L. fulvus* was observed feeding on fruit in this forest in only 7% of the feeding observations, while *L. catta* ate fruit for 34% of the feeding observations.

The main difference between the proportion of fruit eaten by the two species is related to the ability of the animals to use different parts of the forest. The major portion of fruit eaten by *L. fulvus* was from the large *Ficus soroceoides* trees. There were two of these trees in the forest and only five of the 12 groups of *L. fulvus* had home ranges which included one of the trees (Fig. 4). While *Ficus soroceoides* was fruiting, *L. catta* foraged in one or the other of the two trees each morning or afternoon. The fruit of this tree made up 13% of the diet of *L. catta*.

Three other trees provided *L. catta* with fruit: *Vitex beravensis* (5%), *Ficus cocculifolia* (3%) and *Tamarindus indica* (12%). At Antserananomby these three plants were not sources of fruit for *L. fulvus*. During the period of my study, the fruit of these trees was found only outside of the mid-forest area. The only kily trees that still had pods were those which were isolated or in small stands in the brush and scrub portions of the forest. Fallen berries of *V. beravensis* were eaten from the dry river bed by *L. catta*. During the afternoon the animals would sit and rest in the sand of the dry river bed casually eating the berries which had fallen from the trees. *F. cocculifolia* produced fruits the size of large

TABLE VIII

The number and percentage of individual activity records for feeding on identified parts of plants

Part of plant eaten	No. of IARs	% of IARs
Lemur fulvus rufus at Antserananomby		
Leaves	2123	89·16
Fruit	161	6·76
Flowers	90	3·77
Bark	7	0·29
Total	2381	99·98
Lemur fulvus rufus at Tongobato		
Leaves	275	52·08
Fruit	224	42·43
Flowers	26	4·92
Bark	3	0·56
Total	528	99·99
Lemur catta at Antserananomby		
Leaves	670	43·64
Fruit	516	33·61
Herbs	225	14·65
Flowers	124	8·07
Total	1535	99·97
Lemur catta at Berenty		
Fruit	1335	59·30
Leaves	550	24·43
Flowers	137	6·08
Herbs	124	5·50
Bark, sap, cactus	105	4·66
Total	2251	99·97

apples. I saw *L. fulvus* eat this fruit in a forest at the edge of the Mangoky river during my surveys. There was only one of these trees in the forest at Antserananomby, and it was located on the side of the river opposite to the continuous canopy portion of the forest (Fig. 4). *L. fulvus* rarely crossed the river and was never seen in this tree. *L. catta*, on the other hand, crossed the river and fed in this tree regularly for a number of days when the fruit was ripe.

Both *L. catta* and *L. fulvus* ate relatively more fruit in those forests in which they were found alone than at Antserananomby. The intensive study was done at the beginning of and immediately after the rainy season at Tongobato, and at the onset of the rainy season at Berenty. The intensive study at Antserananomby was carried out in the middle of the dry season. During the months of observation at these forests, there were more species of trees bearing fruit at Tongobato and Berenty than at Antserananomby. *L. catta* was seen eating fruit in 59% of the observations at Berenty, and *L. fulvus* ate fruit in 42% of the feeding observations at Tongobato. *L. fulvus* ate leaves in this forest during 52% of the observations and ate the fruit of six of the eight plants in which it was observed feeding. All of these plants were relatively common in the forest. *L. catta* ate leaves in trees during 24% of the observed feeding activity and leaves and stems of ground plants in 5%. At Berenty, in another part of the forest, ground plants made up 20% of the diet of *L. catta* during June through September, 1963 (Jolly, 1966).

L. catta ate flowers between 6–8% of the time and *L. fulvus* ate flowers between 4–5% of the time. Bark and sap were eaten by both species in all three forests, but made up less than 5% of the total observations. *L. catta* was observed feeding on the pulp of a cactus plant (*Opuntia vulgaris*) at Berenty about 4% of the time. At this forest, *L. catta* was also seen chewing dirt in a few observations.

4.6. Drinking

Both *Lemur catta* and *Lemur fulvus* probably obtain most of their water by licking the dew off leaves early in the morning and from the water contained in the fruits and leaves upon which they feed. Animals of both species drank from hollows in trees in which rain-water had collected. They obtained the water by lapping it directly from the hollows. *L. catta* were often seen placing their hands into the hollows and then licking the water from their fingers. *L. catta* also drank from puddles which formed on the ground after a rain and sometimes drank directly from the Mandrare river (Jolly, 1966; Budnitz and Dainis, 1975). I never saw *L. fulvus* drinking water from sources on the ground. Budnitz and Dainis (1975) also report that during long dry spells, *L. catta* had to spend a great deal of time in dry bush and scrub areas of Berenty eating succulent plants (e.g. *Xerosicyos perrieri*, which they ate regularly). In this dry region, groups had to cover more ground in order to obtain the less densely distributed food resources and to find sufficient water.

5. FEEDING BEHAVIOUR AND SOCIAL BEHAVIOUR

The density of *Lemur fulvus* was very high in the forests in which I studied, reaching 1200 animals/km² at Antserananomby. The biomass was roughly 25 kg/ha at Antserananomby and 20 kg/ha at Tongobato. The average size of the groups censused at the two forests was 9·5 (Table I) and groups ranged in size from four to 17 animals. However, the two groups observed with 15 and 17 individuals were noticeably less cohesive than the smaller groups.

In both study sites, the home ranges of groups were quite evenly distributed within the portion of the forest which contained a continuous canopy. Ranges overlapped extensively (Fig. 4) and boundaries of the ranges were not defended. Groups often fed or rested in opposite branches of the same large tree. When encounters between groups occurred, they were usually precipitated by one group surprising another as it moved into the branches of a tree in which the first was feeding or resting. These encounters seemed to function to maintain the integrity of the groups and not to maintain particular boundaries. This pattern of group dispersion and interaction allowed a number of groups to feed on rarely occurring species which happened to be in fruit or flower at any one time without affecting the utilization of the more abundant, evenly distributed kily trees.

Groups of *L. fulvus* were very cohesive. Agonistic encounters within the group were very rare and there were no noticeable hierarchies. Activity of group members was synchronous and animals usually fed, travelled, rested during the day, and slept at night in the same trees. Given the size of the average group of *L. fulvus* and the size of the resource units they utilize, there seems to be no need for competition between members of the same group for food or for feeding, resting, or sleeping sites.

The population densities of *Lemur catta* have been estimated as between 167/km² and 350/km² in different areas in which they have been studied (Jolly, 1966; Sussman, 1972; Budnitz and Dainis, 1975). In my two study sites, the density of *L. catta* was 215/km² at Antserananomby and 250/km² at Berenty, and the biomass was between 4 and 6 kg/ha at the two forests. Although more detailed comparisons remain to be made, there seems to be a direct relationship between the abundance and distribution of resources (including water) and the density, size of home ranges, and number of groups of *L. catta* in an area. In more arid regions with scarce and widely distributed resources, home ranges are large and groups maintain more exclusive use of their ranges. Encounters between groups in these areas are rare and distance is probably maintained between them by spontaneous vocalizations given throughout the day (Sussman and Richard, 1974). Where resources are more abundant, the groups still seem to select for a variety of food items in their diet and cover their whole range in a short period of time, constantly monitoring resources within it. However, there is much more overlap of home ranges between groups and many more intergroup encounters. In these areas, a time plan sharing of resources occurs (A. Jolly, 1972a; Sussman and Richard, 1974).

Agonistic encounters are frequent between members of the same group in *L. catta*. There is a clear and separate dominance hierarchy among the males and females, and females have been reported to be dominant over males (Jolly, 1966; Budnitz and Dainis, 1975). The group is organized around a core subgroup consisting of the adult females, their infants and younger juveniles, and the dominant male or males. As the group travels, the core group usually moves together ahead of the subordinate males and older juveniles. The subordinate males and juveniles also tend to feed and rest together. The group is thus frequently divided into subgroups which separate while moving, foraging and feeding, and resting. The females, and young and more dominant males, get first choice of feeding, drinking and day resting sites. In some cases, certain resources (e.g. small fruiting trees, water holes or bushes) are depleted before all the members of the group have had access to them. In very arid brush and scrub regions, where resource units are small and scattered, the larger group often divides into a number of subgroups and spreads out over a wide area. However, the membership of these smaller subgroups has not yet been analysed. The high frequency of agonistic encounters and the clear hierarchy within the group thus seem to be most clearly related to establishing priority of access to food (and water) resource units of small size and limited abundance by facilitating the division of the group into smaller, foraging subgroups.

L. catta is found throughout the south-west and south of Madagascar. This is the most arid region on the island and most of the undisturbed vegetation is brush and scrub or desert-like, *Didierea*, forest. The ranging and foraging pattern and the group structure are most likely adaptations to these arid environments in which resources are sparse, unpredictable and unevenly distributed.

6. PREDATION

The most dangerous predator of the diurnal lemurs is man. If the animals are approached by a man to whom they are not accustomed, *Lemur fulvus* face the intruder, grunt, and wag their tails and then usually leave, running through the dense closed canopy. If the animals remain aroused, their grunts turn into high-pitched bird-like chirps. This usually elicits chirping in other nearby groups.

Lemur catta make no noise unless certain that they have been noticed. They try to move away silently in the trees until they can descend to the ground. Once on the ground, they run off quietly into the dense underbrush. After a few minutes, they begin to meow quietly and in this way relocate each other. I would often relocate a group after it had been frightened by listening for these quiet vocalizations. Because of the evasive tactics of *L. catta*, the Malagasy often use dogs to hunt this species. If *L. catta* are put into a position where they cannot escape to the ground and run away, they mob the intruder. In these instances, the lemurs will all face the man or dog and bark at him.

There are two potential non-human predators of the diurnal lemurs in the south and south-west of Madagascar: the large hawk (*Gymnogenys radiata*) and the fossa (*Cryptoprocta ferox*). *L. catta*, *L. fulvus* and *Propithecus verreauxi* move into the densest foliage of the closed canopy and give particular loud vocalizations when a *G. radiata* flies overhead. All three species give the calls in unison. These calls are never given to another species of bird nor to the large fruit bat (*Pteropus rufus*) that frequently flies over the trees early in the evening.

The fossa was observed only once during the study. *L. catta* saw the animal and barked and then remained silent, closely watching it as it moved away. *L. fulvus* reacted in the same way as they do to humans. They wagged their tails and grunted. The viverrid passed quickly and disappeared into the dense underbrush.

7. SUMMARY AND DISCUSSION

1. The focus of this field study was to compare the ecology and behaviour of two sympatric, closely related species of *Lemur*: *Lemur catta* and *Lemur fulvus*. By studying sympatric populations, I was able to compare and contrast the manner in which these species utilized potentially identical resources. If differences in the utilization of the environment were noted, hypotheses concerning the relationship

between these differences and differences in individual and social behaviour (as well as morphophysiology) could then be formulated. The two species were also studied where they occurred alone to determine if any of the noticeable differences were caused by the interaction between the populations. In this paper, I describe the differences that were found in the feeding behaviour of the two species.

2. Study areas. Because of the design of the research, three forests were chosen for study, one in which the two species were sympatric (Antserananomby) and two where they were found alone (Tongobato and Berenty). The three study areas were chosen because the forests were similar in structure, the major portion of each containing a continuous canopy dominated by a *Tamarindus indica* (kily) consociation. The more rarely occurring species of trees were also similar at Antserananomby and Tongobato, but many species were not found at Berenty which were relatively common in the other two forests. Antserananomby was studied during the dry season. Tongobato and Berenty were studied during the beginning of the rainy season. A major limitation of the study was that I was only able to study each forest during one season and thus seasonal variation in the behaviour of the animals in the same forest was not known.

3. Sampling methods. Quantitative data were collected at five-minute intervals on the number of individuals engaged in each of six activities—feeding, grooming, resting, moving, travel, and other—and the level of the forest at which activities were performed. The movements of groups within the forest were recorded on prepared maps. When animals were feeding, the place and level at which they were feeding were recorded as well as the plant species and part being eaten. The proportion of feeding records in which the animals were observed eating a particular species or part of a plant was regarded as an estimate of the time which the animals spent feeding on that particular item. Comparisons were made between the quantitative data collected on the two species and between those collected on allopatric populations of the same species.

4. Feeding behaviour.

4.1. Feeding techniques. *Lemur catta* and *Lemur fulvus* were similar and quite variable in the postures they used while feeding in the trees. They usually fed in the small terminal branches. *L. catta*, however, often fed while sitting or standing on the ground. Both species picked food items off the branches directly with their mouths or held food in their hands squirrel fashion while chewing. There was very little manipulation of food items, and no peeling or other food preparation with the hands was observed. However, both species were seen licking water from their hands.

4.2. Feeding heights and feeding sites. Groups of *Lemur fulvus* moved very little throughout the day and had very small home ranges. Day ranges were between 125 and 150 m and home ranges were between 0·75 and 1·0 ha. This species remained in the continuous canopy of the forest and moved horizontally from tree to tree. The animals spent most of their feeding time in the closed canopy level of the forest or at the strata directly adjacent to this level. *L. fulvus* rarely came to the ground or visited portions of the forest which necessitated terrestrial locomotion.

Home ranges of groups of *Lemur catta* were 6 ha (Berenty) and 8·8 ha (Antserananomby), but in very arid regions they have been reported to be as large as 23 ha. Day ranges were about 900–1000 m. The group visited its total home range within seven to ten days, visiting a variety of food resources and constantly monitoring its range. Groups of *L. catta* moved mainly on the ground and spent over 58% of the daytime in areas outside of the continuous canopy portions of the forest, although they slept in the canopy at night. The animals fed in all the available strata of the forest.

4.3. Diurnal activity patterns and percentage of time spent feeding. *Lemur catta* and *Lemur fulvus* are active at different times of the day. The two species do not feed, rest, move or travel during the same hours. *L. fulvus* fed very early in the morning and late in the afternoon. *L. catta* also had two peaks of feeding but they were later in the morning and earlier in the afternoon. Seasonal variations were more pronounced in *L. catta* and seemed to be related to the time of sunrise and the length of the day. *L. fulvus* was active for much less time during the day than *L. catta*. Although both species spent approximately the same amounts of time feeding (25–30% of the day), *L. catta* moved constantly and covered relatively long distances to obtain its food. At Antserananomby, *L. catta* spent 44% of the day feeding, travelling and moving while *L. fulvus* spent only 31% of the day in these activities.

4.4. Species composition of the diet. *Lemur catta* had a much more varied diet than *Lemur fulvus*, eating two to three times as many species of plants. At both Tongobato and Antserananomby, only three species of plant made up over 80% of the diet of *L. fulvus*, with kily accounting for 49% and 76%, respectively. *L. catta*, on the other hand, used one part of its home range for three to four days and then changed to another part. Even when one feeding site was particularly favourable, the group moved continuously while feeding. This movement was rarely related to any noticeable depletion of resources. Groups of *L. catta* often fed on more species of plant in one morning or afternoon feeding session than did *L. fulvus* during the whole study. This difference was related to differences in the use of space between the two species, *L. fulvus* being very restricted in its use of both vertical and horizontal space.

4.5. Parts of plants eaten. Both *Lemur catta* and *Lemur fulvus* ate fruit, shoots, leaves, flowers, bark and sap. However, a very large proportion of the diet of *L. fulvus* was made up of the leaves of *Tamarindus indica.* Kily leaves made up 42% of the diet of *L. fulvus* at Tongobato and over 75% during the dry season at Antserananomby. In the latter forest, *L. fulvus* fed mainly on mature leaves. Like many other species of primate (e.g. *Lepilemur mustelinus*, *Colobus guereza*, *Alouatta villosa* and *Presbytis senex*), *L. fulvus* seems to be able to exist mainly on mature leaves at certain times of the year and this correlates, in all of these species, with low dietetic diversity (Hladik and Hladik, 1969, 1972; Charles-Dominique and Hladik, 1971; Clutton-Brock, 1975a). This agrees with a number of models of feeding strategies which predict that animals that utilize abundant and predictable food resources should choose a small range of food items (MacArthur and Pianka, 1966; Emlen, 1968; Levins and MacArthur, 1969; Schoener, 1971).

L. catta, on the other hand, is a dietary generalist. Its diverse vertical and horizontal ranging pattern was associated with a varied diet. The constant surveillance of a relatively large home range allowed groups of *L. catta* to exploit a number of different resources over a wide area: trees that were in blossom or fruit could be located and utilized, including many food sources which were not available to *L. fulvus* (e.g. those found in the brush and scrub areas at Antserananomby or on the ground). Thus even during the dry season, *L. catta* had access to and ate considerably more young leaves, fruit, and flowers than *L. fulvus.*

The models of feeding strategy mentioned above also predict that with a lower absolute abundance of food, a greater range of items should be taken. Furthermore, the distance between food items and the search time for these items should increase. With low food productivity and patchy, less predictable resources, the size of the home range should also increase. Thus, animals which feed on patchy and clumped resources, such as fruit trees, often tend to have large home ranges (Crook, 1965; Schoener, 1971).

Since *L. catta* and *L. fulvus*, where they are sympatric, have potentially the same resources, it is of course impossible to relate their dietary differences simply to the available resources or to gross differences in the environments in which they live. It is much more likely that food selectivity and specific habitat preferences are related to the evolutionary history of the two species and that these species have developed particular patterns of dealing with specific environmental conditions over a long period of time. Populations of *L. fulvus* are found in the rain forests of the east and in the wet deciduous forests of the north-west and west of Madagascar. They live in the continuous canopy portions of these forests where at least the foliage of some species of trees is always abundant and predictable. Their ability to exist on mainly mature leaves for part of the year provides them with abundant and predictable resources all year round. *L. catta* is found only in the south and south-west of the island and lives in many areas in which there are no lush, canopy forests, but only arid brush and scrub, or desert-like forests. In many of these forests the vegetation is patchy, unpredictable and likely to be very sparse for at least part of the year. The foraging strategies and food selectivity of *L. catta* may well be adapted to these arid environments.

5. Feeding behaviour and social behaviour. The social organizations of *Lemur catta* and *Lemur fulvus* parallel those of other primate species with similar feeding adaptations. *Presbytis entellus* and *Colobus badius*, like *L. catta*, both feed on fruit, select a wide variety of food items and live in large groups with extensive home ranges. *Presbytis senex* and *Colobus guereza*, on the other hand, are more like *L. fulvus*. These species feed largely on foliage, utilize comparatively few species of plant and live in small groups with small home ranges (see Clutton-Brock, 1975a).

A number of reasons have been proposed for large group size in populations utilizing clumped resources which are unpredictable in time and space. These are based on the proposition that each individual must cover an extensive area to obtain a necessary variety of resources but that the total area can support a large number of individuals. Aggregating these individuals into one large group may be advantageous for a variety of reasons. These include: (a) enhanced communication about resources and predators; (b) prevention of overlap in foraging areas of a number of solitary foragers (and, hence, decreased time and energy spent in trial and error while searching for undepleted resources and in aggressive encounters between conspecifics); (c) increase in the area monitored for food; and (d) increased ability to defend against predators (see Schoener, 1971).

It is also quite likely that the small group size found in *L. fulvus* can be related to the distribution, predictability, abundance and size of the resources it selects. We would expect that there will be some relationship between the spacing of resources in the environment and the spacing of those individuals using the resources. However, to explain the adaptive significance of specific differences between the types of social organization found among primates, diachronic as well as synchronic factors must be considered.

A complete understanding of the relationship between specific dietary preferences and foraging strategies and specific types of social structure will most likely have to take into account at least the following factors: (a) the resources and the periodicity of these resources within the total geographical range of the species, as well as those in any particular area; (b) the selectivity of the species—those resources chosen by the species as compared with those available (this is often best done by contrasting resource utilization between a number of species using potentially the same resources, or a number of populations of the same species in varying environments); (c) the evolutionary history of the species [including extrapolations about the present and past geographical distribution and the environments which exist(ed) within these ranges]; and (d) the history of the particular population and group, since conditions in a given area may select for population-specific or group-specific adaptations. This final factor would take into account the flexibility (adaptability) of the species in question given local conditions.

Although *L. catta* and *L. fulvus* coexist in a number of forests in the south-west of Madagascar, they utilize different resources. The data indicate that the differences in resource utilization and habitat preference are not the result of the interaction between the two populations. It is most likely that their patterns of behaviour developed as phylogenetic adaptations to different ecological conditions during the evolutionary history of the two species.

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The Ecology and Sociology of Feeding in *Indri indri*

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1. METHODS

1.1. Introduction

The largest living Malagasy lemur, *Indri indri* (Gmelin, 1788), is the most specialized of the extant "vertical clinging and leaping" primates (Napier and Walker, 1967). Leaping from one vertical support to another is the predominant locomotor behaviour of a small taxonomic family of large-bodied lemurs—the Indriidae—containing in addition to *Indri*, the genera *Propithecus* and *Avahi*. In structure, size and many aspects of behaviour *Indri* closely resembles *Propithecus* (see Richard, this volume) but, unlike the latter, possesses only a rudimentary tail. Although the distribution of *Propithecus* is island-wide, *Indri* are only found in parts of the montane rain forests which line the eastern coast of Madagascar (Fig. 1). *Avahi* is smaller, nocturnal and distributed

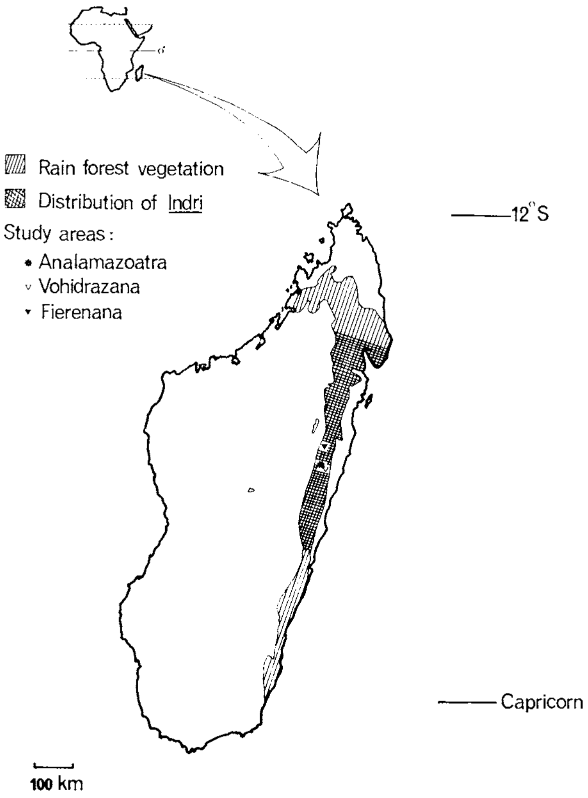

FIG. 1. The distribution of *Indri indri* and the location of study areas mentioned in the text.

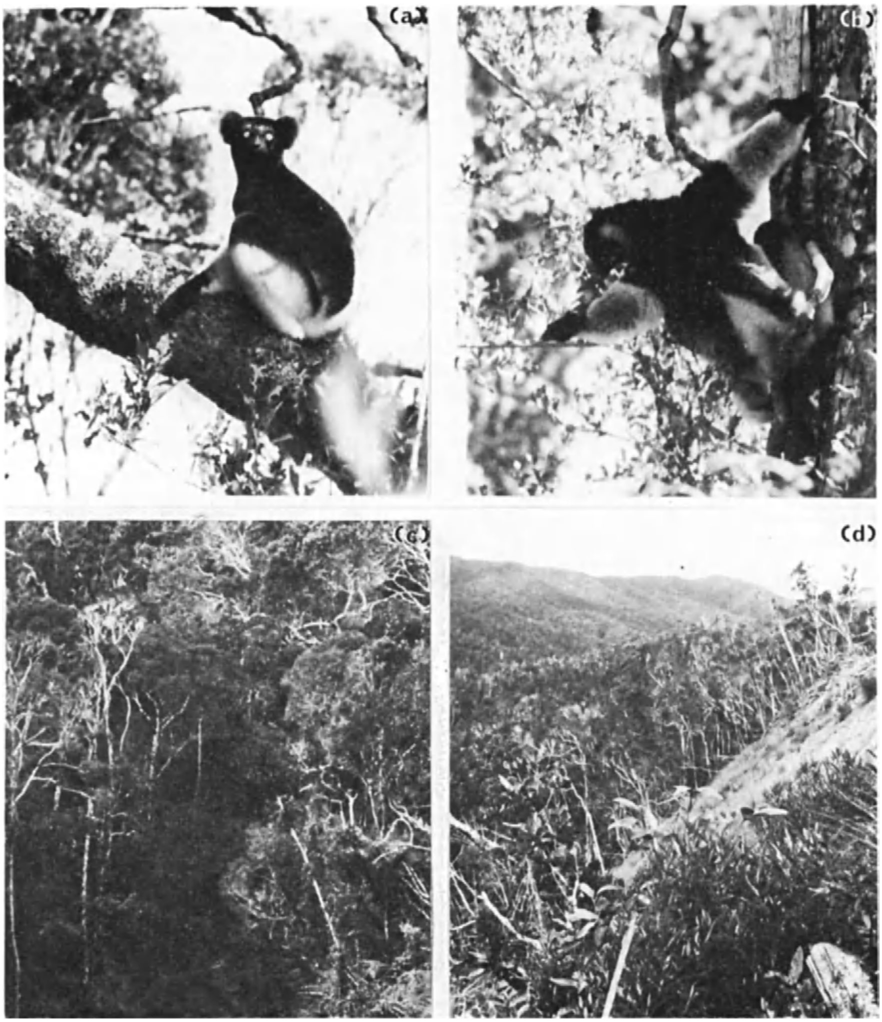

FIG. 2. The study species and its habitat. A partially habituated adult female *Indri* is shown resting in (a) and the group P adult male feeds on "non-supporting" vegetation (*Ficus pyrifolia*) in (b). Parts (c) and (d) illustrate the differences in forest structure within the territory of one study group at Vohidrazana. Tall, slim trees occupy the bottom of the valleys (c), whilst at the top of the ridge a tightly packed vegetation of smaller stature (d) is frequently found.

about both these rain forests and the drier and seasonal forests in the north-west of the island. All three genera are folivore-frugivores (Petter, 1962) and possess the functionally related alimentary specializations: large salivary glands, capacious stomach and lengthy convoluted caeca (Hill, 1953). In the areas visited during this study the three genera were sympatric.

The humid forests of eastern Madagascar are built on a series of highly folded, steep-sided ridges. By influencing patterns of drainage and shelter from prevailing winds these ridges promote a local climatic heterogeneity that considerably affects plant growth. In the wet valley bottoms tall, straight trees grow at low densities to form the closed canopy, conditions typical of climax rain forest vegetation (Richards, 1966). The rapidly drained and exposed ridge-tops, however, support a densely packed vegetation of small twisted trees which often form an impenetrable barrier to observers' movements (Fig. 2d).

Many, if not all, plant species grow at widely varying densities according to their position at different levels on the ridge slopes. Different plant species were found to adapt similarly to the distinct climatic conditions present at each level, causing extensive physiognomical variability within each species. In particular, the size and shape of leaf and leaf-supporting structures of different species of tree were convergent at each level on the ridge, making the task of distinguishing and naming species a difficult one. *Indri*, however, appeared

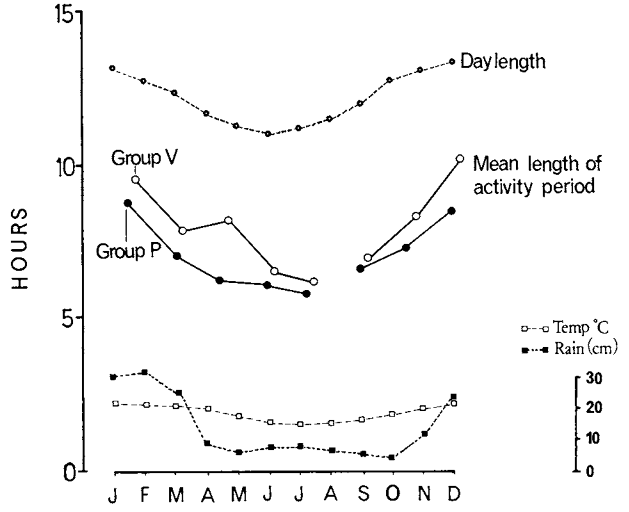

Fig. 3. Seasonal changes in mean monthly rainfall, mean monthly temperatures, astronomic daylength and the study groups' mean activity period duration at Analamazoatra.

to select different foods with equal efficiency at all levels on the ridge slopes.

Mean measures of rainfall and temperature throughout the year (Fig. 3) illustrate the gradually fluctuating temperatures that "peak" in the summer wet season (November to March) when rain falls as afternoon tropical cloudbursts and often throughout the night. Long periods of heavy cloud cover or continuous light rain interspersed with occasional fine days characterize the colder winter months (April to October). Phenological cycles in the forest, if they were at all regular, were of a periodicity that prohibited investigation during the period of field research.

1.2. Study Areas

Three study areas were visited in six-week cycles ("circuits") between June 1972 and August 1973 in order to study the behaviour and ecology of *Indri indri* (Fig. 2a). *Indri* groups were habituated to the observer in the forests of Analamazoatra and Vohidrazana and observed for a total of approximately 2300 hours. A further 200 hours were spent in observations of *Indri* at Fierenana and in other forests.

Indri were found to live in small groups of two to five individuals each comprising a nuclear family unit of an adult male, an adult female, and their dependent offspring (Petter, 1962; Pollock, 1975a). A single infant is born to the adult female at two- or three-year intervals, offspring reaching adult size at about seven to nine years of age. In all study areas the population density of *Indri* lay between nine and 16 individuals per km^2, each group occupying strictly defined territories of 0·15–0·3 km^2 (Pollock, 1975a).

Two groups of *Indri* (group P and group V) were habituated to the observer at Analamazoatra over a period of ten weeks by a repeated

TABLE I

The composition of Indri study groups

Group	Adult ♀	Adult ♂	Adult-sized (03)	Sub-adult (02)	Juvenile (01)	Infant	Total
P	1	1	1 (♂)	1 (♂)	1 (♀)	—	5
V	1	1	—	—	—	1 (♂)	3
IV	1	1	1 (♀)	1 (♂)	—	1 (♂)*	5

The two main study groups, group P and group V, lived in the forest of Analamazoatra. Group IV lived in the forest of Vohidrazana.

* Infant born during the study (May 1973).

process of locating and following a single group. The composition of these two main study groups is shown in Table I. Every individual could be easily distinguished by facial idiosyncracies.

1.3. Methods of Observation

Indri groups were judged to be "habituated" when all constituent members would feed within 5 m of the observer. At this point quantitative observations commenced and groups P and V were followed for 13 and eight days respectively each "circuit". During each period of observation the activity, posture and position of all animals that were visible were recorded at five-minute intervals for ten (group P) or six (group V) successive days. Eight circuits, each containing a single period of observations on each of the two main study groups, covered the year-long period of research.

Each *Indri* group was observed daily throughout their complete diurnal activity period which lasted from five to 11 hours according to the season and the weather. The daily activity period began when the first animal to move from its sleeping position began to feed and ended with the last movement to a sleeping position by a group member. All *Indri* group members usually started to feed no more than a few minutes after the first did so and usually stopped within a few minutes of each other.

One activity record for an identified individual was called an "individual activity record" or IAR. Over the whole year 43·6% of the maximum recordable behaviour[a] of group P and 65·3% of the maximum recordable behaviour of group V was obtained in this way. IARs were equally distributed across individuals, time of day and season, but relatively poor powers of animal identification during the first circuit (56·9% of behavioural records were unidentified compared to a yearly mean of 9·2%) required this month's data to be omitted from much of the subsequent analysis.

1.4. Statistical Analysis

Indri have both a low frequency of behavioural change and a limited repertoire of different activities, thus engaging in long bouts of similar behaviour. Samples of behaviour separated by five, ten and 15 minutes

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[a] The *maximum recordable behaviour* is the total number of individual activity records (IAR) obtained had the behaviour of every individual in the group been recorded at every point-sample during the group's activity period.

were examined to locate the minimum interpoint-sample interval (J. Altmann, 1974) that would enable the greatest quantity of statistically independent records to be used. Behavioural transition[a] frequencies were calculated for each of these three time intervals and compared to distributions expected by chance with a chi-squared (χ^2) test. Only 15-minute transitions were not significantly ($0{\cdot}1 < P < 0{\cdot}2$) interdependent and these were therefore chosen as basic data and considered to represent the optimal compromise between the need for statistical "independence" and the need for minimizing errors arising from sample size limitations.

This treatment fails to solve the problem of dependence between group members as each individual's activity record is considered separately. Only by considerably reducing the amount of data and by applying potentially weighting techniques of data selection could this problem be overcome. As these procedures were inappropriate for the present data reasonably stringent levels of significance ($P < 0{\cdot}05$) are employed and comparable degrees of intragroup behavioural dependence in the main study groups proposed in mitigation.

In the following discussion probability values derive from chi-squared tests unless otherwise stated. Within each group differences between individuals were tried only when the values of all individuals in the group varied significantly.

2. FEEDING BEHAVIOUR

2.1. Feeding Techniques

Foliage, flowers, fruit and leaf buds were generally consumed by *Indri* from branches pulled towards the mouth. Small fruits were picked by mouth and gnawed out of the clenched hand which thus acted as restrainer and support. Large fruits were bitten from their stalks, transferred to the hand and eaten after the animal had moved to a secure position in the food tree. Neither was ever picked manually.

The major source of fruit during the study period consisted primarily of species of the laurel family, all of which were approximately spherical or oval and the size of a large grape. The endosperm of the unripe fruit was scooped out using the "dental-comb" (the prominent battery of

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[a] Strictly speaking, as continuous records of behaviour were not obtained these are *point-sample* and not *behavioural* transitions. In practice the long duration of bouts of activity such as "feeding" or "resting" in *Indri* make this distinction superfluous. In any case the error will underestimate rather than overestimate behavioural independence.

specialized teeth in the lower jaw) as a sharp-edged spoon. Later, the thin sweet pericarps of the same but now mature fruit were gnawed off the underlying kernel.

Mature leaves of rain forest vegetation are thick and rigid and were eaten in bites from the side or apex. The majority of consumed foliage was young, flexible and small and could be clipped off—several leaves at a time—and drawn continuously into the mouth whilst chewing and swallowing.

Indri profit from the high rates of leaf production in young trees by spending a large proportion of their time feeding on sapling vegetation. Although many saplings are unable to support the weight (10–15 kg) of an adult, *Indri* obtain food by pulling them towards a nearby vertical trunk from which they can feed, in the locomotor or "vertical clinging" posture, for several minutes (Fig. 2b).

2.2. Feeding Heights and Sites

Heights were estimated by eye, following calibration by practice with a Zeiss altimeter, to within a 10% maximum error. Since *Indri* changed heights less frequently than they changed activity, height records were taken every 30 rather than every 15 minutes.

All individuals were seen to feed throughout the year at all levels (2–40 m) in the forests. The mean height of individuals in each study group at Analamazoatra was 14 m.

To examine which parts of the trees *Indri* used most, the position of each animal in the canopy was recorded at every point-sample. With the exceptions of the cauliflorous flowers and fruits of a *Tambourissa* sp. and the leaves and fruits of two strangling figs (*Ficus pyrifolia* and *Ficus* sp.), food was canopy borne. The canopy of each tree, irrespective of height, could be allocated to one of three gross structural divisions: (i) cone, (ii) inverted cone and (iii) cylinder. Within each canopy type, four strata were distinguished: "under the canopy" (UC); "canopy bottom" (CB); "middle canopy" (C); "canopy top" (CT). "Middle canopy" comprised the central 50% of the vertical spread of the canopy in each type of tree, "canopy bottom" and "canopy top" equal parts of the remaining lower and higher canopy levels. In addition, two horizontal categories were formed so as to separate the central parts of the canopy from those where an animal was either feeding or was in a position from which it was able (without altering its position) to feed on the outermost regions ("terminal" positions).

An *Indri* located in any of the positions in the canopy would feed, in virtually all cases, on the tree in which it was situated. Feeding "under the canopy", however, generally referred to the consumption of non-supporting (usually sapling) vegetation (Fig. 2b).

Indri at Analamazoatra, where the forest had been subject to selective logging on a small scale, spent approximately equal amounts of time in different canopy levels. Thirty-five per cent of feeding records described animals in the central "middle canopy" category whilst both "canopy top" and "canopy bottom" were used for 17% of the time. About 16% of feeding records involved consumption of a plant other than that in which the animal was situated. Overall, 9% of the records were scored as "terminal" feeding positions.

Group V fed considerably more on non-supporting vegetation than group P ($P<0{\cdot}001$). Within groups certain individual differences were revealed by analysis of each individual's canopy utilization scores. The adult male of group P, for example, differed overall from the adult female and each of the two youngest offspring ($0{\cdot}01<P<0{\cdot}05$, all tests). These differences in canopy use whilst feeding were the only interindividual differences in this group. When the amount of time each group P individual spent in each canopy level when feeding is calculated, these overall differences could be ascribed to specific parts of the trees. Thus the adult male spent significantly less time feeding in "terminal" positions than the youngest offspring 01 ($0{\cdot}01<P<0{\cdot}05$), the subadult 02 ($0{\cdot}001<P<0{\cdot}01$) more time feeding in the "middle canopy" than 02 ($0{\cdot}01<P<0{\cdot}05$), and more time feeding in the "canopy bottom" than the adult female ($0{\cdot}001<P<0{\cdot}01$), as shown in Fig. 4. Feeding sites chosen by one group V adult differed significantly from those chosen by the other ($P<0{\cdot}001$)—the adult male spent significantly less time feeding in the "canopy top" ($P<0{\cdot}001$) and more time feeding in terminal positions ($P<0{\cdot}001$) than the adult female.

The intergroup difference appears to result predominantly from the different feeding positions adopted by the two adult females as no overall differences between males could be determined. The low probability that these two females used the trees similarly for feeding ($P<0{\cdot}001$) could be attributed to the respective amounts of feeding time spent (a) at "terminal" positions (P high, $P<0{\cdot}001$) and (b) outside the canopy on non-supporting vegetation (V high, $0{\cdot}01<P<0{\cdot}05$). Compared to her group P counterpart, the female of group V thus avoided peripheral parts of the canopies of trees in which she fed and chose to spend instead proportionately more time feeding on the young foliage of saplings growing low in the forest.

Assuming that each individual would freely move to similar optimal feeding spots in a food tree, consistent differences between individuals'

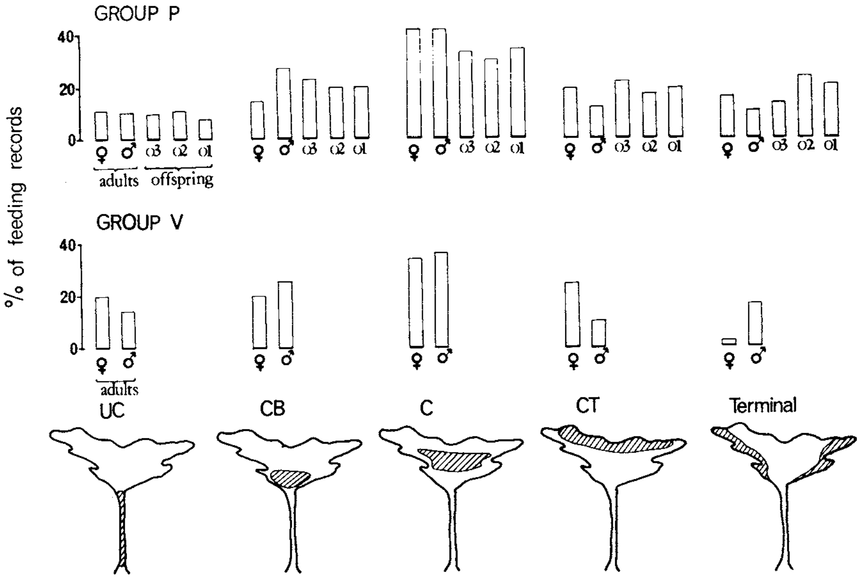

FIG. 4. Individual differences in preferred feeding sites chosen by *Indri* at Analamazoatra. The proportion of each individual's feeding records that were scored as under the canopy (UC), in the canopy bottom (CB), in the middle of the canopy (C), in the canopy top (CT) and in the peripheral canopy parts (Terminal) are shown. Canopy categories are more fully described in the text.

utilization of the various parts of trees are likely to be of social significance. Displacements of the adult male by the adult female in each study group forced the former to feed in lower canopy levels. There the adult male could easily move to another tree if the attack was repeated, but the concentration of food was poorer. Adult female *Indri* were never displaced from their selected feeding positions. Terminal feeding positions were apparently most used by the lightest animals (01 and 02) and some intragroup ecological differentiation may have thus developed to some small extent as envisaged by Kummer (1968) for *Papio hamadryas*.

It is likely that differences in feeding positions chosen by the two adult females were associated with the presence of an infant in group V. Terminal branches broke easily and observed falls occurred usually from these positions. Furthermore, locomotor practice performed by the infant in a small area around its mother whilst she fed in the tops of trees frequently caused branches to break or the infant to lose its grip on weak supports and fall. The mother may have avoided terminal positions in the interest of infant security and chosen to feed more on the young leaves of saplings low in the forest where falls by the infant were inconsequential (see Section 3).

2.3. The Time Spent Feeding

2.3.1. *Overall time spent feeding*

Differences in the overall activity period of the two groups were marked (Fig. 3). The relative proportions of the daily activity period spent feeding over the whole year was 39·2% for group P and 36·6% for group V. After translation into measures of real time group V in fact fed on average for 4·9% longer than group P each day as a result of their longer daily activity period.[a]

The percentage of the activity period devoted to feeding varied from 30 to 60% throughout the year. The data were insufficiently precise to permit an examination of daily changes in this parameter, but the impression gained was of little or no variability. The longer daily activity periods during the summer months were not associated with any correlated reduction in the proportion of time *Indri* spent feeding (Fig. 5). For group P the amount of time spent feeding each day throughout the year rose and fell with the seasonally changing duration of the daily activity period. This group spent significantly less time feeding during circuits VI and VII than at any other time of the year (both tests: $0{\cdot}01 < P < 0{\cdot}05$). Compared to other months least fruit was consumed during these two circuits (see Section 2.3.3).

For group V, however, feeding was more variable, presumably because of non-seasonal influences. Ten significant differences between

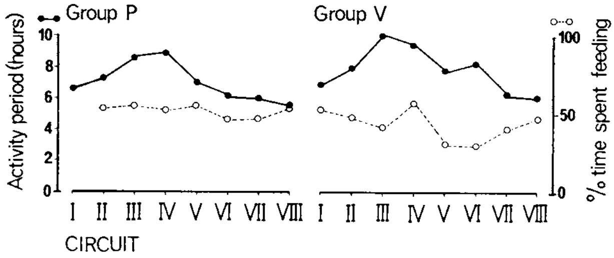

FIG. 5. Changes in the duration of the daily activity period and the proportion of this period spent feeding by each study group at Analamazoatra over the year's observations. The abscissa is marked by the circuit number (see text). Circuits occurred at approximately 6-week intervals from September 1972 (circuit I) until August 1973 (circuit VIII).

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[a] This is a % difference of group P's total number of feeding records per day. A test was conducted in the field to ensure that *Indri* behaved similarly when they were out of the observer's sight as they did when normally seen (Pollock, 1975b).

circuits in the proportion of the activity period spent feeding contained five which focused upon the poor level of feeding exhibited by this group during circuit V.

2.3.2. *Diurnal distribution of feeding*

Indri first show signs of activity two to three hours after dawn and finally take up sleeping positions a similar period before dusk. The total period of activity each day can last as little as five (midwinter) or as much as 11 (midsummer) hours and is often considerably shortened by wet, cold weather conditions. Within this period *Indri* range and feed continuously, gradually building up the intensity of feeding to peak at about midday or shortly after (Fig. 6). Temporary social sessions of loud, intergroup calls, communal bouts of defaecation, and suckling activities were sufficiently variable in their timing and short in duration to be concealed in the overall distribution of feeding records. The longer activity period of group V more than compensated for the proportionately fewer feeding records each hour compared to group P.

Seasonal variation in the hourly distribution of feeding (Fig. 6) indicates for group P earlier morning feeding "peaks" (9.00–10.00h) in the summer months (circuits III–V) than in the winter (11.00–

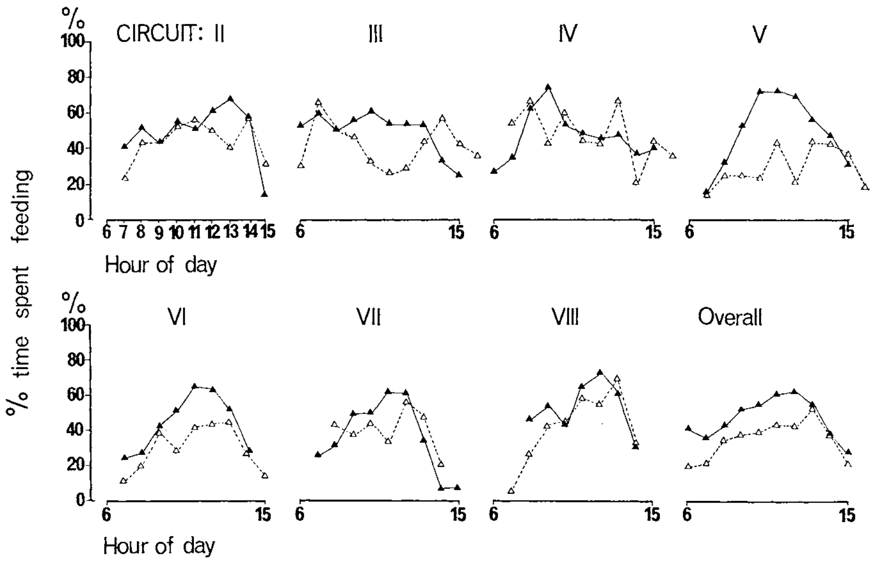

FIG. 6. The hourly distribution of feeding records during each circuit. The proportion of each hour of the daily activity period that group P (closed triangles) and group V (open triangles) were engaged in feeding activities is shown for circuits II to VIII and over the whole year (Overall).

13.00h during circuits VI–VIII). Intense feeding bouts early in the day on the fruits of *Ravensara* sp. and *Cryptocarya* sp. during circuit IV accounted for this peak at one time. In group V the variable daily distribution of suckling times adversely affected smooth daily distributions of feeding records for each circuit. In midsummer (circuit III), for example, an early and late feeding peak is present—a condition typical of diurnal, tropical animals, and indeed lemurs in other regions (see Richard, this volume). Here, however, this bimodal pattern is probably associated with the fact that 65·5% of the time spent suckling by the group V infant during circuit III occurred between 10.00 and 12.00h. Towards the end of the study, as the infant was weaned, the daily distribution of feeding activities (and the activity period itself) more closely approached that of group P.

The hourly distributions of feeding showed no marked variation amongst different individuals (Pollock, 1975b).

2.3.3. *The amount of time spent feeding on different foods*

Indri were seen to eat at least 62 species of plant during the course of the study. All 62 species could be ascribed to a genus, but only 24 were identified at the species level. In 10·8% of the feeding records it was not possible to identify the species of plant being consumed either because the food could not be clearly seen or because it was unknown. Using the classification suggested by Hutchinson (1973) identified foods were located in 19 families, the most frequently represented of which were: Clusiaceae (seven spp.), Annonaceae (four spp.), Lauraceae (three spp.), Euphorbiaceae (three spp.), Sapindaceae (three spp.), and 11 families each represented by a single species. No animal matter was seen to be eaten by *Indri* during the study period although it appeared that objects obtained from the fur and skin whilst grooming were sometimes ingested.

A maximum of 16 plant species consumed by group P were not observed to be eaten by group V and five species consumed by group V were not observed to be eaten by group P. This was most likely due to differences in the period of observation on each group (see Section 1.3) and not to intergroup variation in selectivity. Of the 21 species eaten by one group but not by the other, 14 were eaten on a single occasion during one circuit only, and the remaining seven totalled only 1·1% of the feeding records of group V and 3·3% of the feeding records of group P.

Each *Indri* study group fed much more on some species than others (Fig. 7). Group P spent 13·9% of its feeding time on the top ranking species and 50% on the top ranking five species. Group V spent 19·0%

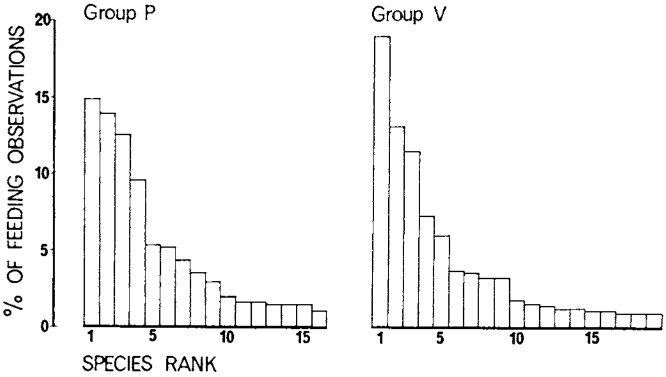

FIG. 7. Species selectivity. The proportions of each group's feeding observations that the most heavily eaten food species were consumed are shown for each study group at Analamazoatra. Species are ranked according to their proportion of the feeding observations and only those species fed on for at least 1% of all the observations are included.

of its feeding time on the top ranking species and 50% on the top ranking five species. Four of the five most-eaten species and ten of the 13 most-eaten species were common to both groups.

Differences in the diet of the two groups appeared to be more related to the amount of time each group spent on each food species than to the choice of species itself. Whether variation in the amount of time spent on particular food species was due to local variation in availability, different needs or personal preferences could not be examined as no measures of food abundance were taken. Clumps of food of one species were in at least some cases largely responsible for concentrated feeding by one group and not the other. Little, if any, seasonal variation in the variety of chosen food species was evident (see Section 2.4).

The two study groups did not differ extensively in the amount of time they fed on various food parts (Table II). Seasonal variation in food-part consumption was clearly associated in most cases with changes in availability resulting from phenological cycling of the food plants. Peaks in the seasonal distribution of consumption of each food

TABLE II

The percentage of feeding observations on each food part category by each study group over the whole year

Group	Leaf shoots and young leaves	Fruit	Flowers	Mature leaves	Unidentified
P	36·1	26·4	2·3	0·9	34·3
V	32·2	23·8	0·0	0·2	43·8

part by each *Indri* study group (Fig. 8) could be generally attributed to a few, specific and repeatedly visited food sources; thus the great increase in fruit-eating during the middle of the study period was clearly the consequence of the synchronized fruiting of a few, large *Cryptocarya olseodaphnifolia* in the territory of each study group at Analamazoatra. Similarly, the small overall amount of time spent feeding on flowers was due to a single species of *Symphonia* in circuit III and *Ocotea* in circuit V.

Young foliage, ranging from leaf shoots to large, flexible but clearly immature leaves, provided the main part of both study groups' diets. Fruit (including the unripe endosperm or seed) seemed to be preferred when it was available, and it was consumed earlier each day and for longer periods than young leaves. Other items, such as mature leaves, were fed on regularly but in small amounts.

The sampling technique employed during this study did not permit statistical comparisons of food-type consumption between groups to be made, but differences were not obviously marked.

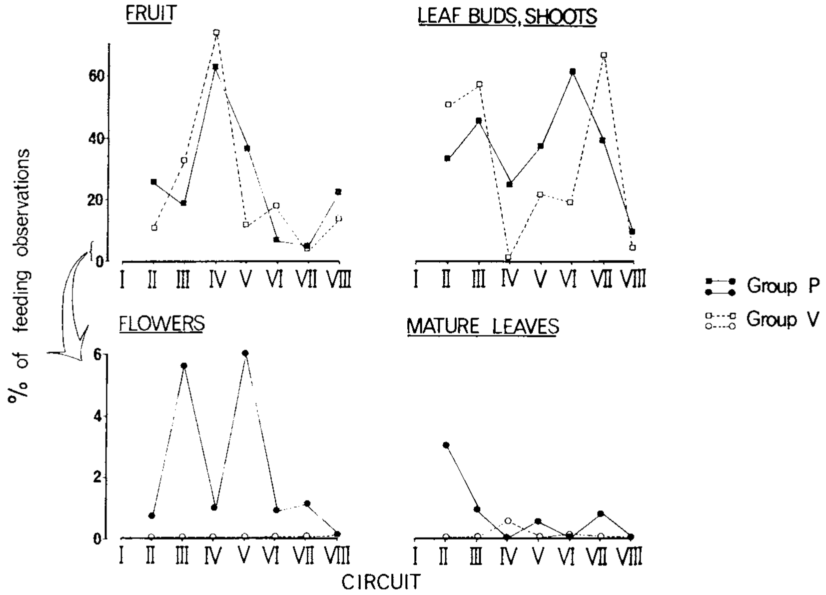

FIG. 8. Seasonal variation in food part consumption. Changes over the study period in the proportion of feeding records involving each major food part category are shown for each study group at Analamazoatra.

On about 75% of the observation days each *Indri* group consumed small quantities of earth exposed by upturned tree trunks. All group members sequentially fed on earth in a specific spot that would be returned to several days later. There appeared to be between five and ten such earth-feeding sites in each group's territory. An analysis of one soil sample failed to show high concentrations of specific minerals (Pollock, 1975b).

2.4. Selectivity

No botanical census of forests inhabited by *Indri* was performed but it was nevertheless clear that most *Indri* foods at Analamazoatra were produced by the commonest trees of the forest (Abraham, pers. comm.; pers. obs.). Using the results of a plant survey carried out in 1970 by a government department in one of the study areas (of a similar botanical constitution), it was found that out of the 20 commonest species of tree, 12 were much eaten *Indri* food species accounting for 82·6% of feeding observations in this study, and 58·7% of the forest's complement of trees.

Several cases of intraspecific selectivity of individual trees, repeatedly ignoring as food other frequently visited neighbouring trees, were observed in group P but not in group V. The significance of this form of selectivity was not understood, but may be cited as evidence for satisfactory levels if not an abundance of food at some times of the year.

2.5. Dietetic Diversity

Measures of the number of species eaten each day and each circuit did not vary greatly between the two study groups (Fig. 9), though the data suggested that group V individuals were slightly more diverse in their daily diet than those of group P. This is further supported by differences between the two groups in the frequency with which animals moved to a new tree (see Section 4.4).

Seasonal variation in dietetic diversity, measured by the number of different species eaten each circuit and the rate of change of food species each day, appeared to be absent in both groups. A particular food species was usually chosen once each day, although several individual trees might be visited within a feeding bout on that species. To this general rule, which conferred on the observer the impression of a highly organized strategy of feeding and ranging, there was a single notable exception: the saplings, young and old trees of *Ravensara pervillei*—the species most consistently consumed in large quantities

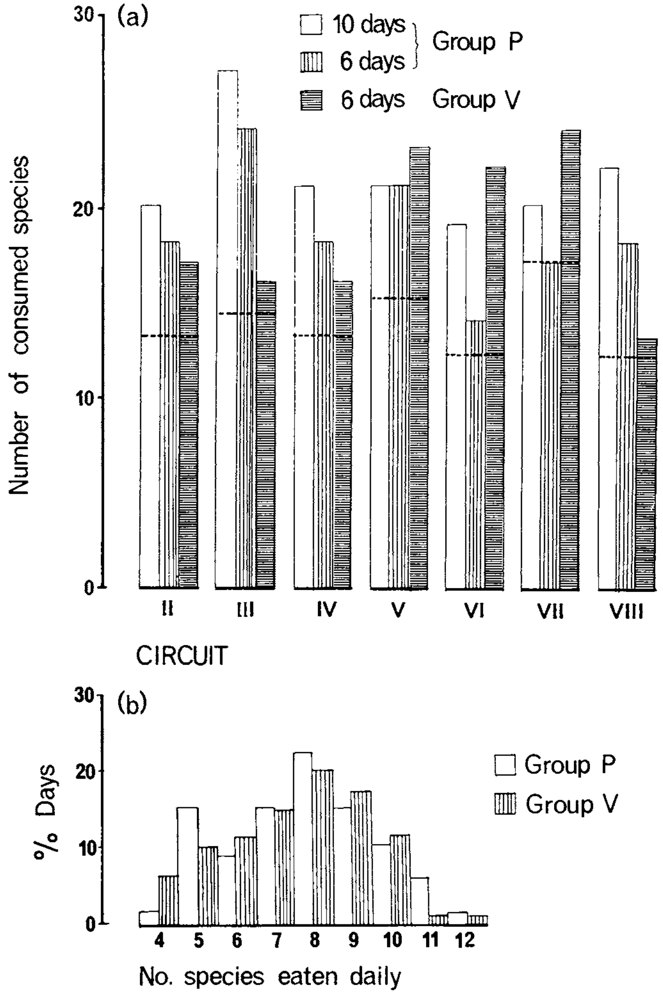

FIG. 9. Dietetic diversity. (a) Shows variation over the course of the study in the number of different food species eaten by each study group in a circuit. The heavy dotted line defines the number of species eaten by both groups during a circuit. (b) Shows the distribution over the whole year of the minimum number of different species consumed daily by each study group. The *minimum* number of species is that number of identified food species—all unidentified foods assumed to have been included in those previously or subsequently identified.

throughout the year—were apparently eaten wherever the group "came into contact" with them.

In any one day a noticeably constant number of species, ranging from five to 12 in number, was consumed by each group. These usually included a concentrated but temporary food source—one or two large fruiting trees, for example—and one or more species eaten throughout the year. In addition a group of five to ten species, which partially changed in composition between successive circuits, would contain three or four species chosen to be eaten each day, some of which were repeatedly fed on during only a single day. It was for this reason that the impression was gained of an organized variability in *Indri* diet. The fact that the degree to which certain foods were consumed more than others did not influence the number of species eaten daily, supports the hypothesis that a precise control of dietetic variety existed.

The presence of regular cycles of food choice over time could not be demonstrated either by measuring inter food-choice intervals or from a stochastic analysis of successive food selections (Pollock, 1975b). Nevertheless, a tendency to feed again on the same species at a different source ("feeding continuity") was present, although the low frequency of changes of food and the short observation periods prohibited statistical confirmation. Feeding continuity was most marked for (a) major foods, and (b) foods rarely eaten, but cannot be proposed for a large proportion of foods. As movements between different sources of the same food species frequently involved considerable progressions, spatial aggregations of trees of one species, though sometimes present, do not satisfactorily explain this behaviour.

There was no evidence that either group ate certain food species or food parts at particular times of the day, although long bouts of fruit-eating would usually begin early in the day.

Generally, the diet of *Indri* changed completely every two or three months. According to the local people, regular phenological seasonality in the forests' constituent species was mostly absent and observations made during the short period of research supported the notion of an apparently "random" occurrence of fruiting both between and within species for many species. From the 22 species eaten either at midsummer or midwinter, 12 were eaten at both times of the year but in only one case was the same part of the same species eaten. In general, dietetic differences between successive circuits were as variable as those between seasons and there is, therefore, no reason to consider parameters of nutrition in *Indri* in terms of slowly changing seasonal variation. For example, midsummer (circuit IV) stands out as the period when most time was spent on fewest species, although the activity period was at its longest and the greatest number of feeding observations recorded. During this circuit the top ranking species accounted for 59 and 55% of feeding observations for groups P and V respectively. Group P retained this highly selective feeding for the following circuit whilst group V returned to a more evenly distributed diet. Dietary specialization at certain times of the year seemed, therefore, to depend largely on specific food sources and did not arise in response to gradually changing seasonal effects. The possibility naturally remains that seasonally consistent changes in *Indri* diet occur regularly at intervals of more than one year.

3. AGE/SEX VARIATION IN FEEDING BEHAVIOUR

Individuals varied widely in all aspects of feeding behaviour. These included the overall time spent feeding, rate of food consumption and type of food consumed.

3.1. Feeding Rate

Only observations of feeding on certain fruits, which could be easily scored as their remains fell to the ground, suggested differences between individuals in feeding rate. The adult female in group V consistently fed more rapidly on the fruit of *Ravensara* sp. than the adult male (Mann-Whitney U test: $P<0{\cdot}02$).

There are insufficient data to compare other individuals but, in general, feeding rate appeared to be greatest in those individuals which fed longest (see below) thus enhancing rather than balancing individual differences in the quantities of food consumed.

3.2. The Time Spent Feeding

Although the degree to which individuals differed in the amount of time they spent feeding was complicated by seasonal variation, tests of individual variation in group P established three important results. Firstly, the adult male fed significantly less (i.e. less by time) than every other group member ($0{\cdot}01<P<0{\cdot}05$); secondly, the youngest individual fed significantly more ($0{\cdot}01<P<0{\cdot}02$) than every other group member except the next youngest individual; and thirdly, the oldest, adult-sized offspring fed significantly less ($0{\cdot}01<P<0{\cdot}05$) than the two youngest offspring.

As in group P, the adult male in group V spent very much less time feeding than the group's adult female ($P<0{\cdot}001$).

There was no difference in the overall amount of time spent feeding by the adult females ($0{\cdot}5<P<0{\cdot}7$) but the group V adult male fed for significantly less time each day than his group *P* counterpart ($0{\cdot}001 < P < 0{\cdot}01$).

Individuals in each group normally fed on the same item at the same time (but see Section 5.3). A cursory, quantitative examination of individual differences in the amount of time spent on food species and food parts was, however, performed. Sample size limitations restricted the analysis to major food items.

In group P the top ranking species, *Ocotea* sp., was consumed less by the adult male ($0{\cdot}01 < P < 0{\cdot}05$) than either 03 or 01 individuals. 01 also fed significantly more than 02 on this species ($0{\cdot}01 < P < 0{\cdot}05$). *Ravensara pervillei*, the second ranking food, was consumed equally by individuals of this group. In group V the two top ranking species were consumed equally by the two adults.

Individual preferences for (i) fruit and (ii) young leaves were then examined. No differences were found within group P but the adult female of group V fed on young leaves for 37·9% of the time compared to the adult male's 19·1% ($P < 0{\cdot}001$).

Adult males therefore fed for less time, may have consumed food more slowly and appeared to eat more fruit and less shoots than adult females and young offspring. In addition the adult male of group V fed far less than any other individual. Increased food intake by growing, pregnant or lactating mammals is a widely observed phenomenon (Sadleir, 1969) and may, if social constraints influence individuals' rate and amount of feeding, account both for overall differences in feeding and specifically the consumption of young protein-rich foliage (Hladik *et al.*, 1971a).

4. FEEDING AND RANGING BEHAVIOUR

4.1. Introduction

Indri groups in all study areas lived in strictly defined, adjacent *territories* surrounded by a narrow border of common ground in which border encounters would occasionally take place. Group P had been known to occupy their territory for at least four years (Pollock, 1975b).

The pattern of movements by *Indri* about their territory seemingly depended only on the distribution of food (Pollock, in press). When a desirable species or group of individual trees was fruiting or growing new foliage, early progressions to the food source (usually from a near central sleeping location) were followed by intense feeding, with very little animal movement, for periods up to three hours. The remainder

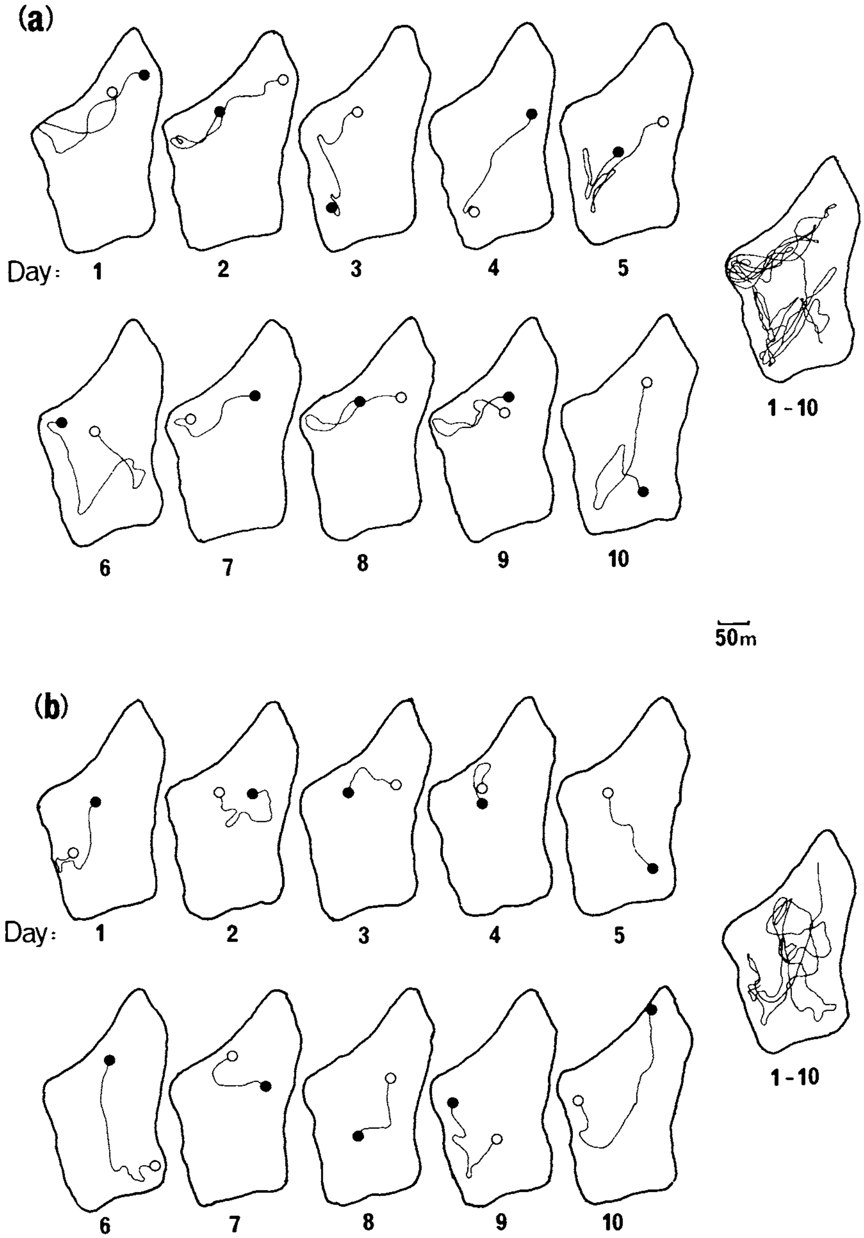

FIG. 10. Ranging for food. Daily travel paths are shown for group P at two different times of the year. In (a) repeated visits to a few fruiting trees resulted in predictable daily travel routes from central sleeping sites. When no food species were in fruit a more random-like pattern of movements occurred (b). Direction of movement can be inferred from the previous night's sleeping site (open circles) to the following night's site (black circles).

of the day was then devoted to sequences of short progressions and feeding bouts on a diverse array of species. Ranging patterns, in this case, reflected the repeated use of small parts of the territory and the specific arboreal pathways separating them (Fig. 10a).

When no concentrated food source was available shorter feeding bouts, interrupted by small progressions, took place. Occasionally a group would travel 200–300 m in one long movement taking them diametrically across their territory. A more even utilization of the territory occurred at these times (Fig. 10b).

The ranging behaviour of *Indri*, considered in terms of the amount of time spent in various parts and the frequency with which parts were visited, was recorded by marking out each territory into 50-m sided quadrats, the event of a group moving into a new quadrat being continuously recorded.

4.2. Territory Utilization and Feeding

Despite concentrating equally on similarly sized portions of their territories (see below), the two study groups differed in the way different quadrats were used. Group V spent relatively less time per entry in low ranking quadrats (quadrats in which only small overall amounts of time were spent) than in high ranking quadrats. This relationship was absent in group P which appeared to use the quadrats they did visit, equally (Fig. 11). There was no consistent relationship

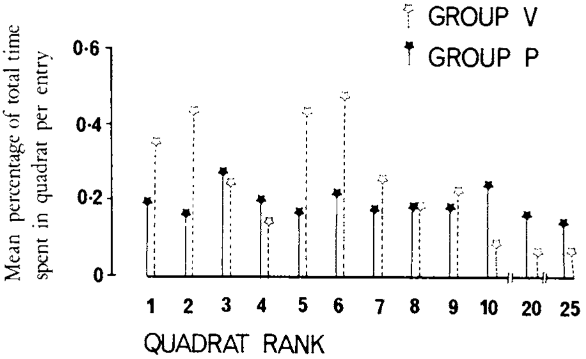

FIG. 11. The amount of time spent in a quadrat once it was entered. The average percentage of the total observation time spent by each group in the most heavily used quadrats each time they were entered. Quadrats are ranked according to the amount of time spent in them overall. In group V (but not group P) less time was spent per entry in quadrats in which little overall time was spent, than in quadrats in which a lot of time was spent overall.

for either study group between the amount of time spent in a quadrat and the proportion of time spent there in feeding activities.

It appeared, therefore, that as the amount of time spent in a quadrat was not significantly correlated with the number of species consumed in that quadrat ($0{\cdot}6 < P < 0{\cdot}7$), group P was probably entering specific quadrats to feed upon specific foods. The movements of group V, however, which spent relatively small amounts of time in little-used quadrats each time they were entered, suggested that although this group was also concentrating on parts of the territory they knew contained food, they were passing more rapidly through other areas.

4.3. Ranging Behaviour and Feeding

Although over the whole year all territory parts were visited several times, during a circuit the study groups moved through, on average, only 41·4% (group P) and 43·5% (group V) of the territory in six successive days. The territorial area was quite discrete and apparently unchanging over the period of research. Territorial boundaries could be defined satisfactorily by the behaviour of the animals in peripheral regions without having to resort to measures of cumulative annual ranges (Pollock, in press).

In ten days a mean of only 57·2% of the quadrats in group P's territory was visited and, therefore, it is not possible accurately to relate *Indri* ranging patterns with seasonal variation in diet, or even closely compare the ranging movements of the study groups themselves. The median number of different quadrats entered daily did not significantly differ between the two groups (median test: $0{\cdot}1 < P < 0{\cdot}2$), and the frequency with which a visited quadrat was subsequently re-entered during the same circuit was likewise similar (Pollock, 1975b). Although both groups appeared to range farthest during the summer months when the activity period was longest, seasonal differences in daily travel distance did not vary significantly over the year's observations either for group P (Kruskal–Wallis test: $0{\cdot}5 < P < 0{\cdot}7$) or group V (Kruskal–Wallis test: $0{\cdot}2 < P < 0{\cdot}3$). Seasonal changes in the amount of rain, the time during which rain fell, temperature and daylength were not closely related to obvious changes in food availability or the type of food consumed, and neither were climate-dependent differences found in most parameters of ranging behaviour (Pollock, 1975b). That groups moved farthest when most fruit was consumed seemed to be associated with the local distribution of a few individual fruiting trees rather than any regular seasonal variation in ranging behaviour.

4.4. Local Movements and Feeding

The impression that group P's ranging movements were organized into a definite pattern was gained from observations of their tendency to travel in straight lines or wide arcs about the territory. Measures of the acuteness of turns performed by each group each circuit were found to be correlated with the proportion of time spent feeding in group V (Spearman correlation test: $0{\cdot}01 < P < 0{\cdot}05$) but not in group P (Spearman correlation test: $r_s = 0{\cdot}07$, n.s.). Attempts to correlate the frequency of each group's angled movements with the proportion of time that each adult spent feeding isolated the adult male in group V as the main contributor to his group's variation in this measure (Spearman correlation test: $0{\cdot}01 < P < 0{\cdot}05$). The group V adult male was found to feed least when most angled movements taken by the group occurred.

Individuals in group V moved from tree to tree more often than those in group P. The frequency with which group V members moved into another tree was three times as great as the frequency in group P, and longitudinal observations of the group V adult male and the group P adult female showed that the former made about three times as many jumps as the latter every day (Pollock, in press). The distance actually travelled by one group P individual was nearly identical to the distance moved by the whole group estimated mathematically from mean inter-quadrat distances (Pollock, in press). As the numbers of quadrats entered daily did not differ between groups, group V appeared to be moving about three metres sideways for each metre travelled in the direction of progression, whereas for group P no considerable lateral movement occurred.

The tendency for group V to move more rapidly through rarely visited quadrats, to move more within quadrats than group P, and to make most angled turns when they fed least, all implied either a poorer knowledge of food location or a dearth of food in their territory. Folivorous primates may require years in order to accumulate a proper knowledge of food location in rain forest environments. The socionomic structure of the group, the recent acquisition of a territory by group V (according to the local people) and the seemingly satisfactory levels of food observed in the forest when the animals fed little, suggest the former interpretation.

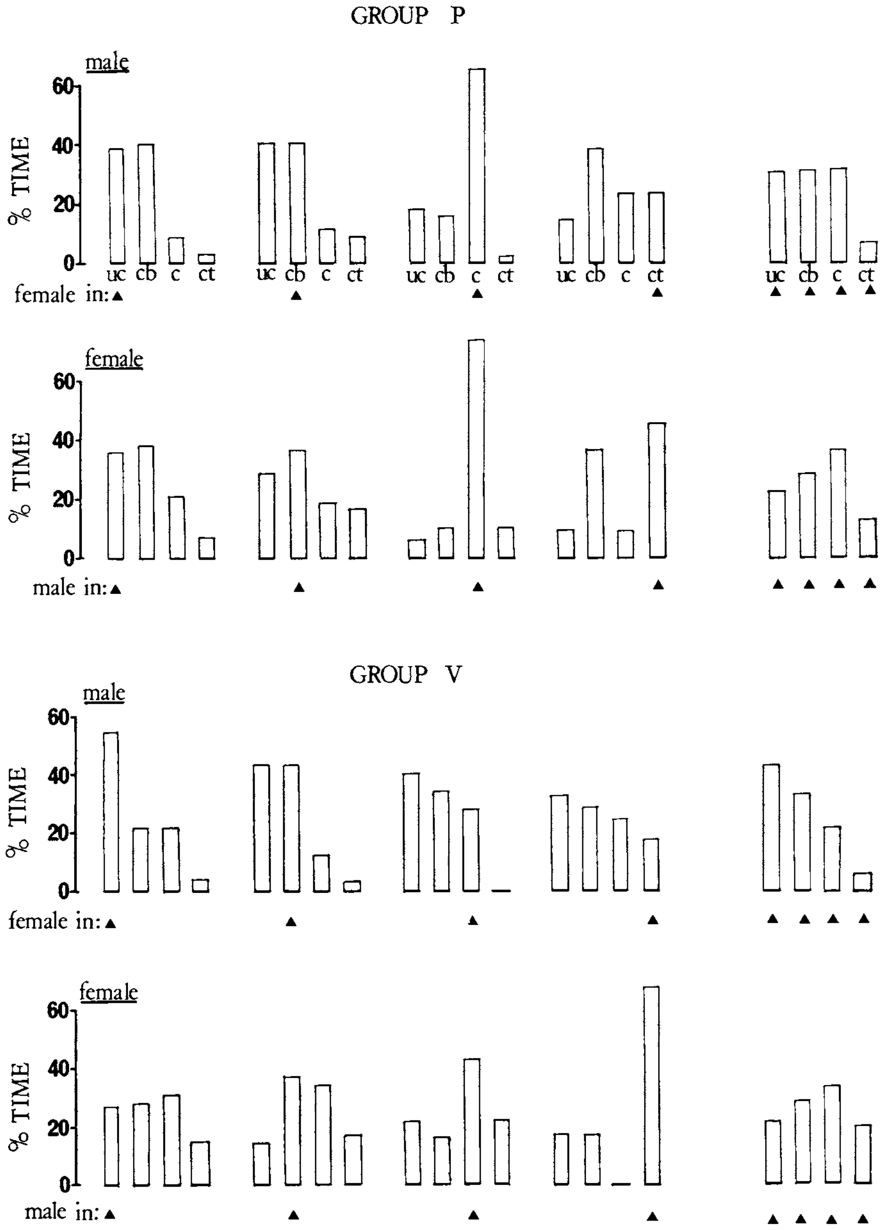

FIG. 12. The relative positions of the adults in each study group. The proportion of observations (% time), when the two adults in a group were seen simultaneously, that different canopy levels were occupied. For each case and in each group the proportion of observations that one adult is in each canopy level (see Fig. 4) when the other adult is in a specified canopy level is shown. Thus when the female of group P was in the bottom canopy position (cb) the male was seen under the canopy (uc) 40% of the time, at the bottom of the canopy 40% of the time, in the middle of the canopy (c) 11% of the time and at the canopy top (ct) 9% of the time. Also shown are the canopy positions taken by one adult when the other adult is in any canopy position.

5. SOCIAL ASPECTS OF FEEDING BEHAVIOUR

5.1. Introduction

Competition for food between *Indri* group members was expressed by frequent aggressive interactions ("displacements") in feeding situations. Most aggressive episodes were observed when many group members were feeding in crowded conditions in a small, dense food source. Adult *female* and young *Indri* are dominant in all such instances but confrontations involving these animals were rarely observed—their status being normally maintained without examination.

The data permitted a fine analysis of social inhibition and facilitation in feeding activities to be made. The social influence one individual exerted on another's feeding behaviour was considered to be manifested in measures of:

(a) "feeding proximity"—the relative positioning within trees and the distances separating animals according to their activity, and

(b) "feeding synchrony"—the relative timing of individuals' activities.

5.2. Feeding Proximity

The spatial relationship between adults in each group was examined in two ways: (a) the relative positions adults took in trees at the same time, and (b) the absolute distances separating adults whose activities varied.

When the two adults in a group were simultaneously seen the adult female was consistently observed to be higher in the canopy than the adult male (Fig. 12). This difference was more marked in group V than in group P and was independent of canopy level i.e. the females spent more time in higher canopy positions than the adult males irrespective of the males' canopy positions. As lower parts of the trees were more structural than food-bearing this probably conferred a feeding advantage on the females.

For both *Indri* study groups the distances between adults when either one or the other or both were feeding were computed (Fig. 13). In group P the adults were closer together when both were feeding than when either adult only was feeding ($P < 0{\cdot}001$). Unlike group P the adults of group V were significantly farther apart when the adult male only was feeding than when the adult female only was feeding ($P < 0{\cdot}01$). Furthermore, group V adults feeding simultaneously were farther apart than group P adults feeding simultaneously ($P < 0{\cdot}001$).

In feeding situations, therefore, female dominance was expressed

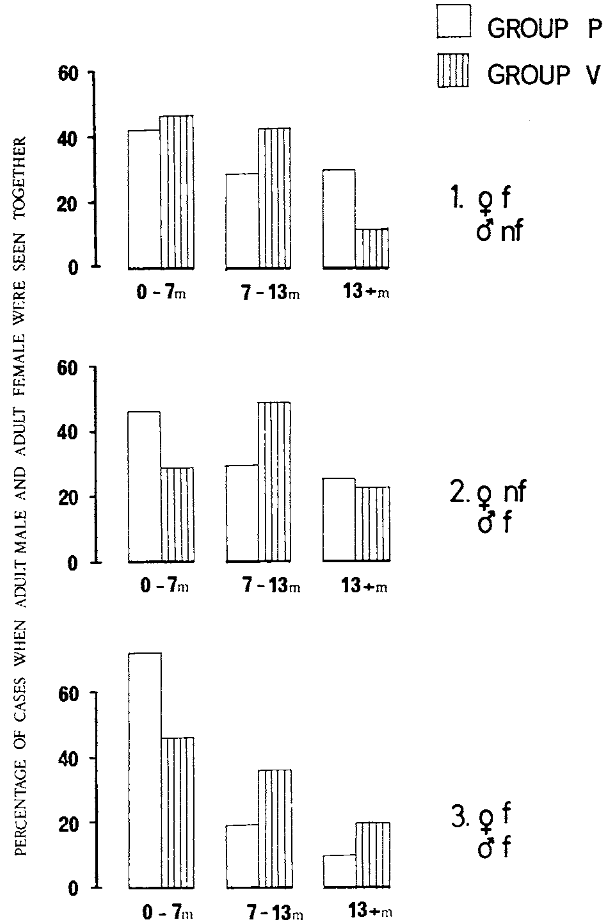

FIG. 13. The distance between adults according to their relative activity. For three categories of distance (0–7 m, 7–13 m and over 13 m) differences between groups in interadult distances are shown when (1) the adult female is feeding (f) and the adult male is not feeding (nf), (2) the adult female is not feeding and the adult male is feeding, and (3) adults are both feeding.

firstly by her advantageous position in food-bearing parts of the trees (both *Indri* study groups), and secondly by the maintenance of greater distances between adults when the adult male was feeding than when he was not (group V only).

5.3. Feeding Synchrony

The group V adult female was found to influence the adult male's feeding behaviour. The proportion of time spent feeding by the adult male in each group during each circuit was calculated for (i) when the adult female, simultaneously seen, was also feeding, and (ii) when the adult female, simultaneously seen, was engaged in activities other than feeding (Fig. 14).

(a) Group P. The overall proportion of time spent feeding by the adult male each circuit was not correlated with the proportion of time he spent feeding either when the adult female was simultaneously feeding (Spearman rank correlation test: $r_s = 0{\cdot}14$, $P > 0{\cdot}1$) or when she was engaged in other activities ($r_s = 0{\cdot}05$).

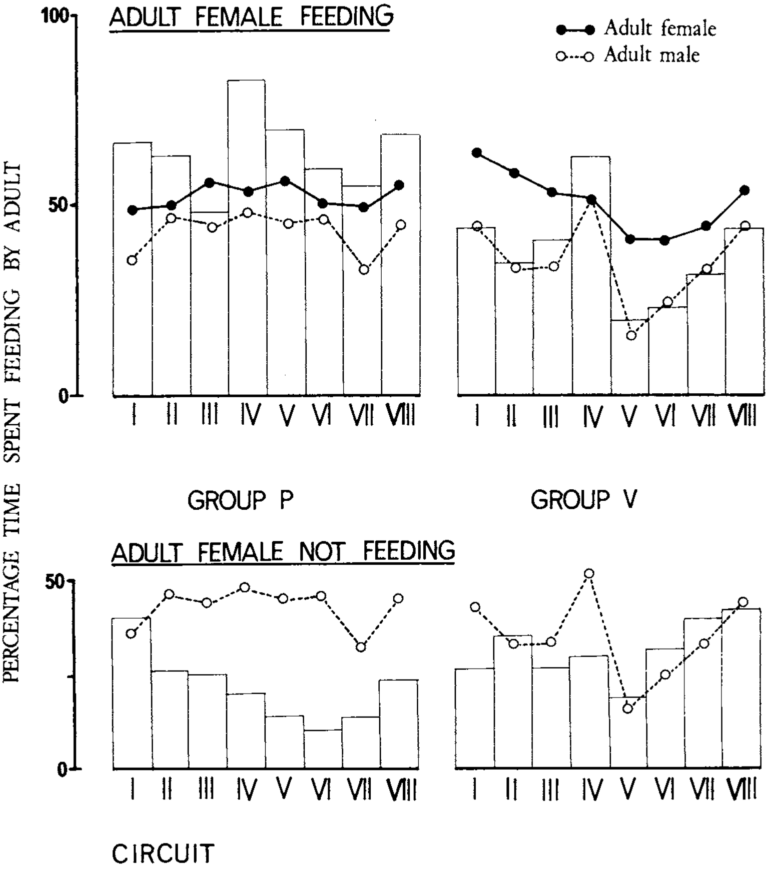

FIG. 14. Seasonal variation in activity synchrony. For each group the histogram represents the proportion of time spent feeding by the adult male when the adult female was either feeding (above) or engaged in other activities (below), during each circuit throughout the year. The total proportion of time spent feeding by each adult are also shown for each circuit.

(b) Group V. The overall proportion of time spent feeding by the adult male each circuit was correlated with the proportion of time he spent feeding when the adult female was simultaneously feeding ($r_s = 0{\cdot}91$, $P < 0{\cdot}001$). There was no significant correlation between the proportion of time spent feeding by the adult male overall and the proportion of time he spent feeding when the adult female was engaged in non-feeding activities ($r_s = 0{\cdot}17$).

It appears, therefore, that the amount of time spent feeding by the adult male of group V was controlled by the amount of time he was "permitted" to feed when the adult female was herself feeding. This relationship could not be defined in the data from group P. There is little doubt that this form of feeding relationship in group V was controlled by the adult female rather than voluntarily chosen by the adult male, as she often actively forced the adult male to move from feeding positions which she subsequently occupied. The adult male, however, was never seen aggressively to approach or displace her.

The effects of other (non-adult) individuals on the feeding behaviour of each member of the group could be determined in different dyadic situations and, whilst their full description is beyond the scope of this chapter, it is clear that continuous elements of social communication influenced which animals aggregated closely and fed together (Pollock, 1975b). In brief, other animals were more likely to feed when (a) the adult male and (b) the oldest (03) offspring were not feeding, and the presence nearby of the adult female and the youngest offspring (01) exerted a mild but clear inhibitory effect on the feeding activities of the rest of the group.

5.4. Feedings Orders and Movements

Because the observer was unable to stay close to a rapidly moving group, the orders in which individual *Indri* left a large food source were preferentially recorded to those of entry. Individual differences were found to exist in this measure: the adult male in group P leaving first on 75% of observations of his position in departure orders. In group IV at Vohidrazana an adult-sized female was consistently the last to enter feeding trees in which the whole group fed, and she usually brought up the rear in group progressions. She also left large food sources last as, to a lesser extent, did 03 in group P at Analamazoatra. 03 was seen to be last in group progressions 44% of the time, considerably more than any other group member. This individual, the oldest and adult-sized offspring in group P, was the animal most often displaced from feeding positions by all other group members (38·3% of all displacements observed in this group), and the least often groomed (10·3% of all grooming interactions).

In group V each adult equally shared the role of progression leader although in group IV, shortly after the birth of an infant in May 1973, it was the adult female who consistently directed movements to new food sources, being essentially followed around the territory by the rest of the group. Leadership in group progressions may confer priority of access to a food source in *Indri* much as it appears to do in the large multimale groups of *Lemur catta* (Jolly, 1966; Budnitz and Dainis, 1975). In both cases it is the adult females which profit from leadership at the expense of adult males.

5.5. Discussion

Social dominance in *Indri*, exerted primarily in feeding contexts, clearly differentiated the adult females and young animals from other individuals. They fed more, and not only had priority of access to food, but could also (in at least some cases) determine group movements and effectively control the amount that others consumed. Adult males fed least of all, fed relatively more in structural rather than food-bearing parts of the trees, and were easily displaced from feeding positions. They also took most responsibility for group defence by participating actively in the repulsion of invading groups from their territory, whilst the adult female rested in a safe central location (Pollock, 1975b). Female dominance in *Indri* (and other lemurs) may be reproductively advantageous in conditions where food is scarce, a pregnant or lactating female being consequently less nutritionally deprived than her reproductive partner. A weighted distribution of resources in this manner would be to the reproductive advantage of both the male and the female of the group (Trivers, 1972).

6. GENERAL DISCUSSION

Identification of adaptive facets of *Indri* feeding behaviour obviously depends on recognition of the amount of food available to the animals. Frequent observations of the presence of "foods" partially consumed or even ignored, at times of low general feeding activity, suggested that *Indri* at Analamazoatra, which eat the commonest plants of the forest and are physiologically able to remain active for longer periods when required to, retain a nutritional credit. The animals, which were active for only five or six hours daily during much of the year (spending approximately half this time feeding), were all in apparently perfect health. Analysis of preserved samples of faeces yielded few traces of internal parasitic infection (File, pers. comm.). The possibility remains, however, that specific foods, perhaps consumed in small quantities, constituted practical limits on *Indri* nutrition. The significance of the high occurrence of food species in the forests, for example, may have been reduced by an intensive intraspecific selectivity. Although there were reasons to believe that the adult female of group V controlled the amount of time spent feeding by the adult male, this was not apparently related to poor levels of food in the forest. Despite the probability that group V knew little about the location of food in their territory, food remained unconsumed on trees during the period of least feeding activity. Furthermore, the amount of time spent feeding may be a poor measure of nutrient intake as feeding techniques, feeding rate, nutrient content and digestibility all vary with the type of food consumed. The requirements of the individuals also differed between circuits as the ambient temperature changed, lactation increased and then diminished, and infant carriage ceased.

The presence of social constraints [relative positioning in trees, proximity influencing activity (or vice versa), and physical displacements of some animals by others] on feeding under conditions where there apparently existed a plentiful supply of food, suggests the maintenance of social controls which, despite being presumably concerned with ensuring survival in suboptimal habitats, persists undiminished at other times. Whether the accentuated form of feeding controls exhibited in group V by the adult female results from the presence of an infant, the unacquired intelligence of food location, or both, remains conjectural until a wider sample of groups can be observed.

7. SUMMARY

1. Two groups of *Indri indri* were regularly observed for 14 months in the eastern rain forests of Madagascar. *Indri* are territorial, family-living, folivore-frugivores with a short, diurnal activity period.

2. *Indri* feed on foliage at all levels of the forest. Locomotor adaptations enable *Indri* to feed on low vegetation incapable of supporting their weight. Differences were found both between and within groups in preferred feeding sites. The presence of an infant in one group probably influenced the feeding sites adopted by its mother and the amount of time she remained active each day.

The proportion of the activity period that *Indri* engaged in feeding

activities varied between months for one group more than it did for the other. Variation in the proportion of time spent feeding was not obviously associated with the seasonally changing daily activity period. *Indri* gradually increase the intensity of feeding until about midday from when there is a slow decline. Discontinuous feeding "bouts" occurred only when suckling by the infant interrupted normal activities.

At least 62 species of plant were eaten by *Indri*. No animal matter was consumed but small amounts of earth were regularly consumed by all individuals. The two groups differed little in their diet. *Indri* probably eat the commonest species of tree in the forest but intraspecific selectivity may limit the amount of food available to the animals. Immediate diversity in diet was assumed over several days but variation in species choice also occurred at longer intervals, the diet changing completely every few months.

3. Individuals varied in feeding rate, the time spent feeding and the type of food consumed. Adult males fed for less time, probably fed more slowly and appeared to eat more fruit and fewer shoots than adult females and young animals.

4. *Indri* range apparently only so as to find food. Differences between groups, in the amount of time spent in entered parts of the territories and the frequency and angle of direction of local movements, were probably related to knowledge of the whereabouts of food. Both groups ranged similar distances each day but no regular pattern of movement was discernible.

5. Priority of access to food is the prerogative of female and very young *Indri*. Dominance in feeding situations affects relative positions in food trees, the distance between individuals according to their activity, and the amount of time individuals spend feeding simultaneously.

6. There were no indications of food shortage during the study period. Fluctuations in the amount of time spent feeding throughout the year may relate more to differences in diet and the animals' reproductive states than to food availability. Strict social controls on group members' feeding behaviour may optimize the chances to produce viable offspring under severe environmental conditions.

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3

The Feeding Behaviour of *Propithecus verreauxi*

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1. INTRODUCTION

An 18-month study of the social organization and ecology of four free-ranging groups of *Propithecus verreauxi* (Grandidier, 1867) was carried out in Madagascar between May 1970 and September 1971. Two groups of the subspecies *P. v. coquereli* were studied in mixed deciduous and evergreen forest at Ampijoroa, in the north-west of the island; the other two groups, belonging to the subspecies *P. v. verreauxi*, lived in Didiereaceae-dominated, semi-arid forest near Hazafotsy in the extreme south (see Richard, 1974). The location of the two study areas is shown in Fig. 1, and the age and sex composition of the four groups is given in Table I.

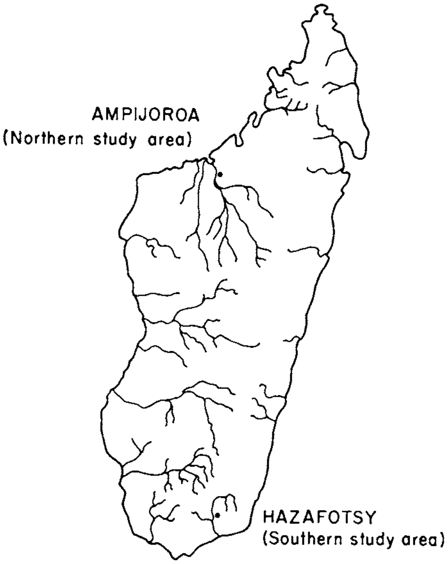

FIG. 1. Location of study areas.

2. STUDY AREAS

2.1. Location

The northern study area (16°35′ S and 46°82′ E) was situated in the forestry reserve at Ampijoroa, in a region known as the Ankarafantsika. It was about 100 km from the west coast of the island, and 2 km from

Lac Ampijoroa. No timbering was permitted in the reserve, and livestock were never seen in the study area. The forest contained six primate species in addition to *P. v. coquereli: Lemur fulvus*, *Lemur mongoz*, *Microcebus murinus*, *Cheirogaleus medius*, *Lepilemur mustelinus* and *Avahi laniger*.

The southern study area (24°85′ S and 46°50′ E) was situated in semi-arid forest 1 km from Hazafotsy, around 1500 km south of Ampijoroa. Hazafotsy lies on the north-west boundary of Reserve Nationale No. 11, and the study area was inside the reserve. Although the reserve has not been burnt or felled in recent times, cattle and goats graze in it much of the year. The sparseness of vegetation at ground level may be an effect of this grazing. Only two primate species other than *P. v. verreauxi* were seen in the southern forest: *Microcebus murinus* and *Lepilemur mustelinus*.

2.2. Forest Structures

In order to compare the two habitats and to assess the availability and distribution of food resources, the vegetation was systematically sampled in both areas; aspects of the structure, density, diversity and phenology of vegetation in each forest were recorded (see also Section 3.3). In the north, most trees were between 3 and 13 m in height, with emergents occasionally exceeding 21 m (Fig. 2). The small stature of trees was probably a function of the poverty of the soil as well as of the age of the forest: except for the forest's low profile, the usual characteristics of a very young secondary succession (Richards, 1966) were absent. In the south, most trees were between 3 and 7 m high, and none exceeded 21 m (Fig. 2). It appeared that there was a critical size beyond which two of the most abundant *Alluaudia* species present, *A. procera* and *A. ascendens*, became top-heavy, with the entire branching superstructure ultimately being torn off the trunk by its own weight. In addition to being generally lower, trees in the southern study area provided less cover than in the north: summing the maximum spread of all trees in each plot of vegetation sampled, the mean summed spread of trees per sample in the south was 214 m. In the north it was 493 m. It should be noted, however, that the estimated density of trees was similar in both areas: 13 878 per ha in the north, and 13 370 per ha in the south.

2.3. Species Composition of Forests

A greater diversity of tree species was found in the north than in the south; 167 species, belonging to 35 families, were identified in the

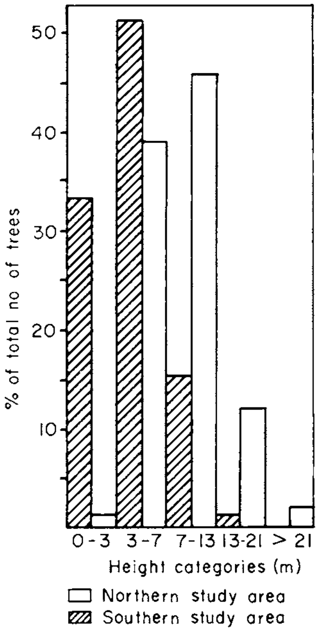

FIG. 2. Distribution between height categories of trees sampled in each study area.

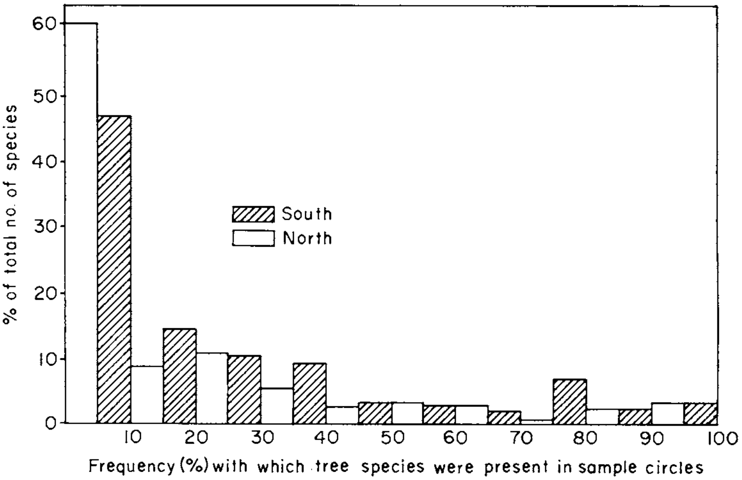

FIG. 3. Tree species grouped according to the number of sample plots in which they occurred.

north compared with only 70 species, belonging to 23 families, in the south. In both forests, most tree species occurred rarely in the plots sampled in the course of the vegetational analysis. Few species occurred in most or all of them. In Fig. 3 species are grouped according to the number of plots in which they occurred. Thus, for example, in the north 62% of species occurred in only 10% of the plots sampled (although not necessarily the *same* 10%—these figures refer only to frequency of occurrence and not to distribution). A chi-square (χ^2) test performed on the counts from each forest showed no significant difference between them. There was a close correlation between the number of plots sampled in which a species occurred and the total number of individuals of that species counted, and in the discussion of food availability (see Section 4.4) the former is taken to be a measure of the latter.

Concerning the distribution of tree species, therefore, it can only be said that a few species were abundant and widely, though not necessarily uniformly, distributed through the forest in each study area. Most species occurred rarely, unevenly scattered amongst the few dominant species.

2.4. Climate

Seasonal changes in climate were clear in the north, and even more marked in the south. In 1970, heavy rain began to fall in the north, particularly at night, towards the middle of October. Between mid-October and December 385·4 mm of the annual total of 1619 mm (data supplied by Météorologie Nationale de Madagascar) of rain fell and maximum and minimum temperatures of 29·5 and 18° C were recorded. These months are referred to as "the wet season". Between July and September, only 1·8 mm of rain fell, and temperatures ranged between 31·5 and 14° C. These months are referred to as "the dry

TABLE I

Composition of study groups when observations were begun in July 1970 (north) and September 1970 (south)

Group	Adult male	Adult female	Subadult	Juvenile	Infant	Total
I	2	5	0	0	0	7
II	1	1	1 (♂)	1 (♂)	1	5
III	2	2	1 (♂)	1 (♂)	2	8
IV	1	2	1 (♂)	0	2	6
	6	10	3	2	5	26

season". In the south, 613·8 mm of the annual total of 629·8 mm (data supplied by Météorologie Nationale de Madagascar) of rain fell during January, February and March (the wet season), and temperatures ranged between 39 and 16° C. During the rest of the year (the dry season), practically no rain fell and temperatures ranged between 36 and 8° C. In both the north and the south, some trees shed their leaves at the beginning of the dry season, while leaf production continued throughout the year in others. Unlike the north, the southern forest was dominated by xerophytic vegetation, however, and many species exhibited water-conserving adaptations, such as extreme reduction of leaf size, huge-girthed bottle trunks or water-retaining tubers.

3. SAMPLING METHODS

3.1. Feeding Behaviour

The northern study groups, I and II, were observed during the dry season months of July and August 1970 and July 1971, and during the wet season months of October, November and December 1970. The southern groups, III and IV, were studied during the dry season months of April, May and June 1971 and during the wet season months of January, February and March 1971. The four groups were habituated to my presence before the start of quantitative data collection. A group was regarded as habituated when all its members would approach and feed within two metres of me.

An animal was recorded as feeding if it was chewing or ingesting. The animals' remarkable tolerance of and apparent indifference to my presence, the low stature of the forest in both study areas and, in the south, the low density of foliage, all facilitated accurate observation of both the food species and the part being eaten. Animals could almost always be seen, and were rarely more than 10 to 15 m away from me. Bias introduced by differential visibility of animals or of the activity being performed by a given animal was thus minimal.

One animal was followed for 12 hours each day, from 6.00 until 18.00h. Each day the age and sex class of the subject was changed so that observations were equally distributed between the different categories as well as between different times of day. Data on feeding behaviour were recorded at timed minute-intervals. Seventy-two hours of data collected in this way were recorded for each group in each of the months referred to above. (Henceforth, *the number of records made at minute intervals* which an animal spent feeding will be referred to as *time spent* feeding.) These sampling techniques were used to collect information on the following aspects of feeding behaviour in the different age and sex classes: total time spent feeding, time spent feeding on different food species and food parts, animals' posture and height above ground when feeding, and their ranging behaviour. Initially I also tried to measure the time animals spent foraging, but no satisfactory definition of this behavioural category was found and the attempt was abandoned.

3.2. Ranging Behaviour

In order to record animals' movements, both study areas were gridded into quadrats with sides of 50 m by trails marked at ground level. This divided each group's range into about 36 quadrats. If a member of a given group was seen in a quadrat more than once, that whole quadrat was included within the range of the group. The criterion of occupancy on at least two occasions was introduced to avoid including areas through which males occasionally passed alone. A definition of the group's range which excluded areas occasionally entered only by males was necessary because, particularly during the mating season, males moved through areas which were never used by the rest of the group. Taking the 50 m quadrat as the minimum size unit in estimating range must still have resulted in an over-estimate of the real area occupied by the group, for there were certain portions of most quadrats where the group was never seen and which they probably did not use. It should also be noted that while all groups lived in a three-dimensional space, their displacements and range were measured in only two dimensions.

3.3. Structure and Composition of Vegetation

A limited analysis of the structure and composition of the vegetation in both study areas was undertaken. Two samples were made in each hectare quadrat delineated by the quadrat system. Within each hectare quadrat the two samples were randomly located, following the "stratified random" sample technique described by Southwood (1966). Each sample consisted of a circle with a measured radius of 5 m. Within each circle, all trees with a trunk diameter greater than 3 cm were counted and identified, and the trunk diameter, height and maximum spread of the tree, height of the lowest branch above the ground and phenology were noted.

Using this method, a total of 2619 trees were described in the northern study area, taken from 24 samples. In the south, 3136 trees coming from 30 samples were described. The total sample covered 1·57% of the surface area of each study area. In both areas, lianas constituted an important item in the diet of *P. verreauxi.* It was not possible to make an accurate estimate of the density of lianas, but a count was made of the number of trees bearing lianas in each sample in order to provide a rough estimate of abundance.

Data on synchrony of leaf and fruit production and their presence in tree species were based on observations made on ten species in each study area. Not all the preferred food species of *P. verreauxi* were known at the outset of the study, and some tree species were selected for sampling because they constituted a large proportion of their diet during the first month of observation in each area, and others because they were abundant. Each month, observations on ten individual trees from each species were tabulated. Different individual trees were sampled each month. Five non-exclusive phenological categories were used:

(1) leaf shoot and/or young leaves and flush (young leaves were differentiated from adult leaves on the basis of their paler colouring and, sometimes, smaller size);
(2) adult and/or dying leaves;
(3) flowers, open and/or in bud;
(4) fruit, green and/or ripe;
(5) dormant buds.

A record of "present" or "absent" was entered for each of these categories, but no estimate of quantity was made. However, in cases where one or two desiccated fruit or dead leaves remained attached to a tree when all the rest had already dropped, "absent" was recorded in these categories.

4. FEEDING BEHAVIOUR

4.1. Feeding Techniques

Animals detached food parts with their teeth, using their hands only to pull food-carrying branches towards their mouths. Occasionally, an animal carried the fruit of one particular *Combretum* species between its teeth or clasped to its chest with one hand: this was an unusually large, rare and greatly relished fruit, and an animal seen eating it by other members of the group was often challenged and chased for it. However, food was generally consumed where it was found. Bark and dead wood were gouged out with the tooth-comb and then torn off, gripped between the upper and lower molars and premolars.

Animals fed in many postures, enabling them to reach almost all parts of any tree (Richard, in press a). In the larger branches they usually sat or assumed their characteristic vertical posture; in the fine branch niche they often fed upside down, grasping a cluster of twigs in each hand and foot with the body suspended below and thereby distributing their weight over a considerable area. There was no evidence to support Napier and Walker's (1967) comment "The limitations imposed by the vertical clinging and leaping habit upon feeding behaviour are also quite marked . . .".

4.2. Feeding Heights and Sites

Five categories of substrate were distinguished in each forest: Ground, Vertical support (over 6 cm in diameter), Horizontal support (over 6 cm in diameter), Branches (between 6 and 1·5 cm in diameter) and Twigs (less than 1·5 cm in diameter). Although animals in both areas spent little time on the ground, all other substrate categories were used extensively. Descriptive notes indicate that most feeding behaviour occurred amongst branches and twigs, however, where the availability of flowers, fruit and leaves was greatest (Richard, in press b). No differentiation was found in choice of feeding sites by the different age and sex classes. However, it should be noted that infants were not included in the analysis: it is possible that infants spent less time feeding on the periphery of the tree but this impression cannot be substantiated.

In both study areas, groups spent considerable amounts of time at all levels in the forest. The two southern groups tended to spend more time at lower levels than the northern groups. Factors contributing to this difference were the overall lower stature of the southern forest, and the fact that most of the taller trees in the south were *Alluaudia ascendens* and *A. procera*. The extremities of the thin, spiny vertical branches of these species provided no regular or firm support for locomotion and were a source of food only when they flowered at the end of the dry season. Animals were rarely seen high on these branches at any other time. A full analysis of feeding levels has not yet been made, but preliminary results indicate that feeding, like other activities, occurred regularly at all levels (Richard, in press b).

4.3. Activity Patterns

In both study areas there were striking seasonal differences in the mean amount of time animals spent feeding each day. Mean time spent feeding per day in the south during the wet season was 246 min (32·8% of total time), while in the dry season it was only 173 min (24·2% of total time). In the north, equivalent figures were 268 min (37%) and 245 min (30·3%). These results were calculated by combining data from all the age and sex classes (including gestating and lactating females), with the exception of data on the juvenile in group III during the wet season. This animal was excluded from the analysis because he fed significantly longer each day in the wet season than did other animals in the two southern groups (Kruskal–Wallis one-way analysis of variance, $P \leqslant 0{\cdot}01$). Combining data for the two groups in the south, the amount of time spent feeding each day in the wet season was significantly greater than in the dry season (Mann-Whitney U test $P \leqslant 0{\cdot}004$). In the north, the difference was not significant although there was a similar trend. Comparing results from the north and south for each season, there was no significant difference during the wet season. In the dry season, however, the southern groups fed significantly less than those in the north (Mann-Whitney U test, $P \leqslant 0{\cdot}001$).

The daily pattern of feeding in each season and the nature of the change between seasons were clear, and similar in both areas: during the wet season feeding began early, reaching a peak between 7.00 and 9.00h. This was followed by a gradual decrease until midday, by which time very little feeding was taking place. Between 13.00 and 14.00h the amount of time animals spent feeding began to increase once more, reaching a peak in the later afternoon. During the dry season, intensive feeding began later and ended earlier in both study areas. In the north, there was still a falling-off in feeding at midday, although it was less marked than in the wet season. In the south, the amount of time spent feeding per hour slowly built up throughout the morning to reach a peak at midday and then decreased in the afternoon at almost the same rate.

Although the group was often widely dispersed during feeding bouts, animals also fed in close proximity to each other. All or most members of the group usually spent part or parts of each feeding bout in a single tree; for the rest of the bout they were more widely dispersed, moving rapidly from tree to tree and feeding for varying amounts of time in each.

5. REGIONAL, SEASONAL AND LOCAL VARIATION IN FEEDING BEHAVIOUR

Regional, seasonal and local variation in the feeding behaviour of the groups of *P. verreauxi* studied were closely interrelated and are considered together in this paper. The term "local" variation is used to describe variation observed between groups living in the same forest.

In the following discussion, data from adult and subadult animals of both sexes are combined. No animal aged five months or more was seen eating a food part or food species which was not also eaten by another animal at some point during observations. Analysis has not been undertaken to establish whether animals had different food preferences, dependent upon their age and sex class or upon their individual tastes, but if such variation did exist, it was certainly not striking. Only infants were excluded from the analysis: between the ages of three weeks and one-and-a-half months infants did attempt to eat food parts not eaten by other members of the group (Richard, in press b).

5.1. Variation in Species Composition of Diet

5.1.1. *Regional*

The species composition of the diet of the groups in each study area was almost totally different. The 12 species on which each group spent most time feeding throughout the study are listed in Table II, together with the percentage of total feeding time the group spent eating each. Regional variation was largely, but not totally, due to differences in the composition of the two forests. Four tree species were found in both forests: *Baudouinia fluggeiformis* (found in 92% of vegetation samples in the north, and 23% in the south), *Cedrelopsis grevei* (17% in the north, and 77% in the south), *Commiphora pervilleana* (66% in the north, and 16% in the south), and *Rothmannia decaryi* (79% in the north, and 3% in the south). The southern groups both spent over 1% of total feeding time eating *C. grevei* whereas neither northern group was ever seen eating it; contrarily, *B. fluggeiformis* was an important dietary component in the north but was untouched in the south. These differences were found although both species were quite commonly occurring in the two study areas. *C. pervilleana* was eaten commonly by the northern groups, but both groups in the south ate it for less than 1% of total feeding time. In contrast, *R. decaryi* was eaten in quantity in the south, and rarely in the north; further, in the south animals ate only the green ripe fruit of this species whereas in the north animals ate only its large white flowers. Here again, the differences did not appear to be an inevitable product of variation in the abundance of the two species. Indeed, given the apparent rarity of *R. decaryi* in the south a converse result might have been expected.

TABLE II

Twelve species on which each group spent most time feeding throughout the study, and percentage of total feeding time spent eating each

Food species	Time spent (%)	Food species	Time spent (%)
GROUP I		GROUP II	
Drypetes sp. no. 1*	12·4	*Drypetes* sp. no. 1	11·7
Cedrelopsis sp. no. 1	5·4	*Cedrelopsis* sp. no. 1	8·9
Combretum sp. no. 1	5·3	*Bussea perrieri* R. Vig.	4·5
Dead wood	5·3	*Commiphora pervilleana* Perr	4·4
Capurodendron microlobum (Baker) Aubreville	5·1	*Bathiorhamnus louveli* Perr	3·9
Rheedia arenicola Jerm and Perr	4·5	Dead wood	3·9
Commiphora pervilleana Perr	4·2	*Rhopalocarpus similis Hemsley*	3·7
Apaloxylon madagascariense Drake	4·0	*Combretum* sp. no. 1	3·6
Liana sp. no. 1	3·7	Liana sp. no. 1	3·3
Protorhus deflexa Perr	3·4	*Boscia* sp.	3·1
Hippocratea sp.	3·3	*Protorhus deflexa* Perr	2·4
Mundulea sp.	2·9	*Capurodendron microlobum* (Baker) Aubreville	2·3
GROUP III		GROUP IV	
Terminalia sp. no. 1	21·5	*Terminalia* sp. no. 1	21·0
Mimosa sp. no. 1	16·8	Liana sp. no. 2	15·4
Liana sp. no. 2	12·3	*Mimosa* sp. no. 1	11·2
Grewia sp. no. 2	7·7	*Grewia* sp. no. 1	9·9
Terminalia sp. no. 2	5·0	*Hagunta modesta* (Baker) M. Pichon	4·8
Diospyros humbertiana Perr	4·1	*Terminalia* sp. no. 2	4·3
Grewia sp. no. 1	5·2	*Grewia* sp. no. 2	2·6
Euphorbia plagiantha Drake	2·3	Liana sp. no. 3	2·5
Liana sp. no. 4	2·1	*Diospryos humbertiana* Perr	1·9
Liana sp. no. 3	2·1	*Rothmannia decaryi*	1·6
Hagunta modesta (Baker) M. Pichon	1·8	*Commiphora* sp. no. 1	1·6
Liana sp. no. 5	1·7	*Grewia* sp. no. 3	1·5

* Where species identification could not be made, samples were numbered serially.

5.1.2. *Seasonal*

The composition of each group's diet changed almost completely between seasons. Only five food species, out of a total of 79 eaten in the course of observations, were eaten by the southern study groups for more than 1% of total time spent feeding in both the dry and wet seasons. The northern study groups ate nine food species for more than 1% of feeding time in all months, from a total of 102 which they were observed to eat in one season or the other.

5.1.3. *Local*

In the north, group I fed on six species for more than 1% of total feeding time each, of which five were eaten by group II for less than 1% of total feeding time and one, *Malleastrum* sp., was never eaten at all. Group II fed on eight species of which seven were eaten by group I for less than 1% of total time spent feeding, but group I was never seen eating the eighth, *Erythroxylon* sp. In the south, group III fed on seven species which were eaten by group IV for less than 1% of total feeding time, and group IV fed on six. No single food species was eaten by one group and not the other in the south.

Within each study area, eight out of the 12 food species most commonly eaten by the two groups were the same, and there was a close correlation between the way the two groups in each area allotted feeding time to these species (Spearman rank correlation coefficient, $P<0{\cdot}01$—north; $P<0{\cdot}01$—south). However, there was proportionately more variation between the diets of the two southern groups than those of the northern groups. Forty-one per cent of the food species eaten for more than 1% each of total time spent feeding by group III were eaten for less than 1% each of total feeding time by group IV, and 33% of the food species eaten for more than 1% each by group IV were eaten for less than 1% each by group III. Equivalent values for groups I and II were 23 and 33%.

5.2. Variation in Food Parts Eaten

In both study areas, there was a clear seasonal change in the parts eaten of trees and lianas irrespective of species. With one exception (see below) the nature of this change was similar in the two groups in each study area. Figure 4 shows the percentage of total feeding time which each group spent eating fruit, flowers and flower buds. Figure 5 shows the percentage of total feeding time which each spent eating leaflets, shoots, young leaves, flush and buds, and adult leaves. Data on synchrony of phenology among trees in the two study areas indicate that changes in the importance of different food parts for the diet of the four groups generally reflected quite closely changes in the availability of these parts in the two forests (Richard, in press a).

In the north, a general peak in young leaf consumption occurred at the same time as a decrease in adult leaf consumption at the beginning of the wet season. Further into the wet season, consumption of young leaves declined too, and there was an increase in the consumption of flowers in November, followed by a large increase in time spent feeding

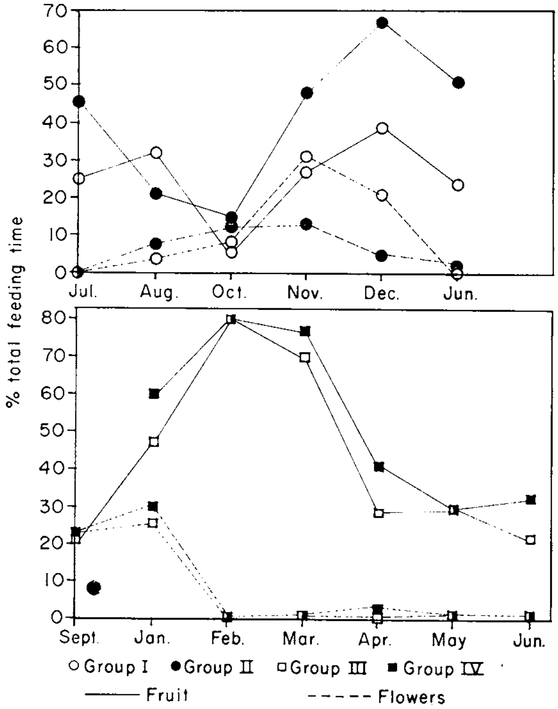

FIG. 4. Percentage of total feeding time which each group spent eating fruit, flowers and flower buds.

on fruit in December. In the dry season, there was a general decrease in time spent feeding on fruit and flowers, and a general increase in time spent feeding on adult leaves. Time spent feeding on young leaves decreased generally in the dry season, but the result for group I, July 1971, did not conform to this pattern: a large proportion of the time this group spent feeding on young leaves was spent in a single tree of *Capurodendron microlobum* which was covered with leaf buds at that time. Phenological data indicate that at that time budding occurred uniquely in this one tree.

In the south, flowers were an important dietary item at the onset of the wet season in January. For the rest of the wet season, however, as in the north, fruit constituted an overwhelming proportion of the animals' diet. At the beginning of the dry season, as in the north, there was a general increase in the amount of time spent feeding on adult leaves, and this trend continued through the dry season until the end of the study in June. Flowers again became an important dietary

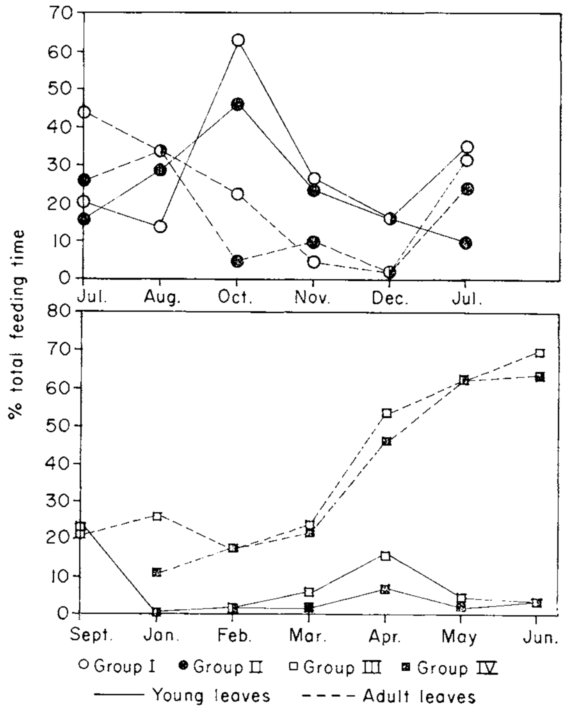

FIG. 5. Percentage of total feeding time which each group spent eating leaf shoots, young leaves, flush and buds, and adult leaves.

component towards the end of the dry season in group III (no observations were made of group IV). These flowers came from *Alluaudia ascendens* and *A. procera*. Both these species were abundant in the forest, and both flower annually in September. Young leaves also constituted a higher proportion of group III's diet in September than at any other time. Again, this reflects changes in the phenology and availability of food parts in the forest. The rapid response of trees to small amounts of rain and the ability of some species to produce young leaves well into the dry season despite a total absence of rain have been documented elsewhere (Richard, in press a): light, but unexpected and atypical, rainfall at the beginning of September 1970 was probably sufficient to stimulate leaf production by many species and it is this sudden availability of young leaves which is reflected in group III's diet at that time.

A high proportion of time was spent eating bark and/or dead wood by the study groups at certain times of year. In the south, bark eating occurred only in the dry season: in September, group III spent 15·5% of their total feeding time eating the bark and cambium of *Operi-*

culicarya decaryi. No animal was ever seen eating dead wood. In the north, both groups ate bark to the exclusion of dead wood in the dry season, and dead wood almost to the exclusion of bark in the wet season. The bark eaten in the dry season came mainly from thin branches of *Commiphora pervilleana.*

5.3. Variation in Breadth of Diet

5.3.1. *Regional*

The southern groups' diet contained fewer species than that of the northern groups. In the course of the field study, group I was observed feeding on 88 known different food species (including five liana species), and group II on 102 (including five lianas). In the south, group III was seen to feed on 79 different food species (including 15 lianas) and group IV on 65 (including 13 lianas). These represented 49% (group I), 58% (group II), 91% (group III) and 74% (group IV) of all the tree species identified in each forest. The lower number but larger percentage of species eaten in the south was probably partly a result of there simply being fewer species in the forest. However, the larger percentage of species eaten may also have been due to an increase in

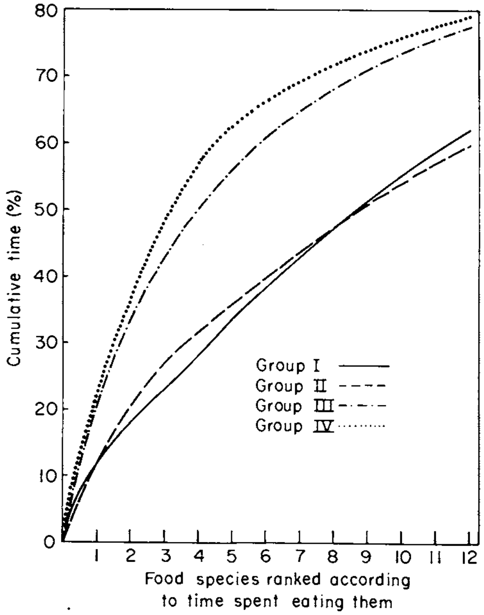

FIG. 6. Mean percentage of total feeding time which each group spent eating the 12 food species fed on by the group more commonly than any other species.

the animals' selection for variety of diet. In both areas, however, many of these species were eaten rarely. Figure 6 shows that all four groups spent at least 60% of total feeding time eating only 12 food species; it also indicates that this tendency to feed primarily on a few species was more pronounced in the south than in the north.

5.3.2. *Seasonal*

Table III gives the number of food species on which each group spent more than 1% of total feeding time, in each season.[a] In both areas, groups spent more time eating fewer species in the wet season than in the dry season (Mann-Whitney U test, $P<0{\cdot}01$ for both areas).

TABLE III

Number of food species eaten by each group for more than 1% of total feeding time, in each season

Month	No. of species		Month	No. of species	
	Group I	Group II		Group III	Group IV
July and August	18	22	May and June	18	19
November and December	13	17	January and February	8	6

5.4. Variation in Diet and the Abundance of Foods

In both study areas groups ate a relatively high number of food species which occurred frequently in the forest, instead of seeking out more rarely occurring tree species. In Fig. 7 tree species are grouped according to their frequency of occurrence in plots sampled; the number of food species coming from each of these groups is shown. Only food species eaten by any of the four study groups for more than 1% of total feeding time are included. In the north, 87% of the total number of tree species identified occurred in less than half the total number of plots, yet only 64% of the northern groups' food species came from these tree species, and the remaining 36% from the 13% of tree species that occurred in more than half the plots. In the south, 84·5% of the total number of tree species occurred in less than half the plots and yet they constituted only 65% of the total number of food species of the southern groups. The remaining 35% of food species came from the 15·5% of tree species which occurred in more than half the plots sampled. Nevertheless, it

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[a] When all food species were included in the analysis, trends in the data were masked by the long tail of rarely eaten food species. However, this is not to dismiss the possibly critical importance of rarely eaten foods (p. 94).

should be noted that rarely occurring tree species did constitute almost two-thirds of the total number of food species. Separate analysis of feeding data from wet and dry season months showed that this was equally true in both seasons.

Figure 7 also shows how many of groups I and III's five most commonly eaten food species come from each group of tree species; 31·6% of total feeding time was spent eating these five species by group I, and 55·1% by group III. The distribution of the results shows that even among the groups' most commonly eaten foods there was a wide range of variation in the abundance of the food species. It must be added, however, that the accuracy of estimates of the abundance of foods based on the frequency of occurrence of tree species is questionable: for example, the 87% of tree species which occurred in less than half the total number of plots in the north may have made up a much lower proportion of the canopy.

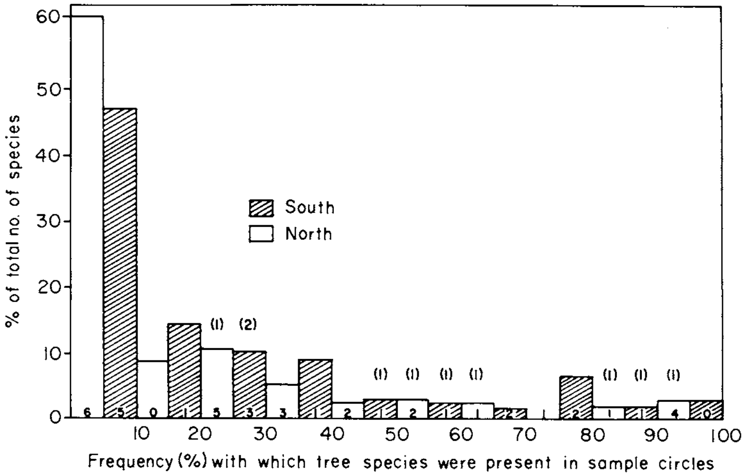

FIG. 7. Tree species grouped according to the number of samples in which they occurred and their frequency of occurrence in sample plots, showing the number of food species coming from each of these groups.

6. RANGING BEHAVIOUR

6.1. General Characteristics of Range Utilization

The group was located by reference to the grid system and the spatial displacement of the animal under observation each day was recorded at minute intervals. Distances were estimated by eye and are therefore approximate. No significant difference was found in the distance moved each day by the different age and sex classes in each study area, and results for animals in the two groups in each area were therefore combined.

Characteristically, each group followed the same general route for two or three days and then suddenly changed both their sleeping tree and direction of movement. Only six days of quantitative data were collected on each group in each month, and it was thus not possible to map overall ranging strategies. However, each group appeared to visit most parts of the range within a period of about ten days.

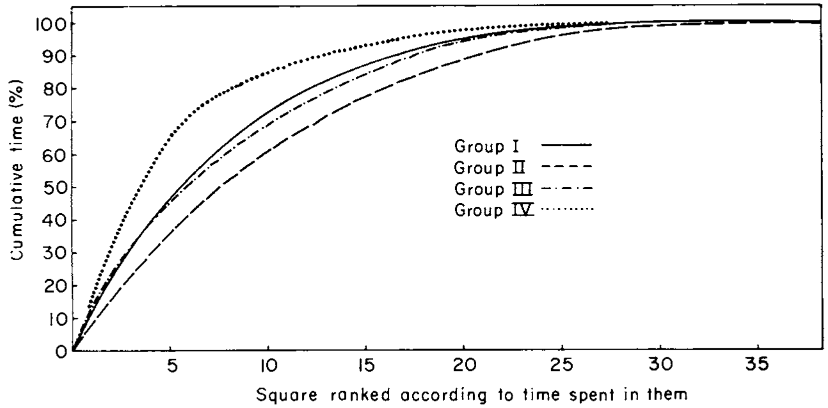

FIG. 8. Variation between each group's allocation of time across its home range.

Range size varied between the groups from 6·75 to 8·50 ha, but this variation was not significant. However, these figures are in a sense misleading, in that all four groups used a relatively large proportion of their range very rarely, spending much of their time in relatively few quadrats. There were, however, differences in the extent to which each group showed this tendency. Figure 8 shows the variation between groups' allocation of time across their range. Quadrats were ranked according to the amount of time spent in them, and this time is shown cumulatively as a percentage of total time.

Although parts of each range could be differentiated on the amount of time spent in them, they could not be distinguished by the type of activity performed in them: there was a highly significant correlation between the amount of time spent feeding and the amount of time spent in other activities in the ten most commonly used quadrats in each group's range (Spearman rank correlation coefficient, $P<0{\cdot}001$).

This was also true when all quadrats were considered, but in the latter case some correlation was to be expected.

6.2. Regional and Seasonal Variation

In the north, mean distance moved each day in the wet season was 1100 m; in the dry season it was 750 m. In the south, mean distance moved each day in the wet season was 1000 m; in the dry season it was 550 m. In both seasons, the northern groups ranged farther each day, on average, than the southern groups (Mann-Whitney U test: $P<0{\cdot}001$—dry season; $P<0{\cdot}05$—wet season).

In both north and south, groups moved farther each day in the wet season than in the dry season (Mann-Whitney U test, $P<0{\cdot}008$—north; $P<0{\cdot}001$—south). Although this was associated with a considerable increase in the total number of quadrats entered during a month's observations, the increase in the number of different quadrats entered was very slight. In Table IV total number of quadrats and total number of different quadrats entered are plotted for each group in each month. The ratio between these figures shows that, in ranging farther in the wet season, groups tended merely to cover the area used in the dry season more rapidly in the wet season, rather than to expand it appreciably. This tendency to spend more time in fewer quadrats in the dry season was more pronounced in the south than in the north.

6.3. Exclusivity of Range Use

All four study groups each had areas of exclusive use within their ranges. Exclusivity of use was not clearly related to amount of use: areas used intensively by a group were not necessarily exclusive to that group and, conversely, little-used quadrats were not necessarily areas of overlap with other groups (Fig. 9). An analysis of the most and least used quadrats in the range of each group showed that an almost equal number of each group's most and least used quadrats were also entered by other groups (Table V). In the north, groups I and II had exclusive use of 29 and 24% of their total ranges. In the south, groups III and IV had exclusive use of 54 and 51% of their ranges. In the north intensively used quadrats were scattered about the range, whilst in the south they tended to form a central block.

Intergroup interactions occurred in most parts of the ranges of the

TABLE IV

Number of quadrats entered, number of different quadrats entered and the ratio between these figures, for each group in each month

Group	Month	No. squares entered	No. different squares entered	Ratio*
I	July	69	22	3·1
	Aug.	62	20	3·1
	Oct.	118	23	5·1
	Nov.	144	25	5·8
	Dec.	137	26	5·3
	July	69	17	4·0
II	July	90	24	3·7
	Aug.	79	21	3·8
	Oct.	122	23	5·3
	Nov.	121	26	4·6
	Dec.	167	27	6·2
	July	85	31	2·7
III	Jan.	119	27	4·4
	Feb.	88	23	3·8
	Mar.	95	19	4·0
	Apr.	69	20	3·4
	May	63	19	3·3
	June	55	17	3·2
IV	Jan.	137	25	5·5
	Feb.	107	24	4·4
	Mar.	130	20	6·5
	Apr.	69	21	3·3
	May	56	18	3·1
	June	64	17	3·8

$$* \text{ Ratio} = \frac{\text{Total no. of squares}}{\text{No. of different squares}}$$

TABLE V

Each group's most and least used quadrats, showing the proportion that was also used by another group

Group	No. of quadrats in which overlap occurred amongst the 10 least-used quadrats in the home range	No. of quadrats in which overlap occurred amongst the 10 most-used quadrats in the home range
I	7	8
II	10	10
III	2	3
IV	4	4

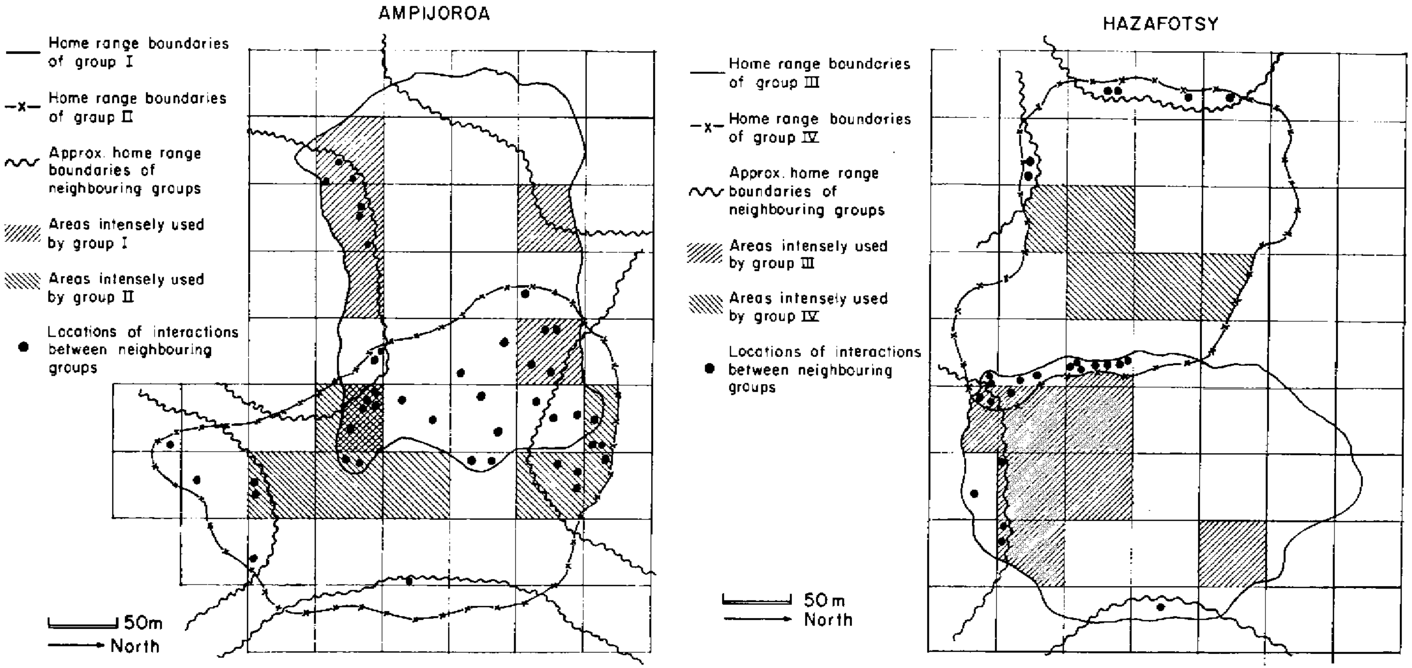

FIG. 9. Maps showing each group's range, areas of intensive use, areas of exclusive use, and the location of intergroup encounters.

northern groups (Fig. 9), so it is improbable that they were defending the boundary of a "territory" during these encounters. Little overt hostility was seen in many of the 59 encounters witnessed in the north: only 18 culminated in the ritualized "battle" described by Jolly (1966). Most of these "battles" occurred with reference to a particular food source in which one of the groups was feeding prior to the encounter. In most other instances, after reciprocal staring and some grunting the groups moved away from each other.

In the south, intergroup encounters occurred round the periphery of the block of exclusively used quadrats. Thus it appeared that the groups had well-defined borders to central areas of exclusive use which were reasserted by periodic hostile encounters with neighbouring groups. Only 29 encounters were observed in the south, but all except nine culminated in "battles".

7. DISCUSSION

In recent years there has been a growing recognition that social organization and social behaviour cannot be usefully studied in an environmental vacuum: emphasis has been increasingly placed on the idea that social organization and the environment form a network of closely interrelated and interacting components (e.g. Crook, 1970; Denham, 1971). However, in practice, in primate studies analysis of both the environment and the social parameters involved has remained at a very general level; in the resulting classifications, within-class variation is often as great as that between classes. It has been pointed out that the lack of correlation may be due in part to different species responding in different ways to comparable environmental pressures (Clutton-Brock, 1974a).

The primary aim of the research reported in this paper was to investigate aspects of intraspecific behavioural variation in *Propithecus verreauxi*. By studying two populations of a single species, it could be assumed that behavioural variation due to genetic influences was minimal. Variation could thus be attributed to environmental differences, or considered random or "neutral", having no adaptive significance (cf. Lewontin, 1974).

The importance of feeding behaviour in the overall "survival strategy" of any species is obvious and has been stressed repeatedly (MacArthur and Pianka, 1966; Schoener, 1971; Watson, 1970). In this study, a number of differences in feeding behaviour were documented between the two populations which were probably related to the distribution and availability of food. It is further argued that regional differences in patterns of group dispersion and in intergroup relationships were integrally related to differences in feeding behaviour. These hypothesized relationships are summarized below.

Considering first the distribution and availability of food species, there were similarities and differences between the two study areas. In both, the profile of the forest was relatively low; in both, most tree species were rarely occurring and widely dispersed, and yet these species constituted a major component of the animals' diet. In the north, however, rainfall was higher and more evenly distributed round the year than in the south, where very little rain fell, and this only in three months of the year. Associated with these differences, vegetation in the north was much more abundant than in the south, trees provided much more cover, and there was a well developed canopy.

Feeding and ranging behaviour varied seasonally in each study area. The direction of the change was generally the same in both areas, but in the south this seasonal variation tended to be more pronounced. Thus, in the dry season in both study areas, animals moved short distances each day and fed for short periods on a wide variety of food species, with leaves constituting a major proportion of their diet. In the wet season, they moved farther each day and fed for longer periods on fewer species, with flowers and fruits predominant in their diet. All these trends, however, were more marked in the south.

On the basis of these observations, the following interpretation of regional differences in patterns of group dispersion (Section 6.3) is suggested: in the north, the scattered distribution of many food species determined the minimum area over which the group must range in the course of a year. Animals covered this range throughout the year in order to monitor these scattered food sources and eat them as they became available: most of these foods were eaten seasonally only, and many were eaten in very small quantities, but it is probable that they were of critical nutritive importance in the animals' diet. A result of this strategy was, however, that at any one time the *total* food available within the range was in excess of the group's immediate needs and overlap between groups could therefore be extensive. It is possible that the scattered, so-called areas of exclusive use were simply areas where I did not see other groups, rather than areas where other groups did not go. The avoiding action generally taken when groups met functioned to increase group dispersion and maintain group integrity. True "battles" almost always occurred at a preferred food source on which one or the other group was feeding immediately before the encounter.

In contrast, in the south the dispersion of groups was determined by *total* food availability at certain times of year rather than by the distribution of a few critical but scattered food sources: the whole range was necessary to support the group towards the end of the dry season, when total food availability was extremely low. It is argued that round-the-year maintenance of a largely exclusive range was a more efficient means of assuring this seasonally crucial resource area than seasonal conflicts to establish exclusivity when total food availability was low.

The interpretations are put forward tentatively, and many other aspects of the data collected remain without any explanation. For example, the function of wood in the animals' diet is largely unknown, although it was an important component. The bark and cambium of *O. decaryi*, eaten in significant quantities in the south, was found to contain approximately 77% water by weight, and it must thus have provided an important source of water towards the end of the long dry season in the south. In contrast, the bark of *C. pervilleana*, eaten in the north, appeared to contain little water and was presumably eaten for its nutritive value rather than as a source of water. The function of dead wood in the diet of the northern groups remains completely obscure. In the wet season, it was a major item in the diet of each group, although the rate of food consumption was low when animals were eating it: they had considerable difficulty tearing off mouthfuls, and the measure "time spent feeding" thus probably over-emphasizes the real proportion of their diet that it constituted. Each group fed on only two dead tree stumps within their ranges, although further dead trunks were present in both ranges which did not differ noticeably from those used as food sources. Close examination of the wood did not reveal any signs of bore holes made by insect larvae: it appeared, rather, to be very dry, very hard and very dense. It is possible that this wood acted as roughage in the diet, at a time when fruit constituted the major component.

Finally, one aspect of intraspecific behavioural variation—local variation—emerged clearly as a significant factor in this study but its basis is still open to speculation. Variation in feeding behaviour was one component of this overall local variation. There were differences between neighbouring groups in the two study areas both in the total range of food species eaten and in the identity of food species constituting the major part of their diet. This "microvariation" may have been the result of differences in the species composition and availability of food species between the particular sections of forest in which the groups ranged: the analysis of vegetation in the ranges of all four groups may have failed to detect such slight variations due to the restricted area sampled. However, it is equally possible that "cultural" differences between groups may also result in group-specific differences in the choice of certain preferred food species [cf. Kawamura's (1959) food lists for *Macaca fuscata* groups]. Further and more detailed study will be needed before other than speculative answers can be provided to these questions.

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4

Feeding Behaviour and Social Organization in Howling Monkeys

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1. INTRODUCTION

My goal in studying howling monkeys (*Alouatta palliata*) was to explain the adaptive basis of their social organization. The adaptive basis of any trait is ultimately that it allows an individual to convert environmental energy into more successful offspring than are produced by the average individual in its population. It is often difficult to demonstrate the connection between social behaviour and successful offspring, but the logical connection can come by relating social behaviour to feeding and foraging efficiency (Smith, 1968). It was with this connection in mind that I studied the foraging behaviour and digestive efficiency of howling monkeys on Barro Colorado Island, Panama Canal Zone. While most of the information in this chapter will deal with feeding behaviour, it will be organized in a way that will allow me to examine

Fig. 1. Adult female *Alouatta palliata*. Photograph courtesy of C. M. Hladik.

arguments about the interrelationship of feeding behaviour and social organization.

2. METHODS

The study had both a field and laboratory component with the field work extending between 1st September 1967 and 14th July 1968. I censused 27 troops on approximately the north-east third of Barro Colorado Island (BCI), mostly in the first three months of the study, in order to compare the population density of the howlers with earlier studies (Carpenter, 1962). In an attempt to speed the process of censusing troops, I tried to disturb resting troops into movement by playing recordings of juvenile distress calls while shaking a black, stuffed dummy or by my own attempts to imitate the loud howls of adult males. Both types of calls caused some movements in resting troops, but they seldom brought all the vocal members of the troop into clear view and I could not be sure that there were not other silent members of the troops out of view. Carpenter's (1934) methods of censusing troops on the move across narrow gaps between trees was still the most reliable method, but very time consuming because of the low frequency of troop movements.

From February through to July we took 407 hours of time budget notes of single monkeys. The monkeys being watched were in view 90% of the time. It is this 90% of the total time that we compiled as time budget notes. I followed the activities of single monkeys rather than whole troops in order not to bias the results towards too high a per cent of the time spent in movement or other activities that would tend to draw my attention. The results may still be biased towards movement because a monkey was most likely to spend long periods out of my sight when it was motionless behind some obstacle. The time budget notes were taken in shorthand symbols for about 50 categories of activity. While taking notes a transistorized timer gave a signal every 10 sec and hash marks were placed under the shorthand symbol for the activity being performed at the time of the signal (Smith, 1968; Richard, 1970). When the timers malfunctioned we counted seconds and placed the hash marks at ten-count intervals. Activities could last for less than 10 sec and not receive a hash mark, but the probability of its receiving a hash mark would be proportional to its length. Adding the hash marks over extended periods of time allowed me to calculate the per cent of time spent in different activities. Activity categories of similar function were grouped after the notes were taken and tabulated.

Most of the notes were taken on members of the "cut-lip" troop (troop AA of Chivers, 1969) which ranged around the clearing and buildings on BCI, but 160 hours were compiled from observation of members of five other troops.

In order to demonstrate diurnal patterns of activity, the period between sunrise and sunset was divided into ten equal periods. Each day's notes were divided into the appropriate periods and then the notes for the same period on successive days were added to get a composite time budget that would include days from over a month or more of time. The composite time budgets were then plotted as bar graphs.

While I censused troops or took time budget notes, I plotted the position of botfly larvae, *Dermatobia hominis*, infecting the monkeys. The botfly larva that infected a captive juvenile monkey remained in the monkey for 29 days before dropping out as a mature pupa. The larva was already large enough to be easily seen in the field when the monkey was captured. Thus, the position and number of botfly larvae can serve as a useful key to the identity of individual monkeys if they are observed at intervals of a few weeks. The number of botfly infections per individual may also be a good indication of its health as will be described later.

The laboratory part of the study was a series of feeding experiments with juvenile monkeys to measure the efficiency with which they assimilate food. The five monkeys used in the feeding experiments were all about one- to four-months-old at capture and were probably still getting most of their nourishment from nursing. They were fed on milk and cultivated fruit in captivity and probably had a very different gut fauna from monkeys living in the wild. Four of the monkeys, which I raised, were probably from nine- to 14-months-old (1·4 to 2·9 kg) during the feeding experiments. The fifth monkey was about 18-months-old when used in the feeding experiments. At nine months, wild monkeys probably get only a small fraction of their nourishment by nursing and are weaned by the time they are a year old. The monkeys were kept in screened cages with dimensions of 60 by 90 by 120 cm. The floor was covered with heavy polyethylene to hold the urine for collection. Some urine was occasionally lost when the monkeys tore holes in the polyethylene, allowing urine to seep into the wooden floor of the cage. The cages were kept in a well ventilated house so that light, temperature and humidity were similar to that experienced by free-living monkeys.

Twice a day I removed the cage floors and separated the faeces, urine, and left-over food accumulated since the last feeding. The monkeys were fed immediately after the cages were cleaned. I fed a

FIG. 2. View of the forest canopy from the top of the steps at the clearing on Barro Colorado Island, Panama. A large tree in the canopy had fallen just before the picture was taken, creating the hole in the canopy in the centre of the photograph.

known wet weight of food at each feeding and converted it to dry weight by determining the loss of weight during drying of food samples. The food samples, faeces, urine and left-over food were all dried at 80° C to a "constant weight". The dried samples were sealed in plastic bags, or vials for urine, and returned to Missouri for analysis. I determined the energy content of all materials by burning a random sample of the material after it had been ground up with mortar and pestle. The techniques of Paine (1964) were used on a Parr semimicro oxygen bomb calorimeter, model 1411, to determine the calorific value of the materials. The per cent nitrogen and calcium content of food and faecal samples were determined by the University of Missouri Agricultural Experiment Station Chemical Laboratories.

I continued the feedings for eight or ten days for each food. Native foods were all picked, weighed, and bagged a few days before the start of an experiment and kept in a refrigerator to prevent spoiling. The materials from the first day were separated from materials from the last seven or nine days because by the end of the first day the nature of the faeces had changed from that produced under the usual diet of milk and cultivated fruit. The percentage of weight and energy assimilated and metabolized is calculated from the materials gathered the last seven or nine days. Assimilated energy is the calories of food ingested minus the calories of faeces produced. Metabolizable energy is assimilated energy minus calories of urine produced.

3. FEEDING BEHAVIOUR

3.1. Time Budgets

Generally it is difficult for an animal to concentrate on doing more than one thing at a time, and howling monkeys are no exception to the rule. The relative amount of time an individual spends on different activities is a good measure of the relative importance of those activities to the organism. If a trade-off of one activity for another were to cause an increase in an individual's contribution to future generations, then the behavioural responses that lead to the trade-off would be under positive selection.

The time budgets of howling monkeys show a great emphasis in resting (Fig. 3). The maintenance category in Fig. 3 includes time spent grooming, defaecating and urinating, but is mainly resting. Urinating and defaecating make up less than 0·3% of the maintenance activity, but as much as 20% of maintenance activity in some hours may be grooming. I never observed allogrooming except between two caged howlers. Free-living monkeys usually use an arm, leg or their tail to rub lightly over some surface of their body at intervals of from ten to 120 seconds. Often the appendage does not touch the body at all. The grooming seems to be directed at moving mosquitoes from the monkey's body. They do not groom during heavy rains. The importance of this activity in preventing parasitism will be discussed later. The monkeys' resting pattern does not seem to be interrupted by the intermittent brushing of mosquitoes. Their resting posture is seldom disturbed and the monkeys use whichever of their five appendages is free. Thus, essentially all of the maintenance time is spent resting. The importance of this great amount of resting time is in allowing the monkeys to concentrate their metabolic activity on digesting a relatively indigestible food. There are slight differences in the percentage of time spent resting between adult males and females and between the wet and dry seasons, but at least 74% of the day and all night are spent resting by all adults at all seasons.

The time spent feeding or moving between feeding sites took up most of the rest of the day, with less than 4% of the day spent in social activities of all kinds. The monkeys could find and consume their daily food requirements during 15 to 22% of the day, because the leaves and fruit upon which they feed are concentrated in large mature trees and require little or no manipulation while being eaten. The low proportion of time spent in social interactions seems unusual for primates, especially when so little time is demanded for feeding and finding food. Actually, the pattern of feeding in trees with an excess of food may prevent aggression between troop members over food or feeding sites. The absence of allogrooming also reduces social interaction, but it is difficult to determine whether its absence is a cause or an effect of low levels of social interaction. Of the 1·5 to 2·4% of the time spent in social behaviour in the wet and dry seasons only one-third was definitely directed at members of the same troop. The remaining two-thirds was spent in vocal activity, most of which was loud enough to function in communication between troops.

A comparison of the activity patterns and diet of the four species of diurnal monkeys on BCI emphasizes the relationship between a high component of leaves in a diet and a high percentage of time resting (Table I). The correlation is actually stronger than the values in Table I indicate because most of the time the *Cebus capucinus* were motionless they were standing and alertly looking for insects. The *Saguinus geoffroyi* were standing and searching all the time they were motionless. In contrast, howlers sit or recline when motionless, brush

TABLE I

Food supply in relation to the time budgets of four diurnal primates on Barro Colorado Island

Species	Where observed	Time observed (hr)	% Time moving or feeding	% Time motionless or grooming	% Fruit* in diet	% Leaves* in diet	% Animals* in diet
Alouatta palliata	Free living	366	21	79	60	44	<1
Alouatta palliata	Caged†	8	17	83	60	40	<1
Ateles geoffroyi	Free living§	§	38	62	80	20	<1
Cebus capucinus	Caged‡	4	41	59	65	15	20
Saguinus geoffroyi	Caged‡	4	35	65	60	10	30

* Date taken from Hladik and Hladik (1969).
† Wide-meshed screened cages in a clearing.
‡ Wide-meshed screened cages under a forest canopy where insects could enter.
§ During 18 days of observation by Richard (1970).

away mosquitoes, and stare into space or sleep. Leaves and small animals appear to be the major source of protein for these four sympatric species of primates. With small animals as a protein source, foraging time is greatly increased, while leaves require little foraging time and much effort to digest. The niche of howling monkeys is at the extreme where most time is budgeted to maximize the effort on digesting food.

3.2. Feeding Behaviour

Howling monkeys appear to have poor manual dexterity compared with most other new world primates (Carpenter, 1934). The thumb and first digit oppose the last three digits. Carpenter gives several examples of how this form of grasping with the hand is used in their typical pronograde locomotion and their feeding behaviour. Usually they grab a branch about 30 cm from its tip and bend it back to bring fruit, leaves, buds or flowers close to their mouth and pick the food with their lips or teeth. The food is manipulated in the mouth, usually without the aid of hands, and may be rejected by spitting it out of the mouth. Most of the food items are either swallowed or spat out without any discrimination between the parts of the food that may differ in their desirability as food. However, I once observed monkeys spitting out the pith of fleshy fruits while swallowing much of the pulp.

3.3. Feeding Heights and Feeding Sites

The fruit, young leaves, buds and flowers which make up the diet of howling monkeys all occur in greatest quantity at the ends of exposed branches near the tops of trees in the forest canopy. Most of the feeding is done in individual trees which are large enough to feed a whole troop during one feeding bout. Monkeys will eat some food, especially leaves, from trees and vines around the main food tree during a feeding bout or at odd intervals when moving between different food trees, but most of the food consumed is in troop feeding bouts from one tree per bout. The trees that can supply enough food for a troop are mature individuals that cover a relatively large exposed area in the canopy. The monkeys generally feed in the top quarter of a tree and travel as high as possible in the canopy when moving between food trees. I never saw a howler on the ground and very seldom on the lower half of a tree. They appear to travel familiar routes through the forest that do not require them to come near the ground (Carpenter, 1934). By staying away from the ground they avoid picking up ticks. The absence of allogrooming in howlers is probably adaptively related to staying away from the ground and avoiding ticks.

3.4. Percentage of Time Spent Eating Different Foods

Fruit and leaves have about equal importance in the diet of howling monkeys. Hladik and Hladik (1969) report 60% of the diet in fruit and 40% in leaves based on stomach contents and field observations of feeding. Richard (1970) and I (Table II) from our pooled notes find a slightly greater emphasis on leaves based on the percentage of time spent feeding on different foods. The slight difference between stomach content and feeding time could result from leaves being consumed at a slower rate than fruit. The seasonal shift in the relative importance of leaves and fruit (Table II) matches seasonal changes in the abundances of these foods. The shift also shows that the monkeys do not follow a rigid balance in the proportions of the two types of food. Buds probably serve the same dietary needs as leaves, and flowers the same dietary needs as fruit (see below). Again the increased use of flowers and buds during the dry season reflects their greater abundance on the trees at that time.

TABLE II

Percentage of time spent feeding on different categories of food

Type of food	% Composition of diet in the dry season	% Composition of diet in the wet season
Platypodium elegans leaves	12·5	14·5
Other species of tree leaves	22·1	43·7
Leaves from various species of vines	6·9	7·7
Total leaves	41·5	65·9
Ficus fruits	28·8	14·3
Other types of fruit	17·3	17·2
Total fruit	46·1	31·5
Flowers of various species	8·7	2·5
Buds of various species	3·6	0
Total hours of feeding observation	27·7	15·4

3.5. The Adaptive Basis of Food Choices

The choice of food is an evolved trait, which in the broadest sense, must be explained in the context of total community structure (Schoener, 1974). Food partitioning among species results from the evolutionary effect of interspecific competition, usually among the species of greatest phylogenetic affinity. Among the primates of BCI, the niche of howlers appears to be at the extreme of the food continuum which includes food that is easy to find, easy to consume, but difficult to digest. Given the extreme of an abundant, but relatively indigestible food, howlers could still improve their diet by choosing a balance of nutrients from among their potential species of food.

Howlers do bias their choice of leaves and fruit to concentrate on a few species and genera on BCI while taking small amounts of a great variety of species (Carpenter, 1934; Hladik and Hladik, 1969; Hladik *et al.*, 1971a). My time budget notes from February through July (Table II) show that howlers had a marked preference for leaves from *Platypodium elegans* Vog. and fruit from various species of the genus *Ficus*. Knight (1975) found on 13 plots, averaging 1·5 ha each, across BCI that *P. elegans* occurred on six plots and species of *Ficus* occurred on nine. The highest percentage composition of trees over 18 cm diameter breast height (DBH) on any one of the 13 plots was 1·0% for *P. elegans* and 0·2% for *Ficus*. However, from 22 to 30% of the time spent eating leaves by howlers was spent on *P. elegans* and 45 to 62% of the time spent eating fruit by howlers was spent on *Ficus*. Knight's data and my observation were not taken in exactly the same area, but the contrast between the percentage composition of the forest and the monkey's diet is probably a good approximation of the degree of preference the monkeys show for these foods.

With one exception, the leaves that monkeys chose to feed upon were either still growing or the youngest leaves on their branch. It is likely that developing leaves have a higher concentration of protein and lower concentrations of cellulose and lignin and possibly secondary plant substances than mature leaves, as Feeny (1970) describes for an oak in temperate forests. The one exception, species of the genus *Cecropia*, made up 2·8% of the total feeding time spent on leaves. The monkeys ate *Cecropia* leaves of all ages including some that were dead and partly freed from the branch by natural abscission. Before natural abscission, many species of trees reabsorb some of the minerals from their leaves, especially phosphorus. However, calcium often increases, rather than decreases, in concentration in leaves during their death and abscission (Biddulph, 1959).

I attempted to explain the above food choices by measuring the monkeys' assimilation efficiency for fruit from *Ficus yoponensis* Desv. and *Ficus obtusifolia* HBK, and leaves from *Platypodium elegans* and an unidentified species of *Cecropia*, along with the concentration of calcium and nitrogen in the food (Table III). The feeding experiments were complicated by the fact that the juvenile monkeys lost weight rapidly when switched to a diet of native food. Therefore, I fed them a mixed diet of native foods and Pet Evaporated Milk diluted with equal amounts of water. In mixed diets I assumed that the milk drunk by the monkeys was assimilated with the same efficiency as in diets of pure milk. This allowed me to calculate the component of the faeces in the mixed diet that came from milk. The remaining component of the faeces could then be subtracted from the native food in the mixed diet to measure the amount of native food assimilated. (The milk mixed in with the roughage of native foods would be less likely to be assimilated than in the absence of roughage.) Therefore, the assumption that milk is assimilated with the same efficiency in pure and mixed diets is probably false and causes the values in experiments 2-B, 3-B and 5-B, Table III, to be underestimates of the real assimilation efficiency of these native foods. A comparison of experiment 4 (Table III) where no milk was added, with experiment 5-B where milk was part of the diet, is an example of the reduction of assimilation rates resulting from my assumptions about the assimilation of milk in mixed diets. The error is greater in the calculation of calories assimilated than in weight assimilated because milk has a higher calorific value than any of the native foods.

The monkeys were fed *ad libitum* with both milk and native foods when their diets were mixed and individuals differed in the relative amounts of the two foods they chose. As the proportion of native food increased, the calculated efficiency of its assimilation increased because the relative effect of the milk error is reduced. For example, an individual which made *F. yoponensis* 18% of its diet had a weight assimilation efficiency of 36% while an individual that made *F. yoponensis* 49% of its diet had a weight assimilation efficiency of 57%.

Taking into consideration all the errors resulting from calculations based on diets mixed with milk, it still seems safe to say that the captive monkeys could not assimilate much more than 50% of their native foods. Even this conclusion requires some hedging because the captive monkeys probably did not have a gut biota as well adapted to aid in digesting native food as do free-living monkeys. None-the-less, free-living howlers do defaecate surprisingly large amounts, and a 50% assimilation efficiency is probably fairly accurate.

The relative efficiencies of assimilation of native foods (Table III) are probably more reliable than their absolute values. *F. yoponensis* fruits appear to have thicker walls and a lower percentage of indigestible seeds than *F. obtusifolia* which would explain the higher assimila-

TABLE III

The efficiency with which five juvenile howling monkeys assimilate and metabolize some common natural foods and Pet Evaporated Milk

Expt. no.	Food	Number of monkeys	% Weight assimilated ± one s.e.	% Calories assimilated ± one s.e.	% Calories metabolized ± one s.e.	kcal per gram dry weight	% Ash	% Ca	% N	% Protein§
1	Pet Evaporated Milk	4	89·6 ± 1·0	89·5 ± 1·0	87·8 ± 1·2	5·64	7·0	1·0	4·7	29·4
2-A	Pet Milk and fruit of *Ficus yoponensis**	3	75·2 ± 3·7	73·8 ± 4·2	72·1 ± 4·2					
2-B	(*Ficus yoponensis*)	3	42·9 ± 7·1	27·8 ± 7·2		4·15	11·0	1·7	1·4	8·6
3-A	Pet Milk and leaves of *Platypodium elegans*†	1	78·1	77·0	74·8					
3-B	(*Platypodium elegans*)	1	37·0	24·4		4·76	4·7	0·5	6·8	42·4
4	*Ficus obtusifolia* fruit and *Cecropia* sp. leaves	2	24·5 ± 1·6	9·6 ± 0·1	8·1 ± 0·5	4·17 3·97	5·2 11·1	1·2 1·6	0·8 2·4	4·7 15·2
5-A	Pet Milk, fruit of *Ficus obtusifolia*, and *Cecropia* sp. leaves‡	2	51·0 ± 2·3	47·0 ± 4·6	45·7 ± 4·5					
5-B	(*Ficus obtusifolia* fruit) (and *Cecropia* sp. leaves)	2	18·7 ± 1·8	− 3·5		4·17 3·97	5·2 11·1	1·2 1·6	0·8 2·4	4·7 15·2

The calorific value, and the % ash, nitrogen, calcium and estimated protein are given for each food. Assimilation rates for foods in parentheses were calculated by subtracting the expected assimilation rate for the milk that was part of the diet.

* The mean percentage of the diet composed of *Ficus yoponensis* was 34·6%.

† *Platypodium elegans* was 18·6% of the diet.

‡ The mean percentage of the diet composed of *Ficus obtusifolia* and *Cecropia* sp. was 55·0%.

§ Assuming % protein = 6·25 × % nitrogen.

tion efficiencies on *F. yoponensis*. *Cecropia* leaves appeared almost unaffected by passing through the guts of captive monkeys which explains the low assimilation efficiency for the mixture of *F. obtusifolia* fruit and *Cecropia* leaves. Generally it would appear that figs are more efficiently digested than leaves and that young *Platypodium* leaves are digested more efficiently than *Cecropia* leaves and probably most other leaves.

The monkeys' choice of *Platypodium elegans* as a major fraction of their leaf diet is more likely to be adaptive because of its extremely high nitrogen (and presumably protein) concentration than because of the efficiency with which its energy can be assimilated. Monkeys could assimilate energy more efficiently from figs or other fruit than from *P. elegans* leaves. However a pure diet of fruit, especially figs, would leave them with a protein deficiency. *Cecropia* leaves would provide a food with a concentration of calcium higher than Pet Milk, but *Ficus yoponensis* fruit has an even higher concentration and is assimilated much more efficiently. *Cecropia* leaves seem to serve as a calcium supplement to the diet only when figs are not available in high enough abundance. From February through May figs made up 28·8% (Table II) of the total diet and no *Cecropia* leaves were eaten, while in June and July figs were only 14·3% of the diet and *Cecropia* leaves were 4·3%.

The major pattern in food choice by howlers seems to be a balance of the various food species to give a nutritionally balanced diet. The balance does not require a rigid proportion of a set of specific food species. The shift in proportion of feeding time on different types of food between the dry and wet season (Table II) follows the relative abundance of the different types of food in the two seasons. Flowers, buds and fruit are more abundant during the dry season and young leaves more abundant in the beginning of the wet season. Buds can be switched for young leaves to supply protein and *Cecropia* leaves for figs to supply calcium. The total nutritional balance is a much more complex picture and will require an analysis of the whole spectrum of mineral, vitamin and nutrient requirements of monkeys and the availability of the requirements in the whole range of potential food species. However, the fact that howlers do show strong preferences for some species of fruits and leaves and that their use of different types of foods shifts in parallel to the abundance of the food indicates that nutrient composition, digestibility, and seasonal abundance are all important variables in the adaptive basis of their choice of a balanced diet. Similar patterns of choice have been demonstrated for domestic animals by comparison with random samples of range forage with gut content of fistulated animals (Jefferies and Rice, 1969; Rao *et al.*, 1974; Krueger *et al.*, 1974).

Together, Carpenter (1934) and Hladik and Hladik (1969) list vegetation of different types eaten by howlers from 69 species in 31 families of plants on BCI and nearby Panama. Additional plant species eaten by howlers in Guanacaste province, Costa Rica, are listed in class reports of the Organization for Tropical Studies. *Alouatta palliata* occurs in a wide variety of forest habitats ranging from aseasonal rain forests along the Caribbean coast to dry, open, seasonal deciduous forests in areas along the Pacific coast of Central America. They range in latitude from Vera Cruz province, Mexico to Ecuador. Within this range of habitats and latitudes the species must feed upon a huge number of plant species. I never observed howlers feeding on animal material other than the insects that probably inhabit some of the leaves and fruit they eat. Stomachs contain less than 1% animal material (Hladik and Hladik, 1969).

4. TEMPORAL PATTERNING OF FOOD CHOICE

4.1. Diurnal Variation in Food Choice

The daily food choice of howling monkeys led to a balance between food rich in protein (leaves and buds) and food rich in digestible carbohydrate (fruit and flowers). In the 16 days in which a troop was followed for at least eight-tenths of the day, each type of food was eaten for at least 5 min, and on all but four days each food was eaten for over 20 min. On three of these four days I did not follow the monkeys all day and at the time of my leaving them or finding them, they were feeding on the food that would tend to balance their diet. The most extreme imbalance of the two types of food on any one complete day of observation was 39 min of leaves to 7 min of flowers and fruit. On the other seven complete days of observation the ratios of the two types of food were all less than three to one.

On four days, flowers rather than fruit served as the source of carbohydrates. I have no direct evidence that the nectar was the main part of the flower digested. However, pollen is apparently difficult for some mammals to digest, except by swallowing urea as a catalyst (Howell, 1974), and it is unlikely that the sepals and petals of the flowers would be rich in either protein or digestible carbohydrates. Nectar is the most likely material of food value to the howlers in flowers. One troop ate flowers and leaves but no fruit for two days in a row, which would be an unusually strong exception to the daily balance in types of food if flowers were not used mainly as a source of digestible carbohydrates.

The monkeys' practice of balancing their diet within each day requires that troops move at least once a day to switch to a preferred food tree for the opposite type of food. On only one occasion did I observe a troop alternate back and forth between two trees, feeding on one (*Ficus obtusifolia*) for fruit and the other (*Platypodium elegans*) for leaves. Sometimes a troop will feed in the same tree in the evening and the morning, but the above observation was the only one I made of a troop returning to a tree during the same period of fruiting. The failure to return in most cases cannot be explained as a result of the troop reducing the supply of fruit to the point where it can no longer be efficiently exploited. In three instances, a second troop entered a tree and fed from it within two days after the troop I was following had left the tree. In one of those instances the second troop was the larger of the two. It may be that the optimum diet is more complex than just a balance between fruit and leaves. There should be selective pressure on trees to make their fruit an incomplete diet for the animals most attracted to them so that the animals will have to move away from the tree periodically and defaecate the seeds far from the parent tree. This argument could be extended for trees using howlers as dispersal agents for their seeds to include only one visit to a tree each fruiting period as the optimum pattern. To achieve this pattern, the fruits of different trees would have to have complementary nutritional deficiencies for howlers. I have no evidence that such a pattern exists other than the usual failure of howler troops to return to the same fruit tree after a feeding bout on leaves.

5. SEASONAL VARIATION

The seasonal changes in the percentage of time feeding on different foods shown in Table II do parallel changes in abundance of those types of food. Flowering among the species of large trees reaches a peak in February and March in the first half of the dry season and fruiting in these trees peaks from April through June, the second half of the dry season and the first month of the wet season. Leaf fall peaks in January and new leaf production peaks in June after bud development during the dry season. Thus flowers and buds are most abundant and are fed on most extensively in the dry season. New leaves are most abundant in the beginning of the wet season at the time I took time budget notes and the use of leaves in the diet increases at that time. Species in the genus *Ficus* fruit at all times of the year and I have no explanation for their more extensive use during the dry season. Although there are seasonal shifts in the use of different types of food, there is a large component of both leaves or buds and fruits or flowers in the diet.

In both the wet and dry seasons there were peak periods of movement and feeding in early morning and late afternoon (Fig. 3). However, in the wet season the activity was later in the morning and earlier in the afternoon than in the dry season. During the wet season the first and last tenths of the day were spent resting (Fig. 3A) while in the dry season these were two of the busiest parts of the day (Fig. 3B). The wet season is generally cooler and more humid. Therefore, the temperature and humidity pattern of the first and last tenth of the day in the dry season would tend to be shifted towards the middle of the day in the wet season. The monkeys would appear to be picking the same climatic conditions for the peak of activity in both the wet and dry season. This pattern of adaptation to daily cycles in climate would be the optimum

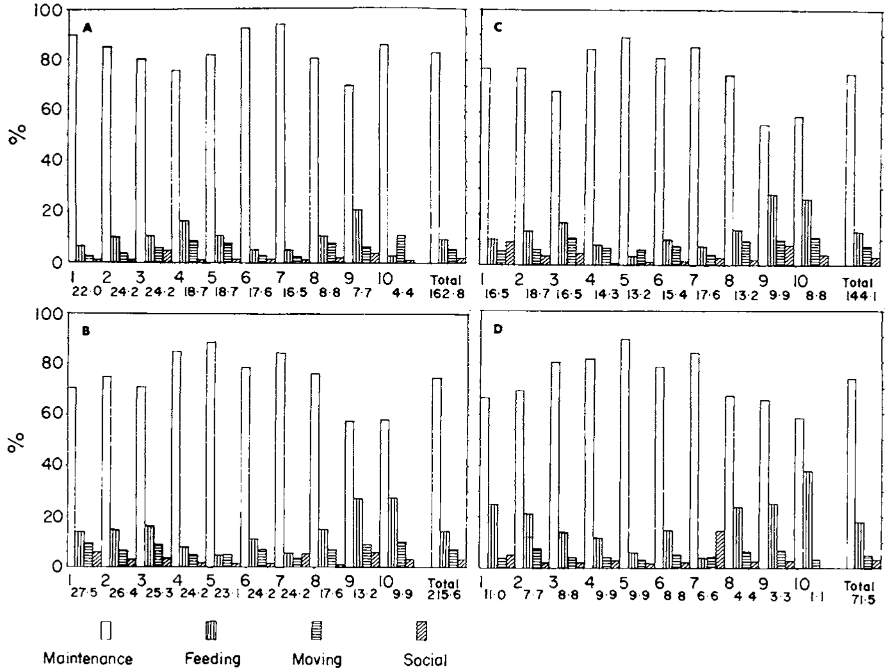

FIG. 3. Time budgets for adult howling monkeys. The types of behaviour grouped to form the categories of maintenance, feeding, moving and social behaviour are described in the text. The period between sunrise and sunset was divided into ten intervals of equal length. These are listed along the abscissa followed by a composite time budget for the total day. The number of hours of observation used to make the time budget for each period of the day is listed under that period. Budget A is a composite of all adults followed during the wet season from 4th June to 5th July 1968. Budget B is a similar composite for the dry season from 20th February to 3rd June 1968. Budgets C and D are for male and female adults respectively during the same period of time as budget B.

one for allowing the monkeys two widely separated periods of activity each day under one set of optimal climatic condition in both the wet and dry seasons.

Howlers rest more but feed, move, and participate in social activity less in the wet season than in the dry (Fig. 3A, B). Chivers (1969) found the same difference in activity between wet and dry days within the wet season. The howlers' response to the heavy rains of the tropical wet season is first to howl, often even at the sound of the rain approaching, and then to sit hunched over until the rain ends. By resting in response to rain their resting time should automatically increase. However, it seems strange that feeding time would be reduced over the whole day. They may eat more hurriedly during the rainy season, but I made no attempt to quantify a difference in the rate of ingesting foods between the two seasons. Their feeding rate is generally slow and there is much leeway for reducing feeding time by increasing feeding rate.

6. SEXUAL VARIATION

Males averaged 14% of the day feeding and females 18% (Fig. 3C, D). The difference is somewhat unexpected because males are heavier than females and should require more food. However, 59% of the notes used to compile the female time budget were taken for females supporting infants. The feeding time of females during the first nine time periods was 14% greater than the feeding time of females without young, or in other words they spent about 1·5% more of the day feeding than did females without infants. The differences between the sexes are not great and could have been biased by the small sample of notes taken during the last tenth of the day for females.

7. PARASITISM AND HEALTH

The extent of parasitism by botfly larvae differed in adult howlers in response to the season of the year, and in adult females in response to the presence or absence of an infant with the female (Table IV). The parasitism was higher from May through July than from October through April. The eggs of botflies are laid on the ventral side of the abdomen of mosquitoes and hatch in response to the warmth of the howler's body when the mosquito comes to get a blood meal. The rise in the number of infestations towards the end of the dry season may result from an increased activity of mosquitoes during the dry season.

TABLE IV

The number of botfly larvae (Dermatobia hominis) *infecting howling monkeys in relation to the season of the year and the sex and reproductive condition of the monkeys*

	Males	Females without infants	Females with infants	Infants	Juveniles	Total
October–April	2·0 ± 0·29	2·8* ± 0·39	1·3 ± 0·53	2·0 ± 0·91	1·6 ± 0·45	2·2 ± 0·21
May–July	3·9 ± 0·61	6·9* ± 0·67	4·4 ± 0·87	3·1 ± 1·47	5·3 ± 1·86	4·9 ± 0·43
t-value	3·19†	5·03†	3·20†	0·52	3·00‡	6·32†

Values are means ± one s.e.

* The difference between the means for females with and without infants in October through April is nearly significant ($t = 1{\cdot}920$, d.f. = 75) and in May through July is significant ($t = 2{\cdot}078$, d.f. = 28).

† Statistically significant at $P < 0{\cdot}01$.

‡ Statistically significant at $P < 0{\cdot}05$.

Its effect may be detrimental to the monkeys most infected. During the 11 months of the study, three monkeys were found dead or dying on the island, all in June and July. Two of these were dead and too decomposed to determine the extent of parasitism, but the third, a juvenile, was still barely alive when found and had been infected with 25 botfly larvae. Many of the holes inhabited by these larvae had been secondarily infested with the larvae of some other type of fly which were eating through the body wall, the peritoneum and even into the liver. It is likely that the heavy botfly infestation was the ultimate cause of the secondary infection of the monkey and its eventual death.

The correlation of high botfly infections in females with the absence of infants could be explained in several ways. (a) The infestations could be the cause of the absence of infants either through death of the infant or failure of the female to come into heat. (b) The poor health of females resulting from some independent cause could cause both the absence of infants and a high infestation of botflies. (c) The presence of an infant could disturb the activity of mosquitoes. The last explanation seems unlikely since infants of Carpenter's (1934) categories 1, 2 and 3 spend 19, 42 and 75% of their daylight hours away from their mothers. In the interaction between the mother and the mosquitoes, an infant can distract the mother as well as disturb the mosquitoes. It seems more likely that there is a causal relationship between botfly infections and poor health in howlers, and that botflies limit howler population density both through adult mortality and reduced reproductive success. Botfly infections are not mentioned in Baldwin and Baldwin's (1972) analysis of howling monkey population limitation in south-western Panama where populations were 12 times as dense as those on BCI. I did not observe botfly infections of howlers in Guanacaste province, Costa Rica.

8. FEEDING BEHAVIOUR AND SOCIAL ORGANIZATION

8.1. Troop Composition

Howlers live in multimale troops which seldom, if ever, intermix. I censused 25 troops in the north-west third of BCI between 7th September and 12th December 1967 and two additional troops on 10th May 1968 (Table V and Fig. 4). The earlier censuses of Carpenter (1934, 1962), Collias and Southwick (1952), and Chivers (1969) are summarized along with mine in Table VI. The recorded history of howlers on BCI starts with relatively few large troops in the early 1930s concentrated in the more mature forests on the southern and western parts of the island. By 1951 the troops had increased in number

TABLE V

Troop composition of the 27 troops whose positions are plotted in Fig. 4

Troop	Adult male	Adult female	Juvenile 3	Juvenile 2	Juvenile 1	Infant 3	Infant 2	Infant 1	Juv. & Inf.	Total
1.	4	8	0	1	1	0	4	0	6	18
2.	4	4	1	1	1	1	2	0	6	14
3.	2	8	1	1	1	1	1	1	6	16
4.	3	3	0	1	1	0	1	0	3	9
5.	3	4	1	0	1	0	1	0	3	10
6.	2	4	0	2	0	0	0	1	3	9
7.	2	4	0	0	0	2	0	0	2	8
8.	4	8	0	1	1	1	1	0	4	16
9.	1	5	0	2	0	1	0	0	3	9
10.	2	9	1	2	0	1	1	1	6	17
11.	3	8	1	0	0	2	3	1	7	18
12.	2	8	1	0	1	0	0	0	2	12
13.	2	5	0	1	0	1	1	0	3	10
14.	2	3	1	0	1	0	0	0	2	7
15.	2	5	0	0	0	0	1	0	1	8
16.	4	11	0	1	0	0	0	1	2	17
17.	6	13	1	1	1	0	2	0	5	24
18.	2	6	0	0	0	0	0	0	0	8
19.	2	3	0	0	0	0	1	0	1	6
20.	1	4	1	0	0	0	1	1	3	8
21.	5	10	0	0	1	1	2	0	4	19
22.	4	13	1	2	1	1	3	3	11	28
23.	1	7	1	0	0	0	0	0	1	9
24.	6	17	1	1	3	1	0	2	8	31
25.	3	5	0	1	0	1	0	0	2	10
26.	4	7	0	2	0	1	2	0	5	16
27.	3	6	1	1	0	1	2	1	6	15
Total	79	188	13	21	14	16	29	12	105	372
Mean no.	2·9	7·0	0·5	0·8	0·5	0·6	1·1	3·9	0·4	13·8
Mean %	21·1	50·1	3·5	5·6	3·7	4·3	7·7	3·2	28·0	

Troops are listed in the order they were discovered.

and spread evenly to all parts of the island, but had decreased to half the average size of the early 1930s apparently as the result of a yellow fever epidemic. The troops had further increased in number by 1959 and their size had recovered to that of the 1930s. Between 1959 and 1967 the number of troops probably doubled, but their average size decreased from 18·5 to about 14.

Comparisons of age structure of troops between different census periods, and especially different authors, are subject to the errors of interpretation of the age of animals in the field. This difference in judgement is part of the cause of differences in Chivers' and my cen-

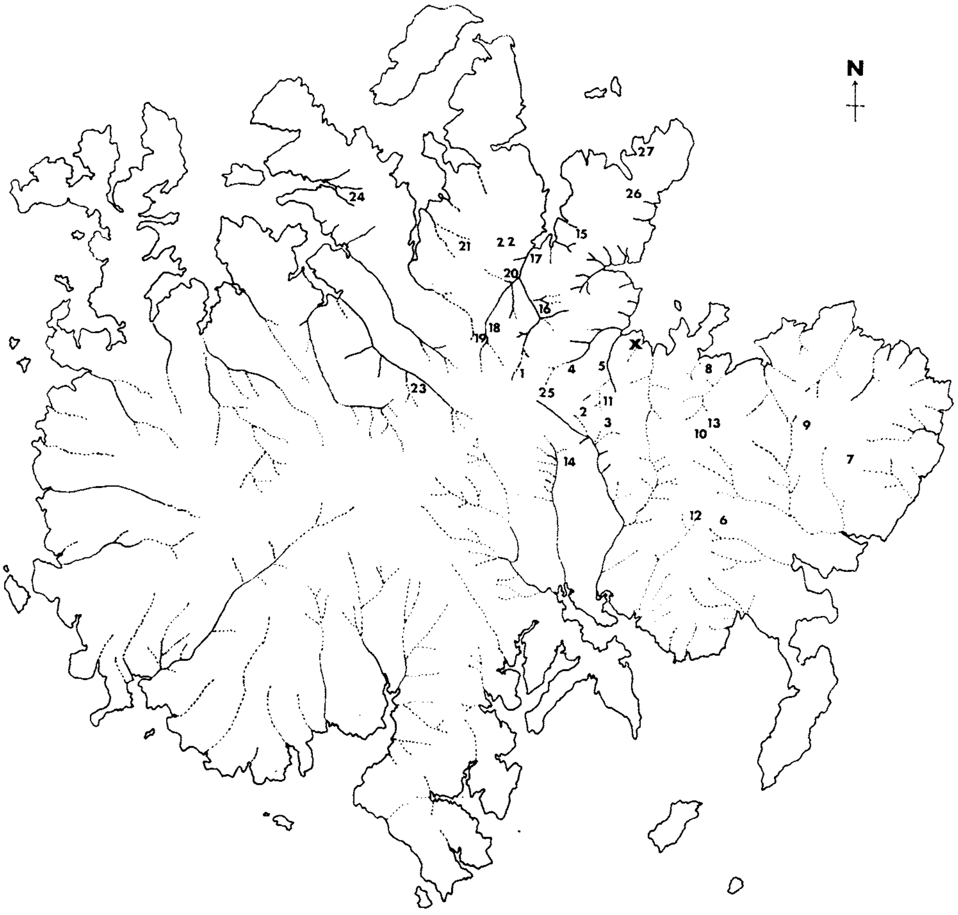

FIG. 4. The position at which troops 1 through 27 of Table V were censused on Barro Colorado Island, Panama.

suses. Chivers' troop YY and my 16 are the same, and yet Chivers found six females, five juveniles, and two infants in August, while I found 11 females, one juvenile, and one infant two months later. Adult males can be easily distinguished from juveniles by their prominent white scrotum. A comparison of the adult sex ratios in Chivers' and my censuses indicates that my pattern of separating adult females from juveniles is probably closer to that of earlier studies by Carpenter.

On the basis of the age distribution of my census there has been a decrease in the proportion of juveniles and infants in the island population starting with over 40% in the 1930s dropping to 33% in 1959 and finally to 28% in 1967. The low of 28% juveniles and infants in 1951 can be explained as resulting from the poor health of the troops during the yellow fever epidemic. The decrease in the proportion of juveniles and infants should be an indication that the population on the island is reaching its maximum population density with a resultant decrease in the animals' health and reproductive rates. The debilitating effects of botfly infections could be the main limiting factor since Baldwin and Baldwin (1972) find healthy populations at 12 times the density in south-western Panama. The eight troops they censused contained 37% infants and juveniles (Baldwin and Baldwin, 1973a). Table VI shows that the main difference in troop composition between the 1930s and 1967 was a reduction in the number of juveniles and infants per troop, and not a marked change in the number of adults.

I censused troops on approximately one-third of the island (Fig. 4). Even in this area I know that I missed one troop, troop XX of Chivers (1969), which ranged just east of the clearing. Because of the extreme overlap of the ranges of troops, I could never be sure that I had found all the troops in an area. By marking the position of botfly infections and comparing successive censuses, I could be sure that I did not use one troop as the basis for two different censuses. I doubt if I missed more than three or four troops in the area of the census. Assuming that the forests on the island had matured to the point that they were all good howler habitat by 1951 when Collias and Southwick found troops fairly evenly dispersed, then there are two eight-year periods of population growth that can be compared on the island since 1951. Assuming that I censused about one-third of the howler population on BCI, then the population increase between 1951 and 1959 was 241%, and between 1959 and 1967 was 37%. The rate of population increase slowed greatly in the second half of the 16-year period indicating that the howler population on BCI was near saturation in 1967.

TABLE VI

Troop size and composition on Barro Colorado Island from 1932 to 1967

Observer	Year of census	Adult males	Sex ratio females per male	Females without infants	Females with infants	Infants	Juveniles	No. of monkeys censused	No. of troops	Mean troop size	Mean no. of adults	% of island censused
Carpenter	1932	0·16	2·7	0·27	0·16	0·18	0·23	398	23	17·3	10·2	100
Carpenter	1933	0·17	2·3	0·19	0·20	0·20	0·24	489	28	17·5	9·8	100
Carpenter	1935	0·18	2·1	0·24	0·14	0·14	0·30	239	15	15·9	10·3	?
Collias and Southwick	1951	0·15	3·8	0·42	0·15	0·15	0·13	239	30	8·0	5·7	100
Carpenter	1959	0·18	2·7	0·33	0·16	0·16	0·17	814	44	18·5	12·5	100
Chivers	1967	0·23	1·8	0·24	0·17	0·17	0·19	176	12	14·7	9·3	16
Smith	1967	0·21	2·4	0·35	0·15	0·15	0·13	372	27	13·8	9·9	33

8.2. Overlap in Troop Range

Carpenter (1934), Collias and Southwick (1952), Altmann (1959), Bernstein (1964) and Chivers (1969) have all plotted the range of movements of the troop of howling monkeys nearest to the clearing on BCI. The population density on that north-eastern side of the island differed greatly during the studies. The north-eastern third of the island had three troops in 1932, 11 troops in 1951, and 28 in 1967. The range of the single troop decreased and the amount of its overlap with the ranges of other troops increased as the density of troops in the area increased over the 35 years. Carpenter's early impression of mutually exclusive territories had to be adjusted by Chivers to one of overlapping ranges with intertroop spacing being accomplished by vocal signals used to prevent troops from meeting in the areas where their ranges overlap.

Figure 5 shows the position of the troop nearest the clearing (troop AA of Chivers and troop 5 in Fig. 4) during a 66-day period starting on 11th May 1968. The position of troops 4, 16 and X were also plotted when they were near the centre of the range of troop 5 during that period. The range of troop 5 overlaps the ranges of troops 4, 16 and X to an even greater extent than Chivers found in June through August of 1967. The area covered by the troop during two months in my study was even greater than the area it used during the 85 days of Chivers' study. The area I have plotted is probably an underestimate of the troop's actual range because there were many mornings when I could not find the troop either because it did not call or it called outside the area in which I expected to find it. There appears to be no part of a troop's range that it uses exclusively on BCI just as Baldwin and Baldwin (1972) report for south-western Panama. Chivers' (1969) report of non-overlapping monthly ranges must have been a coincidence for the period of his study.

8.3. Coevolution of Feeding Behaviour and Social Behaviour

The broad outlines of social behaviour in howling monkeys are similar to other primates that live in multimale troops as defined by Eisenberg *et al.* (1972). The mating system is promiscuous, with some adult females copulating with more than one adult male on the same day. Adult males do not directly participate in parental care, but are more aggressive than females in defending the troop from large potential predators (Carpenter, 1934). My only observation of response to potential enemies occurred when a man climbed a tree within 100

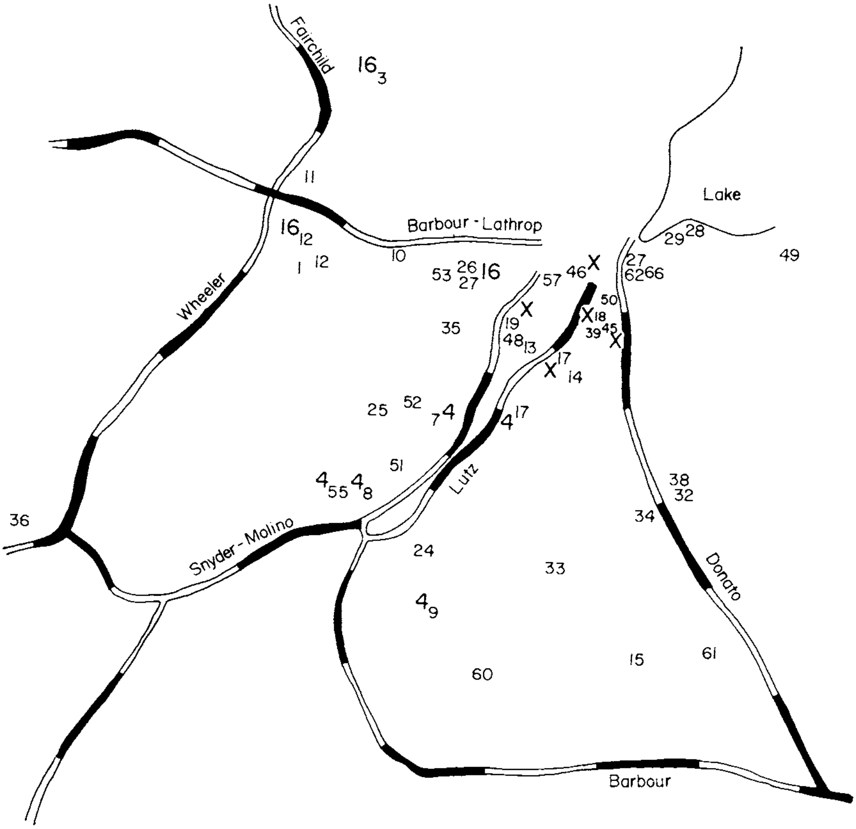

FIG. 5. The position of troop 5 of Fig. 4 on the mornings it was located on 66 successive days starting with 11th May 1968. The small numbers nearest the large symbols 4, 16 and X indicate the days on which these three troops were found near the centre of the range of troop 5.

metres of the troop I was watching. The members of the troop became agitated, but only the males moved towards the intruder, and they covered less than half the distance separating them from the man.

Although the outlines of their social behaviour are similar to other species of primates with multimale troops, howlers accomplish their social structure with a minimum of overt social interaction. There is no allogrooming, no aggression over food, and almost no aggression involved in sex. Adults spend less than one per cent of their time making even the slightest response to other adult troop members, such as turning to look at them as they pass by. Females appear to initiate most sexual interactions by looking in the face of a male and sticking out their tongue repeatedly (Carpenter, 1934). Both Carpenter and I have observed females display to a male with whom they had already copulated earlier in the day and upon receiving no response move to a second male and copulate. On four occasions I have found a male and female separated from any troop by more than 100 metres, but I did not observe copulation between any of the pairs.

There appears to be a learned component to sexual behaviour. A young male gradually moved into troop 5 in December and January, and became the fourth male in that troop. When first seen following along the edge of the troop he had only one testis descended into the scrotum. By 24th May when I first saw him copulate, he was an accepted member of the troop. At that time he copulated with a very small female who might have been classified as a large juvenile. The copulation continued for four minutes and much of the time the male was to one side of the female and did not seem to be penetrating although he was thrusting continuously. Seven copulations I timed for other males each required less than 35 seconds.

I had the impression that the members of a troop treated each other as individuals and had a rank order. However, I was never able to document the social order of even the males of one troop in spite of my efforts to record the interactions of the four males of troop 5 in careful detail. They never did more than watch each other and that with no sign of fear. Chivers' (1969) observation that six of the 40 males he censused had scarred, or freshly torn, lips may be taken as evidence of infrequent fierce fighting among males.

The troops seem to use the same paths through the trees repeatedly and their movements do not seem to be random. They often moved a few hundred metres in the most direct route to a tree in fruit or a *Platypodium* tree to eat leaves. My impression is that they learn much about the position of food and behaviour of other troop members and retain the information for long periods without reinforcement. Such a pattern is hard to document and is pure conjecture.

The evolutionary relationship between feeding behaviour and social behaviour is best explained by demonstrating that one of a group of possible social patterns is most effective in allowing individuals to convert food into offspring. I have argued in earlier sections of this paper that howling monkeys choose a relatively indigestible food supply of fruit and leaves because of character displacement in food choice resulting from interspecific competition with other new world primates in their evolutionary past. Because their food comes from trees, it is highly clumped at any given time in those individual trees which happen to be in fruit or those species of trees whose leaves are particularly rich in some component of their diet not abundant in fruit.

Thus, to maintain a balanced diet the monkeys move daily between trees which supply different components of their nutrient requirements.

The clumping of food in the fruit or leaves of one canopy tree is enough to clump many individual primates. There are many advantages for these clumped primates in moving between food trees as a group. The young individuals can profit from the experience of the old in finding more food. The constant association of the same group of individuals will minimize the learning each has to do in order to anticipate any aggressive action by the others. By moving between food trees as a group each individual may gain whatever advantage arises from group reaction to predators. Howlers are near the maximum weight at which an individual can safely move across the canopy, and any lone predator that can reach them should be routed by large numbers of howlers.

The males of some new world monkeys are involved in parental care by carrying infants (Eisenberg *et al.*, 1972). These monkeys form monogamous family social units at least some of which are territorial (Mason, 1968). The effort the male puts into parental care by carrying infants should tend to offset the female's effort of nursing leading to the evolution of their sexual monomorphism (Trivers, 1972). These monkeys obtain most of their protein by catching insects and small vertebrates; a foraging activity more easily hindered by an infant than foraging on leaves. The sexual dimorphism in howlers could have resulted from selection for male aggression in a promiscuous mating system (Trivers, 1972) and/or from indirect male parental care by a division of labour in troop defence. In either case, the use of leaves as a protein source allows females to forage with relative ease when carrying an infant and provides a food density that can support the large body size necessary for aggressive group defence against predation.

Chivers (1969) contrasts the great overlap of troop movements in howlers with the nearly mutually exclusive ranges or territories of *Cebus* troops. My observation of total overlap of howler troop ranges is probably typical of howler behaviour in unmodified areas. The *Cebus* pattern of extensive troop movement in foraging for animal protein would allow them to visit all parts of a large territory on a daily basis and make aggressive defence of an area possible. The howlers' pattern of moving once or twice a day between preferred feeding sites would not allow them to patrol on a daily basis the whole area through which they range. Accepting Brown's (1964) arguments that territoriality evolves only where there is an immobile, defensible resource in short supply, howling monkeys could not effectively defend the area in which they range without greatly increasing their daily movements.

The dawn chorus of loud howls allows troops to avoid contacts (Chivers, 1969). I observed only two instances in which one troop approached another and eventually displaced it from a food tree. The approaching troops howled almost continuously until the troop originally in the fruiting tree moved away. The displaced troop had fed in the tree the previous night and sometime during the morning it was displaced. The system of avoiding contact by vocal signals in the morning can keep troops isolated when each makes only one or two moves to a new food supply each day if, as Chivers found, they tend to move away from the troops nearest to them. More mobile foragers, like *Cebus*, would have to call at much more frequent intervals in order for troops with overlapping ranges to avoid contact.

By avoiding interaction with other troops howlers avoid the social conflict and aggressive behaviour that accompany establishing social relations with unfamiliar individuals. This avoidance, coupled with the low level of overt social interaction within a troop, is adaptive in minimizing the use of the voluntary musculature and allowing maximum circulation to the gut. Their whole pattern of social and feeding behaviour is a trade-off between minimizing the physical and social effort needed to obtain food so that a maximum effort can be exerted in digesting the relatively indigestible food which is so easily obtained.

9. SUMMARY

1, 2. The aim of the study was to relate feeding behaviour to social organization in howling monkeys. Field methods included censusing free-living troops and taking detailed time budget notes of the daily activities of individual monkeys. Assimilation rates for milk with wild figs or leaves preferred by free-living monkeys were calculated from eight- to ten-day feeding experiments with captive monkeys from nine- to 18-months-old.

3. The time budgets of free-living howlers show a great emphasis on resting. Among diurnal primates on BCI howlers are extreme in the high percentage of leaves in their diet and the high percentage of time spent resting. Their diet is found in the tops of canopy trees and is easily consumed but relatively indigestible. Among these relatively indigestible foods monkeys prefer leaves and buds high in protein, and perhaps calcium, content to balance their source of carbohydrates from fruit and flowers. Their balanced diet does not require specific species of food but rather is chosen from a wide variety of species in relation to their seasonal abundance.

4, 5, 6. Howlers balance their diet between protein-rich leaves and buds and carbohydrate-rich flowers and fruit each day. Seasonal diets, both in the use of species of food and in the balance between leaves, buds, fruit and flowers, are shifted in relation to the relative abundance of the different types of food. Males averaged less feeding time in a day than females, perhaps because of the greater demands of parental care for females.

7. Howlers have a higher level of infection by botfly larvae during May through July than from October through April. Females without infants have a higher level of infection than females with infants. Botfly infections may limit the density of howler populations on BCI through both adult mortality and reduced reproductive success.

8. Through 35 years of censusing howlers on BCI, the number of troops has increased threefold but the average size of troops has decreased. The troop in the young forests near the clearing on BCI has experienced a marked increase in the number of other troops in its area. Its range has increasingly overlapped with neighbouring troops to the point that in 1968 it probably did not have exclusive use of any part of its range. The social organization of howlers is similar in outline to other species with multimale troops. However, howlers have an unusually low level of overt social interaction. Patterns of social behaviour within troops, troop movements, and interactions between troops all seem to be adaptive in allowing individuals to minimize the use of their voluntary musculature so that their bodies can concentrate physiological activity on digesting a relatively indigestible food that is easily obtained.

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5

Diet and Feeding Behaviour of *Callicebus torquatus*

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1. METHODS AND STUDY AREA

This paper is based upon an initial study of *Callicebus torquatus torquatus*, the yellow-handed titi monkey, in north-eastern Peru during June, July and August 1974 (Kinzey *et al.*, 1977). The study consisted of 138 hours of observation. An additional 249 hours of observation were made during a second study in the same months of 1975, but were not completely analysed prior to this writing. Except where otherwise stated, all information presented pertains to the initial study.

During the initial study a troop of three animals (adult male, adult female and infant male less than one-year-old) was followed on 25 days between 25th June and 18th August, 1974, including six complete days from dawn to dusk. Data were recorded simultaneously for all three members of the troop by time sampling the activity every five minutes. Activity was scored as "feeding", "travelling", "resting" or "animal not observed". Most of the time the animals were observed through × 10 binoculars; however, they were sometimes close enough (*i.e.* within 10 m) to observe without any visual aid.

Activity was scored as "feeding" when the animal was reaching for a food item, chewing or actively engaged in looking through the foliage for a food item (as determined by the subsequent behaviour). Each food eaten was categorized as fruit, leaf or insect, and "fruit" was further subdivided on the basis of food structure (see Section 2).

The proportion of foods eaten was calculated as (a) percentage of daily activity devoted to feeding, (b) number of food trees, and (c) number of major feeding bouts. The amount of time spent in each feeding tree varied from a few seconds to 52 min. Trees fed in only briefly, between (but not during) time samples, were not included in the sample. There were limited numbers and kinds of trees in which all three animals remained feeding for ten minutes or more. Such a sequence of time samples was called a major feeding bout and was defined empirically as any series of three consecutive time samples in which all three animals were feeding in the same tree.

Summaries were prepared for each animal, each day, each type of activity, each vegetation zone, and each level of the forest canopy. In order to avoid a bias for time of day, summaries were made for the six complete days of data, unless otherwise stated.

The troop was active for slightly less than ten hours every day, from the time of first movement to the time the troop entered the night sleeping tree. In order to standardize the measurement of activity for each day, the "day" was arbitrarily taken as ten hours. Thus, a day consisted of 120 time samples for each animal, or 360 individual time samples for the troop. All percentages of daily activity were based on these time samples. The time sampling began with the first movement of the first animal away from its sleeping position in the morning and ended arbitrarily ten hours later with from 5 to 60 min of "resting" (including grooming) at the end of the day. The home range during the period of the initial study consisted of 20 ha (however, it was larger during the 1975 study).

The study area, in continuous tropical lowland rain forest of the western Amazon basin, consists of gently undulating hills, interspersed with small streams, supporting a diversity of types of vegetation. The local Spanish terminology is adopted for the vegetation zones. (See Revilla, 1974, for a more detailed description of the flora at the study site.) Based on relative openness of canopy and abundance of ground cover, there are two broad classes of forest vegetation at the study site: palm forest and *varillal*. Varillal is non-inundated forest with a relatively closed canopy and reduced ground cover. Found on the tops of hills, it is named after the relative abundance of vertical tree trunks. Varillal comprises 60% of the territory of the troop studied. (In this paper the term "territory" is used to designate the 20-ha area utilized by the troop during the 1974 study.) There are many types of varillal, three of which occur within the troop's territory (Table I and Fig. 1).

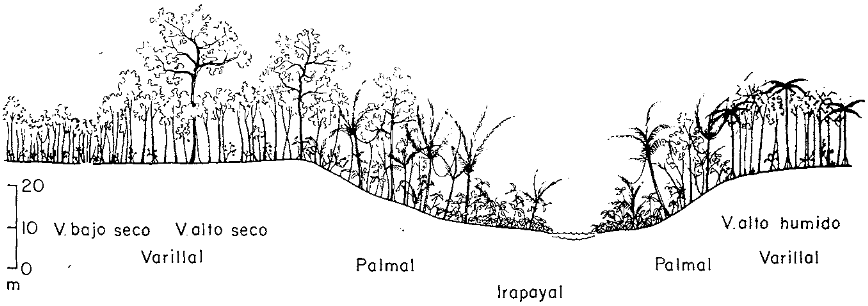

FIG. 1. Vegetation zones in the territory of *C. torquatus* in north-eastern Peru.

(a) *Varillal alto seco*. This is the most frequent varillal and consists of a lower storey (up to 10 m in height) of a few short slender trees, a middle storey (from about 15 to 25 m) consisting of a dense closed canopy, and an upper storey of occasional emergent trees (up to 30 or 35 m) with undivided trunks up to about 20 m height. The ground is a well-drained white arenaceous soil with a thin layer of densely matted roots and dead leaves. Palms are virtually non-existent and the variety of species of trees is great. *C. torquatus* spends more than half of its time in this vegetation zone where emergents such as *Clarisia*, *Virola* and *Brosimum* are among the most important feeding trees.

(b) *Varillal alto humido*. The density of trees is slightly greater than in the varillal alto seco, but species diversity is less, emergent trees are rare and *Euterpe* palms are present. The ground is damp and spongy, apparently with poor drainage. Large numbers of legumes, such as *Pithecolobium* and *Inga*, provide the only fruits eaten by *C. torquatus* in this area.

(c) *Varillal bajo seco*. The density of small trees in this area is very great. (When all trunks greater than 2 cm diameter are included the density is more than 1/m^2.) There are few trees of large diameter, however, the emergent layer is completely lacking, and palms are absent.

Of particular interest to *C. torquatus* here are the large number of berry bushes, including *Psychotria axilaris*, reaching only 3 m in height.

In contrast to varillal in which palms are few or lacking, there are several types of palm forest, named either for the most prevalent species of palm or, when no one species is dominant, simply palmal. Whereas the varillal has a relatively closed canopy, the various palm forests tend to have an irregular canopy with a rather dense ground cover. Two types of palm forest occur within the troop's territory.

(a) *Irapayal.* Along the edges of streams, at the bottom of slopes, the vegetation is irapayal, named after the irapay palm, *Lepidocaryum.* The streams are of clear brown water over white sand, typical of the "black-water" streams described by Janzen (1974). Irapayal consists of a tremendous undergrowth of young irapay palms, lianas, a discontinuous canopy of irregular height and no upper storey emergents. The ground is always damp and may be temporarily inundated after heavy rains. Ungurahui palms (*Jessenia polycarpa*) occur here and offer the only fruits eaten by *C. torquatus* in this area.

(b) *Palmal.* Along the slopes, between irapayal and varillal, lies palmal. The undergrowth is heavy, though not so dense as in the irapayal. The canopy is irregular and discontinuous, but there are occasional emergent trees, and the variety of palms (perhaps 20 species) is greater than in the irapayal. Ungurahui palms are present and other fruiting trees of interest to *C. torquatus* occur here also.

Applying Beard's (1955) classification of Neotropical vegetation-types, the above five vegetation associations have features of both Rain Forest Formation and Evergreen Seasonal Forest Formation. Features of the Rain Forest (Beard, 1944) are present except for the lack of outstanding trees over 40 m in height and the tendency, especially in varillal alto seco, for emergent trees to have broad spreading crowns. These two features are reminiscent of Evergreen Seasonal Forest. The remaining features of Evergreen Seasonal Forest are absent, presumably because rainfall is more constant from month to month than in eastern and central Amazonia (Langenheim *et al.*, 1973).

2. FEEDING BEHAVIOUR

During the initial study, *C. torquatus* spent 26% of its day (2·6hr) feeding, based upon five-minute time samples. The food items eaten included, by percentage of time spent eating each item: 67% fruits, 14% insects, 13% leaves and 6% unknown (Table IV).

Fruits were categorized according to the relative ease in obtaining and ingesting the edible portion. It was hoped that this scheme would facilitate eventual determination of energy harvested as a result of energy expended in food-getting. "Nuts" required considerable preparation to remove the relatively hard edible portion from the tough inedible husk. "Liana nuts" had a brittle shell which was quickly and easily removed to obtain the comparatively soft seed inside. Both kinds of nuts were widely dispersed within a single (usually emergent) tree. "Palm fruit" (of the ungurahui palm) was very hard and required a great deal of incisal action to remove the edible pericarp from the pit. Palm fruits were concentrated on a single inflorescence and many fruits could be eaten without moving from a single feeding location. "Drupes and pomes" consisted of relatively soft edible pulp which was removed by the teeth from a seed or pit. "Berries", like drupes and pomes, consisted of soft edible pulp, but the seed was eaten, too. (Future analysis of faeces will determine whether or not the seed passed through the digestive tract.) "Arilloids" were the edible gelatinous coatings around a seed or seeds; the shell or skin was removed with the teeth and the aril or arilloid sucked from the seed which itself was not eaten. "Seeds" were legumes which required very little preparation to remove the "pea" from the "pod". Since seeds were small and widely dispersed in the canopy, a considerable amount of locomotor activity within and/ or among trees was required to obtain any substantial number of them.

The fruits eaten included, as defined above, 25% nuts, 24% liana nuts, 15% palm fruit, 12% drupes and pomes, 10% berries, 8% gelatinous arilloids and 6% seeds (see Table IV). During the six complete days of time samples upon which these data were based, the animals fed on 66 trees representing 35 different species. This was an average of 11 trees per day (range 6–15). There were 26 species from which they ate fruit and nine species from which they ate leaves. Except for the palm fruit, *Jessenia polycarpa*, represented by nine individual trees, and the legume, *Pithecolobium*, represented by six individual trees, no other species was represented by more than four trees each.

Leaves eaten were mostly immature, or flush, although probably a few mature leaves were also eaten. New growth at the tips of lianas was also included in this category as were leaf petioles which were occasionally selectively eaten.

Insects included ant nests (although it is possible that the nest itself rather than the ants were the food source), as well as insect galls, selectively eaten from leaves, small flying insects grabbed in the air, beetles and hymenoptera larva.

The eating of flowers was not observed during the initial study; however, flowers were eaten during the second study, and comprised less than 0·1% of feeding time samples. No instance was observed of eating invertebrates (other than insects), or other animals or birds' eggs. Water was apparently obtained from fruit and leaves, since no drinking behaviour was observed.

Major feeding bouts accounted for 50% of all feeding time samples (range for the six days, 27 to 60%), and 73% of all fruit-feeding time samples. The day in which only 27% of the feeding time samples was devoted to major feeding bouts was unusual in that a very high percentage of leaves (30%) was eaten that day. There was an average of 3·5 major feeding bouts per day (range, 2 to 5). Of the major feeding bouts, 46% took place in the varillal alto seco, 41% in the palmal and 13% in the irapayal. More than half the major feeding bouts in the palmal and all the major feeding bouts in the irapayal were devoted to palm fruits.

The following 12 fruits were eaten entirely, or almost entirely, during major feeding bouts: *Jessenia polycarpa* (Fig. 2, ungurahui palm); *Clarisia* (Fig. 3) and *Brosimum* (Fig. 4) (Moraceae); *Cordia* (Boragina-

FIG. 2. *Jessenia polycarpa*. Fifteen fruits dropped by *C. torquatus*, showing amount of pulp eaten

FIG. 3. Nut of *Clarisia racemosa*. Husk was broken open by *C. torquatus* and nut was partially eaten before being dropped.

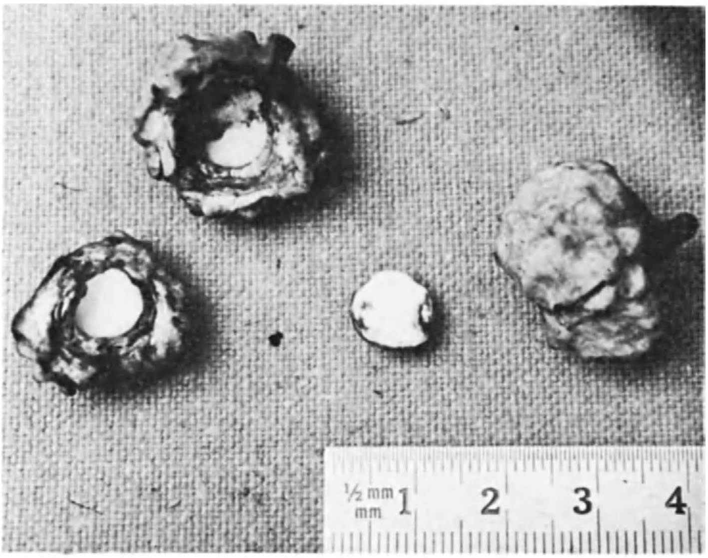

FIG. 4. Nuts of *Brosimum* broken open by *C. torquatus*.

Fig. 5. Fruit of *Rheedia*. Shells were broken open by *C. torquatus* and, after removing the gelatinous arils, they dropped the four seeds. (Scale in mm.)

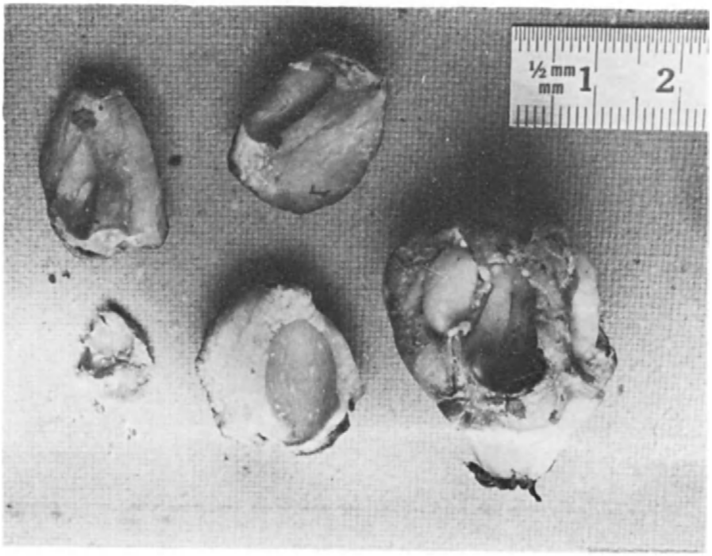

Fig. 6. Fruit of *Tovomita*. The almond-shaped nuts inside the thick pericarp were the edible part.

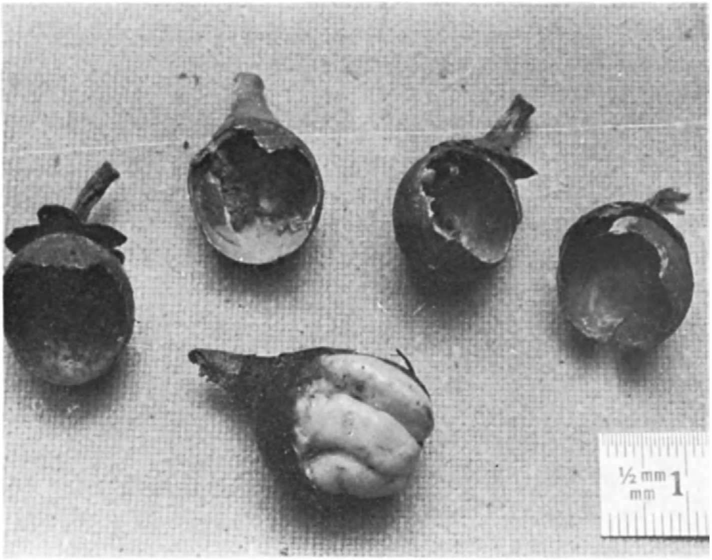

FIG. 7. Liana nuts of *Maripa*. The edible nuts were removed from the top four shells by *C. torquatus*.

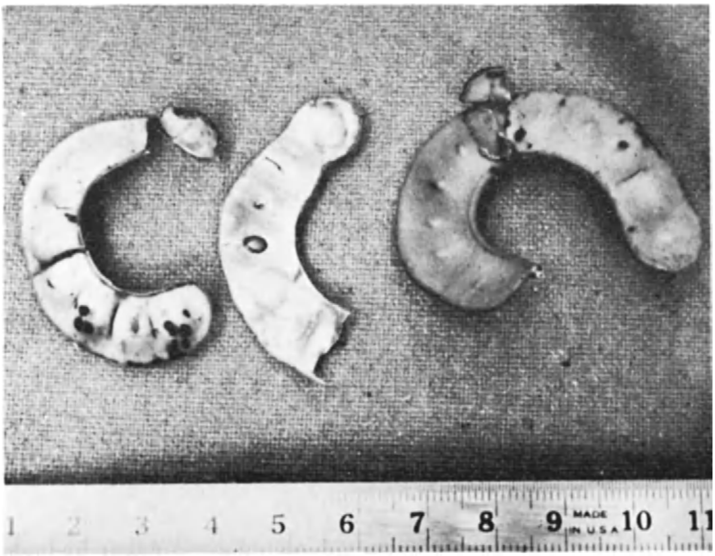

FIG. 8. *Pithecolobium* seed pods. One seed was removed by *C. torquatus* from the pod on the right. (Scale in mm.)

ceae); *Rheedia* (Fig. 5) and *Tovomita* (Fig. 6) (Guttiferae); three different species of *Maripa* (Fig. 7), a liana nut (Convolvulaceae); *Virola* ("cumala") (Myristicaceae); *Machaerium* (a legume); and, *Coccoloba* (Polygonaceae). *Pithecolobium* (Fig. 8), a legume, and *Psychotria axilaris*, a small berry, contributed significantly to the number of feeding time samples, but were not included in major feeding bouts by definition (see Section 1). Major feeding bouts accounted for the bulk of the frugivorous part of the diet, since they included almost all fruit except some berries, arilloids and seeds.

Feeding rates varied for different foods eaten. In major feeding bouts feeding was highly concentrated. Two measures of feeding time were obtained: (a) the time required by an animal to eat one individual fruit, from the time it was placed in the mouth until all chewing stopped and another fruit was searched for; and, (b) time spent in the feeding tree, divided by the number of fruits eaten.

Rates for individual fruits. The average feeding time in minutes for individual *Jessenia* palm fruits was: male, 2·02 ± 0·25 ($n = 11$); female, 1·10 ± 0·16 ($n = 17$); infant, 3·98 ± 0·98 ($n = 4$). The hardness of the fruit probably contributed to the infant's difficulty in eating it; hence his longer eating time. Feeding duration was particularly easy to determine for *Jessenia* because the inflorescence averaged only 18 m from the ground and usually was in full view. Feeding times were more difficult to determine for fruits in emergent trees, but a few determinations were made. The following averages were for adults only. *Brosimum*: 32 ± 4 sec ($n = 5$); *Virola*: 2·12 ± 0·43 min ($n = 3$); *Clarisia*: 2·31 ± 0·92 min ($n = 3$). In both the latter two the husk was very tough and required considerable time to remove to get at the nut inside.

Rates for trees. The "feeding" time spent in a feeding tree included both chewing and looking for edible fruit. For example, a total of 65·6 min was spent in palm trees in four feeding bouts, during which time a total of 98 fruits was eaten by the three animals. Using the rates determined above the troop could have eaten the 98 fruits in 59·7 min if all time was spent chewing; thus, approximately 91% of time in the tree appeared to be utilized for chewing, and about 9% of time reaching for and picking fruit. Most other fruits were considerably more dispersed in the tree than palm fruits, so that a greater proportion of "feeding" time was probably spent looking for edible fruits.

Ripe *Jessenia* fruits weighed about 13·4 ± 0·7 g ($n = 4$) of which 5·0 ± 0·4 g was edible; the remainder, pith. During an average 16 min feeding bout in which 24 fruit were eaten, the troop could have consumed a maximum of 120 g of fruit, or about 66 g by the female, 36 g by the male, and 18 g by the infant. Since most palm fruit was only partially eaten before it was dropped and another picked, this was certainly an overestimate (see Fig. 2).

The average weight of the edible nut of *Clarisia* was 1·4 g ($n = 25$). During a major feeding bout of 24 min each adult animal could eat up to ten nuts or 14 g of food, and the entire troop could thus consume somewhat less than 42 g of food. Unlike *Jessenia* fruit, however, very little of the edible portion of a *Clarisia* nut was ever dropped.

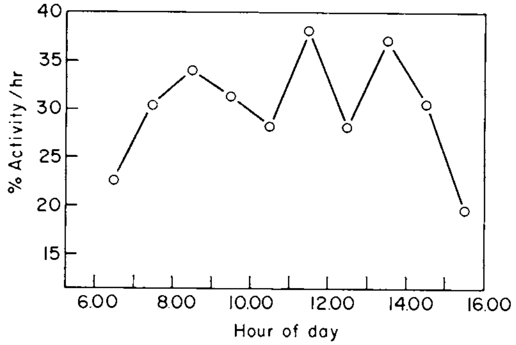

FIG. 9. Hourly variation in feeding activity. Average of time samples for ten days.

The percentage of feeding time samples was calculated for each hour of the day; there was a consistent diurnal pattern of feeding activity. Every day there was a peak of from 40–92% of time samples devoted to feeding during at least one hour, between 7.00 and 9.00, 10.00 and 12.00, and/or 13.00 and 15.00h. Every day there was also an hour of reduced feeding behaviour of 0–17%, beginning at 6.00, 9.00, 12.00 or 15.00h. The average of percentage feeding times for each hour is given for ten days in Fig. 9. (This is an average of six days in July 1974 plus four days in July 1975.) The feeding activity falls off both in late morning as well as in early afternoon; however, the data do not demonstrate a continuous low in feeding activity throughout the middle of the day.

Nearly half of all feeding time was spent in the second storey, roughly between 15 and 25 m in height (Table II). Feeding height depended, however, upon the nature of the food eaten and the vegetation zone. In the varillal alto seco, in which most of the feeding was done, nearly half of the feeding time was in the emergent layer. This was because the dominant fruits in this area (e.g. *Clarisia*, *Brosimum*, *Virola*) grew in tall emergent trees. Feeding upon both legumes and insects in the varillal alto humido was in the second storey only, and the animals appeared

TABLE I

Distribution of vegetation zones in the 20-hectare home range of group I of Callicebus torquatus

	Varillal alto seco	Varillal alto humido	Varillal bajo seco	Palmal	Irapayal	Total all areas
Average number of trees/ha*	400	567	100*	300	467	365
Area, as % of home range	42	8	10	27	14	101
% of day spent by troop in each area	53	9	14	21	3	100
% of feeding time spent by troop in each area	51	6	13	28	2	100
Distribution of fruit trees fed upon (%)	45	2	14	30	9	100
% of feeding time (fruits only)	50	3	9	35	3	100
% of major feeding bouts in each area	46	0	0	41	14	101

* Tree density was estimated in each of the five vegetation zones by a count of all trees larger than 15·25 cm diameter in a 10 × 30 m area. The density of trees was actually greatest in the varillal bajo seco, but most of the trees were less than 15 cm in diameter, and did not reach into the middle storey.

TABLE II

Feeding activity (%) in each canopy level by vegetation zone

	All zones combined	Varillal alto seco	 alto humido	 bajo seco	Palmal	Irapayal
1st storey	29	25	0	98	14	0
2nd storey	45	27	100	2	82	100
3rd storey	26	48	0	—	4	—
Total	100	100	100	100	100	100

Average of six days' time samples.

to move into the third storey there only for occasional resting. In the varillal bajo seco the animals fed mainly on *Psychotria* berries which grew on bushes in the first storey. In the palmal and irapayal most of the feeding was upon palm fruits in the second storey. Liana nuts were often found in the emergent trees in the palmal, but there was no emergent layer in the irapayal. All in all virtually every level of the forest above ground level was utilized for feeding in one area or another. No feeding was observed on the ground, except, occasionally, on insects.

One aspect of feeding behaviour was rather uniform. All three animals frequently fed at the same time and in the same tree upon the same type of food item. In 41% of feeding time samples, all three animals were feeding simultaneously; in 61%, at least two animals were feeding simultaneously. Among the time samples in which only two animals were feeding, the third animal (not feeding) was the female 57% of the time, the male 41% of the time, and the infant 2% of the time. That is, whenever one of the adults was feeding, the juvenile was feeding also.

In most cases (except while feeding on berries in the varillal bajo) the animals adopted a sitting posture while feeding. Usually the animal sat at the fork of two small branches, with feet gripping the branch and tail draped over a nearby branch (see Fig. 12). It reached for a fruit with both hands, and either ate with both hands, or placed one hand on a branch (often the same one grasped by the feet) and ate the fruit with the other.

When feeding on berries in the first storey a different posture was adopted with the torso erect and parallel to the vertical tree trunk (Kinzey, 1975). The hind limbs were drawn up (flexed at hip, knee and ankle), the feet inverted and powerfully adducted with each pollex grasping the vertical trunk. Usually both hands reached toward the berries; one hand held the bush while the other picked the berries and put them in the mouth.

Although most fruit appeared to be placed in the corner of the mouth where canine or premolars apparently tore off the husk or removed the edible pulp, a different method was used to obtain the edible portion of a palm fruit. The fruit was held between the two hands and the upper and lower incisors were used together to scrape the thin layer of hard pericarp from the pith. This behaviour very well may have accounted for the characteristic wear previously noted on *C. torquatus* incisors (see Plate 11 in Kinzey, 1974).

3. TEMPORAL PATTERNING OF FOOD CHOICE

The diurnal pattern of all feeding time samples was presented in Fig. 9. Despite the diurnal variation noted above, the overall distribution of feeding time samples was such that 50% occurred during the first five hours of the day and 50% during the second five hours. The animals appeared to prefer different food items at different hours (see Fig. 10). There was a tendency to eat insects during the middle of the day, to eat leaves toward the end of the day, and to eat fruit both early and late in the day. There did not appear to be any tendency to feed on leaves immediately after feeding on fruit.

There may have been a temporal preference for certain fruits. Although *Jessenia* (palm fruit) and *Maripa* (liana nuts) were eaten at virtually all hours of the day, "nuts" appeared to be preferred early in

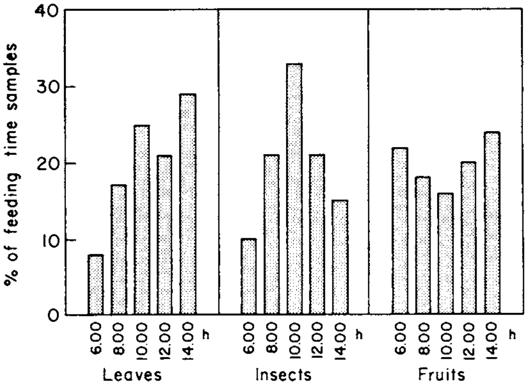

FIG. 10. Variation in food choice, by two-hour intervals. Average of time samples for six days. Intervals begin at 6.00, 8.00, 10.00, 12.00 and 14.00h.

the day. There were four major feeding bouts on *Virola*; all started before 10.30h. There were three major feeding bouts on *Brosimum*; all began before 7.30h. There were four major feeding bouts on *Clarisia*; of these, three began before 8.30h. A considerable body of data was also available on the eating of *Clarisia* in 1975. Of a total of 22 major feeding bouts between 21st June and 3rd August 1975, eight (36%) began before 8.00h; the rest were more or less evenly spaced throughout the day. Despite the increase in eating of fruits after 14.00h (Fig. 10) there were relatively few major feeding bouts between 14.00 and 16.00h. During this time, however, considerable numbers of time samples were devoted to the eating of legumes, especially *Pithecolobium*.

Food choice varied from day to day. For the six days in 1974 the ranges of foods eaten were: fruit, 63–87% per day; insects, 2–25% per day; and leaves, 4–30% per day. There seemed to be a general tendency to eat fewer insects when more leaves were eaten and vice versa.

TABLE III

Percentages of fruits, insects, and leaves eaten on nine consecutive days in July 1975

	Fruit	Insects	Leaves	Unknown	Total
9th July	63	17	9	11	100
10th	85	3	1	11	100
11th	92	4	2	2	100
12th	90	6	4	0	100
13th	70	26	4	0	100
14th	72	14	3	11	100
15th	61	29	9	1	100
16th	74	18	0	8	100
17th	58	38	3	1	100
Average	71	20	4	5	100

Data on feeding are available for nine consecutive days in July 1975 (Table III). The average time spent feeding on these nine days was 28·0% with a range of 10 to 36% per day. The average for eating fruits was 71% (range 58–92%); for insects, 20% (range 3–38%); for leaves, 4% (range 0–9%). The average of unknown food items was 5% with a range from 0–11%. Summarizing, for each of the 15 days more time was spent eating fruits than any other food item; some insects were eaten every day; the animals were observed to eat leaves on every day but one; a greater proportion of time was spent looking for or eating insects than eating leaves.

4. SEASONAL VARIATION

The data were collected during June, July and August; therefore, little can be said at this time about seasonal variability. During these same three months some species of fruit were ripe in 1974 that were not ripe in 1975 and vice versa. An annual pattern of fruiting, therefore, while probably present, is not constant from year to year. Analysis of seasonal variation in feeding will have to await the collection of data at other times of year.

5. SPATIAL VARIATION BY VEGETATION ZONE

Tables IV and V provide the basic data on location of feeding by food type and vegetation zone (compare also Table I). Seventy per cent of all feeding was done in varillal, which comprised 60% of the troop's territory. Most feeding was in the varillal alto seco. Fruits were the preferred food item in all areas except varillal alto humido where only 6% of total feeding time was spent. Leaves were eaten in all areas and they comprised roughly the same percentage (7–20%) of feeding time in each vegetation zone. Insect foraging occurred in all zones except the irapayal, and with very low frequency in the palmal; it was by far the dominant feeding activity in the varillal alto humido.

TABLE IV

Percentage of food items eaten in each vegetation zone

	All zones combined	Varillal alto seco	Varillal alto humido	Varillal bajo seco	Palmal	Irapayal
Fruits	67	67	32	48	87	75
Nuts	25	48	0	0	0	0
Liana nuts	24	20	0	0	46	0
Palm fruit	15	0	0	0	31	100
Drupes and pomes	12	10	0	0	9	0
Berries	10	9	0	82	0	0
Gelatinous arilloids	8	7	0	16	14	0
Seeds	6	6	100	2	0	0
	100	100	100	100	100	100
Insects	14	12	57	30	4	0
Leaves	13	17	7	20	9	17
Unknown	6	4	4	2	0	8
	100	100	100	100	100	100

Average of six days' time samples.

TABLE V

Percentage by vegetation zone of each food item eaten

	Varillal alto seco	Varillal alto humido	Varillal bajo seco	Palmal	Irapayal	Total
Fruits	50	3	9	35	3	100
Nuts	100	0	0	0	0	100
Liana nuts	38	0	0	62	0	100
Palm fruit	0	0	0	80	20	100
Drupes and pomes	59	0	7	34	0	100
Berries	38	0	62	0	0	100
Gelatinuous arilloids	35	0	10	55	0	100
Seeds	41	55	4	0	0	100
Insects	42	22	29	7	0	100
Leaves	58	3	18	18	3	100
Total, all food items	51	6	13	28	2	100

Average of six days' time samples.

The varillal alto seco, in which most of the feeding was done, provided the greatest variety of fruits in the diet. Every type of fruit eaten, except palm fruit and perhaps some species of legume, was found here. As may be seen from Table II, the animals fed in all canopy levels in this part of the forest, although the tough-husked nuts in the emergent trees of the third storey provided the major source of food and accounted for most of the major feeding bouts in this area.

The varillal alto humido appeared to be a preferred location to forage for insects. Even though only 6% of total feeding time was spent here, 22% of all insect-foraging was done here; and 57% of the feeding time samples in this area were for insects. The only fruits eaten in this area were legumes.

The varillal bajo seco was the primary source of berries, especially those of *Psychotria axilaris*. Berries comprised 82% of the fruit-feeding time samples in this area, and 62% of all berries eaten were eaten here. Insect foraging comprised 30% of feeding time samples in this area.

The palmal and irapayal provided the source of palm fruit, *Jessenia polycarpa*. On every occasion that the troop went into the irapayal they fed on the palm fruit, and it seems reasonable to suppose that they went there primarily for that purpose. Palmal was more widely distributed throughout the troop's territory so it appeared that although they may have gone there to seek palm fruits, they also often passed through this vegetation on their way, for example, to a particular feeding tree in the varillal. *Jessenia* trees occurred primarily near streams. Although the animals spent most of their time in the varillal they descended through the palmal on the slopes to the irapayal along the streams to feed upon palm fruit. This occurred almost every day during the season when the palms were ripe.

6. AGE AND SEX VARIATION

The adult male, adult female and infant spent about the same proportion of time feeding. The adult male and female each spent 2·4 hr/day feeding, and the infant, 3·1 hr. The difference between the infant and the adults was not significant ($P > 0{\cdot}10$).

There was no significant difference among the three animals in proportion of time spent feeding on fruits or on leaves; however, the infant spent more time looking for or eating insects than did either of the adults. Of all the insect time samples, 21% were for the adult male, 22% for the adult female, and 36% for the infant ($P = 0{\cdot}07$, Friedman test). Although the infant spent more time looking for insects, it was less successful at catching them and therefore the greater time spent almost certainly did not represent a larger quantity of insects eaten. The infant also took longer to eat individual fruits such as the palm fruit (see Section 2). Thus, it probably obtained less food than either of the adults. It also spent one, two or three periods of up to 1·5 min each day at the female's breast, but it was uncertain whether the infant was actually obtaining milk.

The data on feeding time for palm fruits (Section 2) indicated that the male took longer than the female to eat an individual fruit. Since the size of the dentition is the same in male and female, there does not appear to be any morphological reason for this. It is interesting that male siamangs also took longer than females to eat figs (Chivers, 1974).

7. FEEDING AND RANGING BEHAVIOUR

The 20-hectare territory utilized during the 1974 study was over-laid with a grid of one-hectare squares resulting in 27 squares or quadrats covering the area. (Edge quadrats were partially utilized.) Feeding trees were located in 24 of the quadrats with up to eight feeding trees per hectare. About 74% of the feeding trees were located in only 12 (50%) of these quadrats (Fig. 11a). Trees used during major feeding bouts were even more concentrated: 89% of major feeding bouts were located in 12 quadrats (see Fig. 11b).

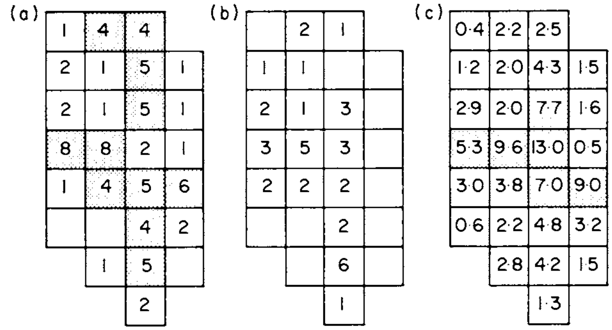

FIG. 11. Territory of *C. torquatus* in hectare quadrats, showing (a) location of feeding trees (no. per ha), shaded area contains four or more feeding trees per hectare, (b) location of major feeding bouts (trees per hectare), and (c) location of paths of travel (% of total length of travel paths per ha), shaded area contains 52% of all travel paths.

The correlation with ranging pattern was high. Of the roughly 10 000 m of path length that the troop was followed, six quadrats contained 52% of the total path length (see shaded area in Fig. 11c) and these same six contained 45% of the feeding trees. In contrast, the same six quadrats contained only one-fourth of the sleeping trees, indicating that location of feeding trees was more important than the location of sleeping trees in relation to ranging pattern.

The effect of feeding on ranging pattern is well illustrated by the following example. On two consecutive days the troop fed in a particular *Brosimum* tree immediately after waking. On the first day the troop slept only 30 m from the *Brosimum*, and moved quickly into the feeding tree upon awaking. On the second day the troop slept 240 m away. Upon awaking they travelled 35 min directly from the sleeping tree south to the *Brosimum* in order to feed there, even though later in the day they moved back as far north as the previous night's sleeping tree.

As the amount of travel per day increased, the resting time appeared to increase also, whereas the feeding time appeared to decrease. The inverse correlation with feeding time was at least in part related to the pattern of feeding in long major feeding bouts, since the amount of feeding time per day was positively correlated with the number of such bouts.

Despite the inverse correlation of daily path length with total daily feeding time, path length was not correlated with feeding time on each individual type of food item (fruits, insects or leaves). One might have expected a larger area covered on those days when insects represented a large proportion of the diet, but this was not the case.

During the 1975 season the home range was expanded compared with

1974, but these data have not yet been analysed in relation to dietary patterns.

8. FEEDING BEHAVIOUR AND SOCIAL BEHAVIOUR

Because the titi monkey travelled in small groups (of two to five) it was usually possible for the entire group to feed simultaneously in one tree. This was certainly true for all the large third storey emergent trees such as *Clarisia*, *Brosimum*, *Virola* etc., and the large lianas such as *Maripa*. It was also true of the *Jessenia* palm, at least for a group as large as three animals. These trees tended to occur singly as isolated trees rather than in groups. The main food sources for which it was not possible that the entire group feed in the same tree were the legume, *Pithecolobium*, and the berry bush, *Psychotria axilaris*. In both these cases, however, the trees grew in clusters and the entire group still fed simultaneously as a close-knit unit while in different trees. Rarely was the troop ever dispersed over more than 20–30 m. The small size of the troop was advantageous in permitting the entire troop to feed together, especially in small trees such as the *Jessenia*.

Within the social group there was a division of foraging roles. The adult female of *Callicebus torquatus* was the animal who searched for new food resources for the day, and who led the group throughout its daily ranging pattern; the male and infant followed. She was usually the first animal of the troop to enter a feeding tree, and similarly the first one out of the tree at the end of a feeding bout. In most feeding situations, whether in a single large emergent tree or in a cluster of *Pithecolobium* trees, the male and juvenile always sat near each other and the female sat some farther distance away from them. Even as the troop moved about the tree or trees, this set of relative distances was maintained.

An important contrasting role of the adult male was to care for the infant. He and the infant always fed close together, but even when not feeding they were usually close together. The male was especially tolerant of the infant. This was important in relationship to feeding since the male frequently allowed the infant to take food from him that was partially eaten.

9. DISCUSSION

Callicebus torquatus is primarily frugivorous, and the pattern of eating fruits differed from that of eating insects and leaves. Fruits were eaten largely in concentrated periods of time, "major feeding bouts", generally three to four per day, with all animals in the troop feeding simultaneously. There was sometimes a directed effort to eat at a particular fruit tree, as evidenced by long rapid travels toward particular feeding trees. No similar long movements were ever made immediately prior to reaching sleeping trees. There was a pattern to eating the most preferred food item: nuts of emergent trees such as *Clarisia* and *Virola*. They were most frequently eaten during the first two hours of the day. Was this an attempt to try to obtain the preferred food source first, even if it meant travelling a long distance immediately upon awaking?

Palm fruits provided another major item in the diet, but feeding on palm fruits was not concentrated at any particular time during the day. This may have been related to the dispersion of palm trees around the periphery of the troop's territory. Only when they were near irapayal did they appear to make a foray into the palm forest and feed on *Jessenia*. Since the palm trees were located near streams and *C. torquatus* spent most of its time on tops of hills and slopes, the irapayal with its ungurahui palm trees formed the boundary (at least on the west) of the troop's territory. (During the 1975 season the ungurahui palms were still not ripe in August and at no time during the 1975 season did the troop venture into the irapayal.) The palm fruit may also have been important as a source of protein since *Jessenia* nuts were relatively high in protein (Snow, 1962). (Nutritional analysis of the other food items is not yet available.) It is perhaps relevant in this regard that there was an inverse correlation between the amounts of time spent eating insects and palm fruits.

The feeding behaviour of *C. torquatus* was similar to that observed in the spider monkey in certain types of fruit trees. In *Ateles belzebuth*, in contrast with *Alouatta seniculus*, *Saimiri* and *Cebus* (Klein and Klein, 1975), rarely were two animals seen feeding on different food items at the same time. They fed in small groups when the dominant fruiting trees, such as palm fruit (Klein's type V trees), were widely dispersed and fruited over long periods of time. *Ateles* differed from *Callicebus* in aggregating in large groups when feeding in other types of trees.

In contrast to the concentrated pattern of feeding on fruits, leaves were eaten opportunistically, in relatively equal proportions in each of the vegetation zones, and never in major feeding bouts. The animals never appeared to make a long directed movement toward any tree just to eat leaves. Unlike the siamang described by Chivers (1974) there was no tendency to eat leaves immediately after eating fruit. However, there was a tendency to eat leaves late in the day (Fig. 10). Although fruit and/or insects were sometimes eaten after the last feeding of leaves, there was no instance of a major feeding bout after the last leaf-eating episode in the day.

Insects, like leaves, appeared to be eaten somewhat opportunistically; however, there was a definite preference for insects in certain parts of the forest, especially in varillal. More than half the feeding time in the varillal alto humido was devoted to eating insects. Few insects were eaten in the palm forests. Whether reduction in insect foraging in the palm forests was due to a reduction in incidence of insects there, to competition from other insectivorous species, or to lack of preference is not known.

There are some data available on feeding in captivity. Dr William Mason has successfully managed a colony of titi monkeys, including both *C. moloch* and *C. torquatus*, since 1965 (Lorenz and Mason, 1971). The average quantity of food provided was approximately 250 g per animal per day. Using the data on weight of food consumed during major feeding bouts (Section 2), it appeared that an adult female might have obtained about 60% of that amount (150 g) in 3·5 major feeding bouts consisting of 2·0 bouts of palm fruits and 1·5 of *Clarisia nuts*. This was probably quite adequate, since about 50% of feeding time was during the major feeding bouts. If the observations of eating times were anywhere near representative, it is difficult to understand how the adult male obtained a sufficient quantity of food. Does the male possibly have a lower energy requirement? According to Lorenz and Mason, "individual and day-to-day variations in food preferences are clear. We suspect that some variation in the food offering may be necessary to sustain adequate food intake in *Callicebus*". In the wild *C. torquatus* had considerable day-to-day variation in kinds of food eaten. Lorenz and Mason noted that "water intake is low" which also accorded well with the naturalistic data.

To the best of my knowledge there are only three other references to the diet of *C. torquatus* in the wild. Izawa (1975) observed two animals feeding along the Rio Caqueta in south-east Colombia. One animal was feeding on leaves and the other on the "thumbnail orange-coloured juicy fruit" of a large Cafeto tree. The stomach contents of two adults were examined. One had only fruit and the other had both fruit and leaves in the stomach. Moynihan (1976) observed that *C. torquatus* in the Putumayo region of southern Colombia fed on the pulp of *Jessenia polycarpa*. Hernandez-Comacho and Cooper (1973) observed *C. torquatus* feeding on fruit and insects in Colombia. These data do not contradict the quantitative data herein presented.

FIG. 12. *Callicebus torquatus* feeding on berries of *Psychotria axilaris*.

10. SUMMARY

1. The diet and feeding behaviour of a troop of three *Callicebus torquatus torquatus* were studied in north-eastern Peru. On the tops of small hills the typical *varillal* vegetation zone, where the animals spent most of their time, contained approximately 400 trees per hectare, providing a continuous canopy between about 15 and 25 m high. The animals fed in about 1% of these trees, many of them emergents above the continuous canopy, during the six full days of observation in July and August 1974.

2. An average of between 2·5 and 3 hours per day was spent feeding. The diet was primarily frugivorous with about 70% of feeding time devoted to fruits. The remaining feeding time was divided between insects and leaves. More time was usually spent foraging for insects than eating leaves. Major portions of the frugivorous portion of the diet consisted of nuts with a relatively tough inedible covering or pericarp, and ungurahui palm fruits. Leaves appeared to be eaten opportunistically in all areas of the forest; insects were consumed primarily in certain areas of vegetation. Feeding occurred at all levels of the forest above the ground but, depending upon the nature of the food source, different levels of the canopy were preferred in different vegetation zones. All animals of the troop tended to feed together, most often in the same feeding tree. Rarely were two animals in the troop observed simultaneously eating different food items. Feeding on fruit was done primarily in blocks of time of from 10 to more than 50 min, termed "major feeding bouts". There were from two to five major feeding bouts per day, usually one in the early morning, one in late morning, and one in the afternoon.

3. Food choice varied from day to day. Combining data from 15 complete days of observation in 1974 and 1975, the amount of time devoted to feeding on fruits varied from 58 to 92% of feeding time per day.

4. Since data were collected only during June, July and August 1974 and 1975, seasonal variation has not yet been studied.

5. Seventy per cent of all feeding was done in varillal which comprised 60% of the troop's 1974 territory of 20 ha. In the palm forests (palmal and irapayal) insects comprised a very small portion of the diet and ungurahui palm fruits were an especially important food source.

6. There was relatively little difference among the adult male, adult female, and infant in amount of time devoted to feeding. How-

ever, the male took longer than the female to eat certain individual fruits.

7. Feeding pattern was correlated with ranging pattern. Fifty-two per cent of the troop's movement occurred within 6 ha. These same 6 ha contained 45% of the feeding trees but only 25% of sleeping trees.

8. A major role of the adult female was to search for food resources; the male and infant followed.

9. The location of ungurahui palm trees marked the approximate (western) boundary of the troop's territory during the duration of the (1974) study.

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Feeding Behaviour of the Colombian Spider Monkey

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1. INTRODUCTION

With the exception of C. R. Carpenter's early report (1935) on a natural population of *Ateles geoffroyi* Kuhl 1820, little first-hand information on the feeding habits of spider monkeys had been published before the onset of our field study of *A. belzebuth* E. Geoffroy 1806, in 1967.

Carpenter described *A. geoffroyi* as frugivorous, and an estimated 90%

FIG. 1. Group of individually identifiable spider monkeys.

of the items they consumed during his field observations of 48 days were said to be either fruits or nuts. The stomach and intestinal contents of collected specimens were used to verify and extend the feeding data obtained by behavioural observations; however, the contents of only one digestive tract were reported. It contained the seeds of a single variety of fruit, illustrating that adult spider monkeys characteristically swallow the large seeds and adhering pulp of many of the fruits they eat, and supporting Carpenter's belief that at times spider monkeys may be subsisting on just one or two kinds of fruit. Few data on substances other than fruit were reported by Carpenter, although he inferred that adult insects and larvae might also have been eaten. This inference, despite its reiteration by Wagner (1956), Hill (1962) and Richard (1970) has not been supported by any real evidence and is discussed below.

In 1969 the first of a series of excellent reports by Hladik and Hladik (1969, and Hladik *et al.*, 1971a) on the comparative feeding behaviour of four neotropical taxa were published. These included, among other things, detailed protocols of feeding behaviour, and quantitative and chemical analyses of many of the foodstuffs used by a group of *A. geoffroyi* which had been released on Barro Colorado Island (BCI) in 1960–61. Many of their results are discussed below in conjunction with our own observations.

2. STUDY AREA, DURATION AND GENERAL OUTLINE OF SPIDER MONKEY POPULATION DENSITY AND SOCIAL ORGANIZATION

Our data on the feeding behaviour of the Colombian spider monkey were collected between October 1967 through November 1968 on a flood plain forest of the Guayabero river within the current boundaries of the Colombian National Park, La Macarena, about 2°30′ N of the equator (see Fig. 2). Our actual study site was a very small portion of what was then a much larger, generally evergreen, forest broken only by natural waterways, lakes, marshes and small tree falls. Most of the study site terrain was inundated annually for periods of time varying from about two to 16 weeks. In 1968 flooding was severest in the months of July and August.

As the result of over 600 hours of behavioural observations by L. Klein, and 500 hours by D. Klein, it was discovered that three distinct and mutually exclusive social networks of spider monkeys (about 20 adult animals) ranged over the approximately 8 km^2 sample

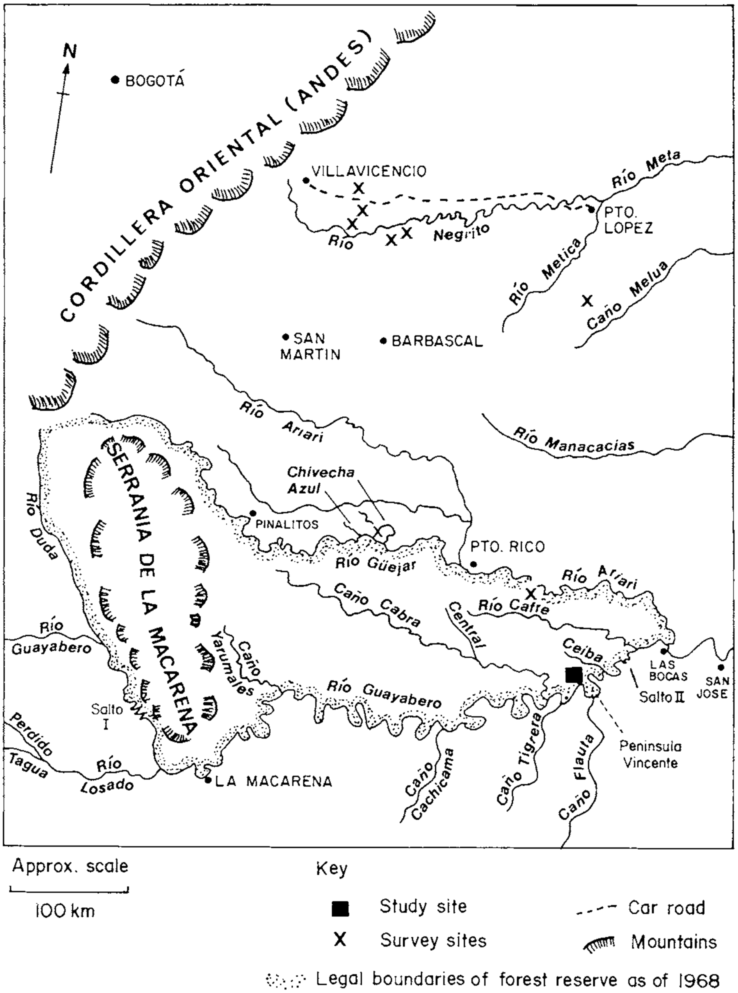

FIG. 2. Location of study area.

plot, and were almost always dispersed into small subgroups averaging over the year about 3·5 animals. Temporarily isolated adults of both sexes were frequently observed, as were temporary groupings of 2–20 spider monkeys.

Distances between subgroupings and isolates of the same social group were known to have ranged between 180 m to 1·5 km, and to have persisted for periods at least as long as two days. There was no indication that subgroups assembled into larger units or reassembled at specific "lodge" trees before nightfall (cf. Carpenter, 1935). (For greater detail, see below and Klein, 1972.)

3. FEEDING BEHAVIOUR

3.1. Study Methods

Many methods are available for studying the natural feeding habits of free-ranging animals (Elton, 1927; Dasmann, 1964; Leopold, 1933; Schaller, 1965; Korschgen, 1969). The methods we used had to be compatible with continuous observations of social behaviour. Consequently the data are based almost entirely upon observations of feeding animals and occasional checking of observations with examinations of fresh faecal material to ensure that the feeding observations were qualitatively and quantitatively representative with what the animals were actually ingesting. From our experience with captive spider monkeys we were able to ascertain that ingested solids, i.e. seeds and rinds, pass through the intestinal tract as solid faeces from four to 12 hours after consumption.

Attempts were made to collect specimens of all of the fruits, leaves and wood which were observed to have been eaten by *Ateles belzebuth.* Items eaten by other primate taxa and birds were also collected when feasible. (All specimens collected and preserved were delivered to the Herbario del Instituto de Ciencias Naturales de la Universidad Nacional de Colombia.)

Recording the number of simultaneously feeding spider monkeys and timing the duration of their feeding whenever it occurred was standard procedure. In those instances in which the animal was encountered while feeding, the initiation of feeding was considered to occur at first sighting. To facilitate computation and subsequent comparison, these observations were divided into feeding bouts: the length of time a single animal was recorded eating continuously on a single type of substance. Individual bouts were considered to have ended when the spider monkey (a) clearly ceased eating; (b) was observed engaging in an activity incompatible with feeding, e.g. resting; (c) moved into another tree; or (d) was clearly observed eating a different substance. When animals were not fully visible, the cessation of branch and leaf movements and moving into another tree were used to determine feeding termination. Moving out of the tree they had been feeding in followed shortly after the termination of feeding in almost all fully observed cases. On only three occasions were adult spider monkeys observed eating more than one type of substance successively in the same tree.

In this latter respect they differed from the insectivorous, foraging *Saimiri sciureus* Linnaeus 1758 and *Cebus apella* Linnaeus 1755 who were frequently observed successively eating fruit and catching insects in the same tree.

Out of the 2156 feeding bouts recorded, scoring errors as large as 5–10 min could not have been a factor in more than 40 of the bouts. These were recorded during inclement weather or when an unusually large number of animals were rapidly moving into and out of trees. Feeding bouts of 1 min or less were all treated quantitatively as if they were 1 min long. There was a considerable degree of variability from under 1 min to as much as 45 min.

Except where otherwise indicated, conclusions concerning the importance of particular items and classes of food in this report have been arrived at on the basis of *relative percentage of time eating different foods*, although this criterion is scarcely comprehensive and for some purposes inappropriate. (For further discussion see Klein, 1972.) The percentages were calculated by multiplying the number of *A. belzebuth* observed eating a particular substance by the amount of time they were observed eating it (animal-feeding minutes) separately for each month during the last 11 months of the study, and for intervals of approximately two weeks. Only the feeding data of the terminal 11 months of the study have been treated quantitatively because it was only during this period that the observers were able effectively to follow *A. belzebuth* for long periods of time.

3.2. Results

Table I shows the relative amounts of time between 1st February 1968 and 22nd November 1968 that *Ateles belzebuth* were observed eating either (a) fruit, (b) leaves or buds of trees, (c) leaves or stems of epiphytes, (d) dead and decaying wood, (e) flowers, (f) insects, animals or eggs. These measures clearly revealed that the animals spent most of their feeding time (83%) eating fruit. This is very close to Carpenter's (1934) estimate that about 90% of the diet of *Ateles geoffroyi* was composed of fruit or nuts and the Hladiks' estimate (1969) of 83% by weight. The remaining percentage of feeding time was spent on tree leaves and buds (5%), epiphytic leaves and stems (2%), and dead or decaying wood (10%). Flowers were observed to have been eaten on only two occasions by *A. belzebuth* juveniles. No clearcut instance in which either invertebrates, mammals, birds, reptiles or amphibians, or the eggs of insects, amphibians or birds were eaten was observed. (See below for further discussion.)

TABLE I

Relative amounts of time spent by A. belzebuth *between 1st Feb. and 22nd Nov. 1968 eating fruits, leaves, stems, flowers and wood*

Types of edible substance	% of total feeding time observed consuming
Fruit	83
Tree leaves and buds	5
Epiphytic leaves and stems	2
Dead wood	10
Flowers	<0·1
Insects, animals and eggs	0

3.2.1. *Feeding heights and sites*

Thirty-one of the 33 species of fruits eaten frequently were borne on trees which varied in height from 15 to 45 m, and in crown width from approximately 8 m to more than 60 m in diameter. In almost all cases fruit was borne at least 12 m from the ground. *A. belzebuth* were never observed to feed on fruits that had either fallen to the ground or were less than approximately 8 to 9 m above it. The height they fed at above 10 m depended almost entirely upon the plant variety being utilized and was usually between 15 and 35 m from the ground.

3.2.2. *Fruit maturity*

Almost all of the fruit *A. belzebuth* were observed to eat appeared either from colour and/or taste to be fully mature. The ratio of observed animal feeding time devoted to ripe versus unripe fruit was more than 100 to 1. Immature fruit was eaten in quantity only during periods in which ripe fruit was scarce or non-existent. Moreover, when ripe and unripe fruit was available within the same tree for at least some tree species, a considerable amount of selective feeding appeared to be occurring even when the fruit was tiny and densely clustered (e.g. *Hyeronima* sp. and *Brosimum* sp.). Although the amount of fruit dropped varied with plant species, it was clear that in at least some cases it was principally the unripe fruit of a cluster that fell to the ground.

3.2.3. *Fruit size*

Fruits eaten frequently by *A. belzebuth* ranged in size from less than 3 mm in diameter, e.g. *Hyeronima* sp., to more than 50 mm, *Rheedia madrono* Planch and Triana, to certain *Inga* species whose fruits frequently exceeded 300 mm in length. This wide range in fruit sizes meant that *A. belzebuth* also shared and may have competed with arboreal feeding vertebrates of disparate sizes represented at the extremes by birds as small as *Forpus* spp. parrots (12–15 cm long) and mammals as large as coatimundis, *Nasua narica* (approximately 0·6 m from head to base of tail).

3.2.4. *Fruit structure and feeding techniques*

Almost all of the fruits frequently eaten by *A. belzebuth*, with the exception of the genus *Ficus*, contained a single seed or seeds clearly distinguishable and harder than the surrounding flesh, pulp, juice or aril. In addition, about 50% of the fruit had a leathery or hard outer covering (pericarp). Adult *A. belzebuth* usually swallowed the seeds of these fruits along with the surrounding softer material, and the intact and recognizable seeds comprised in most cases the major part, by volume at least, of their faeces. On the other hand, the hard outer coverings were either split apart, or bitten into and then dropped. In contrast, juvenile spider monkeys spat out the seeds of fruit larger than 20 mm diameter, eating only the flesh and pulp. While most figs were eaten whole, the skins of one large banyan-type fig tree were spat out both by adults and juveniles after the flesh and seeds had been removed. Sorting of skin from flesh in these cases occurred orally, without the use of fingers.

Spider monkeys frequently ingest large quantities of food within relatively brief periods of time. One spider monkey, for example, was observed to have eaten about 100 *Pouteria* fruit, about 20 to 25 mm in diameter, within a seven-minute period.

3.2.5. *Palms and figs*

Several types of palm fruit were an important part of the diet of *A. belzebuth*. In certain periods (see Table III and Appendix) from 20 to 60% of their feeding time was spent eating palm fruit, and some palm fruit was eaten throughout the year. In number, palm trees were not a prevalent part of the forest's flora and tended to be evenly dispersed (see Klein, 1972). Moreover, individual trees did not bear particularly large numbers of ripe fruit at any one time. The intensive use of palm fruit tended to coincide with periods in which other types of fruit were either scarce or non-existent.

In contrast to palms, the fruit of fig trees (*Ficus* spp.) appears to play a relatively less important role in the diet of *Ateles*. Certainly in comparison to *Alouatta* (see below) most types of figs constituted a far smaller part of *Ateles*' feeding time, and on occasion were among the few fruits actually observed to have been ignored. A similar feeding difference is characteristic of the two genera on BCI (Hladik and Hladik, 1969). Of additional interest is the fact that the genus *Ficus* with respect to the characteristics of (a) tree size, (b) distribution of fruit within the tree, and (c) length of fruiting period, is radically different to palms. In general, those figs that by growth pattern are or become trees (strangler figs) are usually among (a) the largest trees in the evergreen forest, (b) bear large quantities of fruit throughout their crowns or at least on many of their branches, and (c) bear ripe fruit over an extremely brief period, generally of the order of three to four days (Hladik and Hladik, 1969; Condit, 1969; L. Klein, pers. observ.).

3.2.6. *Daily variety*

Individual spider monkeys were usually observed to have eaten two or more varieties of ripe fruit on any one day. On those days in which we were able to follow and observe spider monkeys for periods of four or more hours, on only one out of 67 such days were they observed to have eaten just one variety of mature fruit (cf. Carpenter, 1935). On the remaining 66 days of four or more hours of observation, the number of different taxa of mature fruit eaten ranged from 2 to 9 with a median of 3·3 varieties (see Table II).

TABLE II

Rates at which a different variety of fruit was utilized per minute of daily observation time for approximately 2-week intervals between 1st Feb. and 22nd Nov. 1968

Inclusive dates	No. of actual taxa utilized	Sum of the no. of different fruits observed eaten each day	Minutes of observation	Rate at which fruit taxa eaten varied per minute of daily observation time (no. fruit/min)
1–14 Feb.	9	46	3252	1 per 71
15–29 Feb.	11	45	4252	1 per 94
1–12 Mar.	13	35	3679	1 per 105
1–13 Apr.	15	45	3822	1 per 85
18–30 Apr.	14	27	2410	1 per 89
1–14 May	12	34	2480	1 per 73
16–27 May	10	24	1267	1 per 53
18–24 June	4	5	245	1 per 50
5–13 Sept.	5	13	1818	1 per 140
16–29 Sept.	7	24	2329	1 per 97
2–14 Oct.	5	12	2314	1 per 193
15–22 Oct.	8	14	2175	1 per 155
11–22 Nov.	13	22	2360	1 per 107

TABLE III

Percentage of time spent in each month feeding on different foods

	Feb.	Mar.	Apr.	May	June*	July*	Aug.*	Sept.	Oct.	Nov.
Total wood, fungus, bark	9	12	10	18	2	—	—	>1	1	—
Total leaves, shoots, buds	4	8	3	4	—	—	—	12	17	22
Total fruit	87	80	87	78	98	100	—	87	82	78
Palms	>1	>1	>1	>1	>1	61	26	30	2	4
Figs	7	—	8	—	—	—	—	—	6	13
Spondias sp.	—	—	>1	4	—	—	—	—	—	—
Xylopia	—	—	—	—	—	—	—	>1	2	—
Protium or *Bursera*	5	15	7	—	—	—	—	—	—	—
Licania	7	27	—	—	—	—	—	—	—	—
Hyeronima	50	29	>1	—	—	—	—	—	—	—
Xylosma or *Homalium*	—	—	—	—	—	—	—	—	—	37
Calophyllum	—	—	—	—	—	—	—	>1	4	—
Rheedia sp.	—	—	3	>1	—	—	—	—	—	>1
Licaria	—	—	—	>1	30	—	—	1	—	—
Inga spp.	—	—	2	5	—	—	—	—	—	—
Brosimum spp.	—	—	>1	—	—	—	—	45	67	14
Pseudolmedia spp.	10	5	1	—	—	—	—	—	—	—
Virola spp.	5	3	9	3	—	—	—	2	—	—
Heisteria	1	—	—	—	—	—	—	—	—	—
Chrysophyllum	—	—	—	11	50	31	84	—	—	—
Pouteria	—	—	47	44	18	—	—	—	—	—
Other†	2	1	10	10	>1	8	>1	7	1	10

* Very few observations.

† Includes fruits eaten in very small quantities and fruit which was not identified.

Over the entire year, an average rate of one different taxa of ripe fruit per 95 minutes of daily observation time was recorded, but the variety of ripe fruit available and eaten by *A. belzebuth* varied from period to period. The diet of *A. belzebuth* at its most monotonous level consisted of one variety of ripe fruit per 195 minutes of daily observation time per animal; their diet at its most diverse level consisted of one new variety of ripe fruit approximately every hour. Generally, since within the category of ripe fruit individual spider monkeys appeared to try to maximize the number of varieties eaten in any one day, dietary diversity appeared to be limited by the number of tree taxa bearing ripe fruit at different times of the year.

3.2.7. *Leaves, stems and buds*

A. belzebuth spent about 7% of their feeding time consuming leaves, stems or buds. About one-third of this was feeding on the vegetative structures of plants which were either parasitic, epiphytic or tree climbers rather than the leaves, buds or stems of the trees themselves. The plant which was most frequently and consistently eaten was a variety of *Sphaeradenia* which appeared to climb exclusively on palm trees. A leaf and stem were usually torn from the palm trunk and the stalk then chewed from the bottom up. Although one of the most important non-fruit food sources for spider monkeys, *Sphaeradenia*, was rarely eaten for more than one minute at a time. The longest observed bout persisted for three minutes. The stems of this plant were estimated to comprise 0·3% of the diet of *A. belzebuth* over the year. Of the remaining 5% of their feeding time, about one-half of it was spent on either leaf buds, or non-turgid new leaves. Proportionately more time (up to 22%—see Table III) was spent by *A. belzebuth* feeding on leaves when ripe fruit was either scarce, or restricted in variety.

3.2.8. *Wood*

A. belzebuth spent approximately 8·81% of their feeding time eating decayed wood, 0·7% eating bark and twigs and approximately 0·11% eating the outer covering of abandoned tree termitaria. On some of these occasions a few termites may have been ingested but observation suggested that this was probably coincidental since pieces of wood were frequently discarded which contained many termites, and termites moving along the tops of branches were never observed to have been eaten. Dead wood which definitely contained no termites was eaten most often.

Wood eating was generally confined to specific decayed or decaying trees, and several were known to have been used repeatedly by the same animals for periods at least as long as a month. Several looked as if they might have been used for years, and their remnants were no more than 25 to 35 feet above ground level. Although specific trees were used repeatedly, periods of utilization appeared to depend upon whether subgroups of spider monkeys were spending significant amounts of time feeding from nearby fruiting trees.

3.2.9. *Insects*

In this study, spider monkeys were not observed to eat birds, bird eggs, insects or arachnids, and none of the faeces inspected contained insect fragments, egg shells or vertebrate bones. This finding contrasts with previous reports of the feeding behaviour of *Ateles* (Carpenter, 1934; Wagner, 1956; Hill, 1962; Richard, 1970). However, evidence of spider monkeys eating animal foods in these studies is largely circumstantial and may, at least in part, be based on misinterpretation of the animals' behaviour. For example, Richard (1970) observed *A. geoffroyi* licking dry leaves and suggested that they were eating insects, while Carpenter (1934) describes the same species "searching through leaves, under bark and dead limbs, apparently for larvae and insects". We frequently observed adult spider monkeys sniffing or licking urine from the tops of leaves (Klein and Klein, 1971; Klein, 1971). In addition, dead wood and bark were eaten in substantial amounts and were frequently handled. It seems unlikely that the absence of records of insect-eating in spider monkeys in this study was a result of observation conditions since sympatric species (*Saimiri sciureus* and *Cebus apella*) were frequently observed investigating places where small invertebrates are likely to be found, and catching, killing and ingesting insects and arachnids.

3.3. Discussion

3.3.1. *Feeding heights and sites*

Our results on feeding heights are somewhat at variance with those who have observed *A. geoffroyi* primarily on BCI. Richard (1970), for example, notes that *A. geoffroyi* spend about 2% of daylight time locomoting "bipedally" on the ground, and Eisenberg *et al.* (1972) diagram "average stratum heights" for neotropical monkeys which place *Ateles* clearly below *Alouatta*, and not much above *Cebus capucinus*. A similar diagram appears in Hladik and Hladik (1969). These estimates, if applied to natural populations, are erroneous, and their implications concerning niche separation and overlap are misleading.

At the study site, forest level differences between diurnally sympatric taxa were rarely apparent when they were feeding on the same substance. Where differences in height above the forest floor occurred, they were in large measure, although not exclusively, the consequence of feeding and searching for different food items. For example, howler monkeys, *Alouatta seniculus* Linnaeus 1776, were never observed feeding on palm fruit (see below); therefore they spent relatively less time than spider monkeys between 15 and 21 m from the ground. On the other hand, spider monkeys were not observed to eat either frog's eggs or cicadas which occasionally brought *C. apella* and *S. sciureus* as close as 6 to 8 m to the ground.

3.3.2. *Fruit maturity*

In general, *A. belzebuth*, particularly in comparison with *C. apella*, did not appear to disturb potentially edible but unripe fruit in the process of obtaining and consuming ripe fruit. There were, of course, occasions when an entire branch broke off as the animal drew a branch or twig containing fruit to it. These occasions were, however, infrequent and sometimes produced a "surprise" reaction by the feeding animal (Klein, 1972). The fact that flowers were so infrequently eaten, and then only by juveniles, reinforced the impression that the undisturbed and non-agonistic behaviour of *A. belzebuth* did little to adversely affect the eventual production of ripe fruit in those trees in which they fed, rested or moved through.

In comparison, on several occasions both adult and juvenile *A. seniculus* and *C. apella* were observed consuming the flowers of trees of which both they and *A. belzebuth* also ate the fruit (e.g. *Euterpe* sp. and *Iriartea* sp.). The observations on this aspect of the fruit eating behaviour of *A. belzebuth* accords with the observations by Hladik and Hladik (1969, pp. 72, 74) of *A. geoffroyi* on BCI, despite the fact that the released spider monkeys there continue to utilize significant amounts of pilfered food.

3.3.3. *Palms and figs*

The different usage of fig and palm fruits between *Ateles* and *Alouatta* may have a physiological basis. Several types of figs are known to be very high in nitrogen (Hladik and Hladik, 1969; Hladik *et al.*, 1971a) and a proteolytic enzyme, ficin (Condit, 1969). On the other hand, the flesh of many palms contains exceptionally large amounts of vegetable oils (Corner, 1966). The dietary difference between *Ateles* and *Alouatta* with respect to figs and palm fruits illustrates one of the dangers of labelling primates in terms of gross dietary categories such as frugivorous, insectivorous, etc. Furthermore, it also illustrates one of the problems with using a more refined approach based on percentage differences as long as categories as gross as "fruits", "leaves", "insects" etc. continue to be used. Such categories may be overtly simple and even misleading when more specific dietary substances are the actual differentiating factors. Although howler monkeys are definitely more herbivorous (folivorous), and less frugivorous than spider monkeys, they also eat more immature fruit and ripe figs than spider monkeys. Overlooking differences of this sort is bound to make the task of understanding relationships between social behaviour and ecology more difficult, if not impossible.

3.3.4. *Leaves, stems and buds*

Relative to respective amounts of observation time, *Alouatta seniculus* were observed feeding on leaves much more frequently than *Ateles belzebuth.* It was not possible to make any estimates on the amount of leaves, stems or buds in the diets of *Saimiri sciureus* or *Cebus apella. C. apella*, however, were observed eating leaves, and on many occasions the stalks (petioles) of palm leaves. In contrast, spider monkeys were not seen eating any vegetative palm tree parts, although on one occasion an adult was observed behaving in a way which suggested that she may have been drinking liquid coming from a bruised palm bud.

Superficially, the estimate of the percentage of leaves, stalks and buds in the diet of *A. belzebuth* appear to be somewhat smaller than the estimates of Hladik and Hladik (1969) for *A. geoffroyi* on BCI. It is impossible, however, to determine the actual degree of discrepancy between their estimate of 20% and the proposed estimate of 7% since Hladik and Hladik included bark, wood, latex and flowers in the same category as leaves and buds. The estimates are actually quite close if the same items they included in a single category are combined, since about 10% of the total observed feeding time of *A. belzebuth* was spent consuming decayed and decaying wood. Spider monkeys spent about 17% of their feeding time collectively on leaves, stems, buds and wood at the study site; about 20% on BCI.

The percentage by weight estimates of Hladik and Hladik (1969) for similar substances in the diets of *Alouatta palliata* Gray 1849 and *Cebus capucinus* Linnaeus 1758 were, respectively 40 and 15%.

3.3.5. *Wood*

Several decaying tree remains utilized as food by spider monkeys were also used by groups of howler monkeys, sometimes simultaneously with spider monkeys. However, neither *Cebus apella* nor *Saimiri sciureus* were observed eating wood from similar or the same trees, despite the fact that on several occasions they were known to have passed close by. Hladik and Hladik (1969) note examples of bark eating in *A. geoffroyi* Kuhl 1820.

Although several other non-human primates have been observed eating significant quantities of decayed wood (see e.g. Schaller, 1965; Bernstein, 1968; Ripley, 1970) neither the nutritional value nor dietary basis for these behaviours has been investigated.

3.3.6. *Insects*

The field observations indicated that *A. belzebuth* rarely if ever sought out and consumed insects or arachnids. If any animals were eaten at all, they must have been inconspicuously tiny, immobile and eaten in exceptionally small quantities at any one time. Observations on several taxa of captive, but wild born, neotropical primates support the field observations. In comparison to *Cebus apella*, *Saimiri sciureus*, *Lagothrix lagothrica* Humboldt 1812, and *Saguinus* sp., *A. belzebuth* are not attracted to small mobile objects unless their attention is first drawn to such objects by the actions of individuals of other taxa. Moreover, they are not, nor do they become, adept at catching or killing insects such as moths, grasshoppers, mealworms, mantids etc. even after they have been enticed to accept and swallow a few. Breaking into or splitting twigs and branches and extracting objects within, a frequent practice of captive specimens of the genus *Cebus* (Thorington, 1967; Klein, pers. observ.), is not a class of behavioural patterns we have ever observed performed by either feral or captive spider monkeys, despite continuous contact with insectivorous taxa. Hladik and Hladik (1969) arrived at a similar conclusion.

4. ACTIVITY BUDGETS AND CYCLES

4.1. Methods

In this study the data were recorded as activity duration times and not as point-samples taken at the beginning of each minute (Eisenberg and Kuehn, 1966) or at 10-sec intervals (Richard, 1970). A spider monkey was considered to be feeding as long as (a) it had an edible item either in hand or mouth; or (b) it remained active within a tree containing food substances in which it had been observed eating during the immediately preceding period of 2 to 3 min. It was considered to have stopped feeding if (a) it moved out of the tree it had been feeding in; (b) it remained stationary within the tree it had been feeding in without taking objects into its mouth for a period of approximately 3 or more min; or (c) began performing activities inconsistent with feeding, e.g. allogrooming. As defined here, feeding bouts frequently included intermittent periods of time lasting longer than 10 sec (cf. Richard, 1970) in which the animals did not have an edible item either in mouth or hand. Spider monkeys were considered to be moving as long as some consistently directional progression between or through a tree was occurring. If stationary for periods longer than 3 to 4 min, the animal was no longer considered to be moving, but resting. Sustained periods of movement between trees always included frequent pauses ranging in duration from 5 sec to 2 min, although most pauses occurring during intertree progression were between 10 and 30 sec duration. In contrast to resting, spider monkeys while pausing usually maintained an alert rather than relaxed posture, frequently peered around and often maintained a suspensory or semi-suspensory posture. Resting comprised all daytime activities which occurred from a stationary position with the exception of feeding, drinking and short pauses. Periods of social grooming and adult play were also included since they comprised only a small percentage of the time during which the adult animals were stationary. All observed juvenile and infant play took place around resting or grooming adults. The frequent play of the released *Ateles geoffroyi* females on BCI, then infantless, caused Eisenberg and Kuehn (1966) to consider adult play, but not social grooming, a general and separate category of activities.

For our initial analyses 25 of those days during which we were best able to continuously follow and observe spider monkeys were analysed. They represent observational periods at all times of the year except between 1st December 1967 and 1st February 1968 when only sporadic attempts to follow individual spider monkeys were made, and the months of July and August in which extensive flooding occurred. The mean length of continuous observation for these days was approximately 7·5 hr and the number of days selected was sufficient to ensure that data were recorded for all 12 diurnal hourly intervals for a minimum of four 60-min observational periods. The minimal figure of 4 hr represents the period between 5.00 and 6.00h when it was very difficult to locate and observe animals unless they had been followed to sleeping sites. Moreover, the amount of time between the hours of 5.00 and 6.00h, and 17.00 and 18.00h, during which the spider monkeys under observation were considered to be sleeping (Klein, 1972) was not included in the computations.

The number of adult and juvenile animals engaged in feeding, resting and moving at any one time was multiplied by the number of minutes during which the activity was performed. These resulting animal/minute activity scores were then grouped according to the time of occurrence into 12-hourly intervals between 6.00 and 18.00h. Superficially, this procedure appears to give greater weight to observations of large rather than small subgroups, but as the relative importance of each activity was assessed on the basis of a ratio derived from the total (lumped data) of animal/activity minutes occurring only within the same hour, and since the same number of animals was almost always under observation for that interval of time, animals were usually being compared against themselves and little or no biasing was involved. However, since pooling and averaging obscures the pattern of differential activity onset and termination in individual animals (see Klein,

TABLE IV

Percentage of time engaged in either resting, feeding or moving based on 25 daily protocols of A. belzebuth *collected between February and November 1968*

	Hour of day (h)												
Activity	5–6	6–7	7–8	8–9	9–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18
Rest	22	25	44	43	65	63	62	67	46	54	36	29	21
Feed	41	37	22	31	20	16	21	17	26	19	32	36	38
Move	37	38	34	26	15	22	17	15	29	26	31	35	41

1972) and since animals were probably more likely to be encountered and observed if they were moving or feeding, 11 protocols of either individual or parties of two adult animals were also analysed separately. These data were collected during February, March, April, May and September 1968.

4.2. Results

The results of our analysis of 25 days are presented in Table IV. Table V summarizes the data for the 11 protocols considered separately. The overall results are not too discrepant. Together they suggest that the usual percentage of daylight time spent by feral spider monkeys feeding varied between 15 and 25%, resting between 50 and 65%, and moving between 5 and 20%. However, a portion of the time (roughly estimated as one-third) that a spider monkey was scored as moving was actually spent pausing and looking around from a stationary position. Moreover, a small percentage of the daylight time spent resting (provisionally estimated to be less than 5% of the resting time, i.e. less than 25 min daily) was usually spent by adults engaged in activities such as allogrooming and play.

Diurnal activities revealed by consideration of the individual protocols separately were periodic alternations of intervals of activity and inactivity with three to five lengthy periods of rest each day. In most cases long rest periods appeared to follow intensive periods of feeding (see Figs 3 and 4). This pattern is obscured when data collected on more than one animal and on different days are averaged (Table III). However these averages do reflect and emphasize, as a consequence of the greater data, the general tendency for rest periods to lengthen and become more frequent toward the midday hours.

As is exemplified from the same graphs, the time at which bouts of activity and rest began varied widely as did their relative duration. Both the timing and bout length appeared to be affected by weather conditions, social factors and availability and dispersion of food supplies, though our data were insufficient to demonstrate this conclusively. The study suggested that (a) heavy rainfall, particularly at dawn or early in the morning, delayed the onset of moving and feeding, although continuous rain did not entirely inhibit feeding and moving. (b) Sudden rain occurring at any time during the day usually, but not invariably, resulted in resting. Sometimes it initiated extremely vigorous but brief periods of activity. (c) Intergroup contacts could result in unusually delayed feeding bouts by initiating periods of rapid and continuous movement, and (d) the distribution, abundance and variety of types

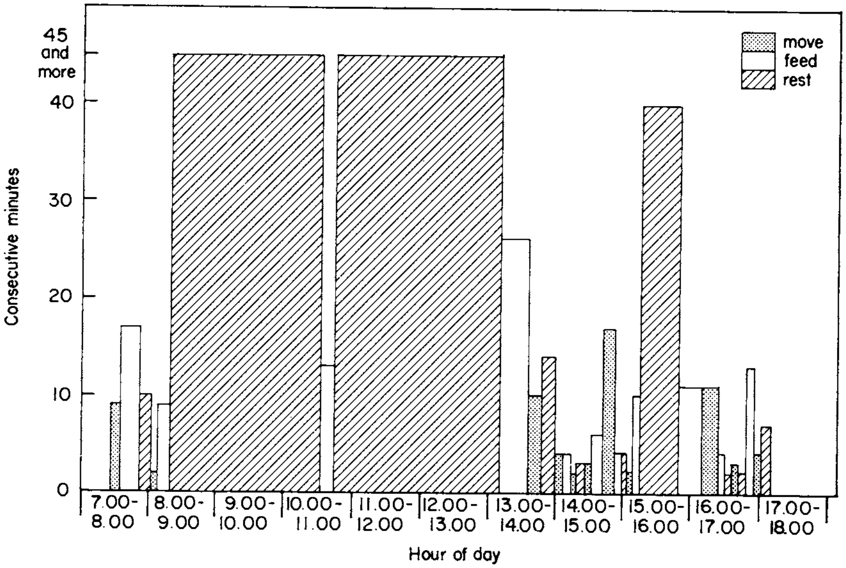

FIG. 3. Duration of moving, feeding and resting bouts of one adult female throughout the day of 9th March 1968.

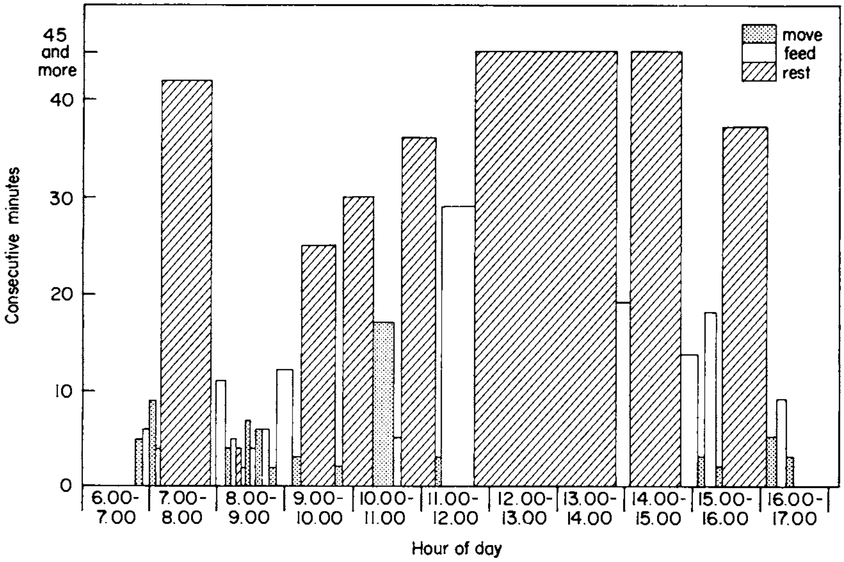

FIG. 4. Duration of moving, feeding and resting bouts of two adult females with infants throughout the day of 7th September 1968.

of ripe fruits available had an important effect upon the relative duration and frequency with which either feeding or moving occurred. Scattered supplies of scant ripe fruit appeared to be correlated with relative inactivity; abundant but concentrated and non-diverse supplies with lengthy travel and long rest periods; and abundant, diverse and relatively scattered supplies with more frequent moves and shorter rest periods.

4.3. Discussion

These results can be compared to the activity budget prepared by Richard (1970) for the BCI *Ateles geoffroyi* (see Table VI). Richard estimated that the spider monkeys on BCI spent about 11% of their time feeding and 28% of their time moving, while our data suggested that 22% of the time was spent feeding and 15% moving. These differences in estimates were probably a result of (a) differences in recording techniques, (b) differences in sample distribution (Richard's

TABLE V

Percentage of daylight time spent by A. belzebuth *engaged in feeding, resting or moving*

Activity	% of daylight time
Feeding	22·2
Resting	63·0
Moving	14·8

Mean value for 11 protocols of either individual animals or subgroups of two.

TABLE VI

Percentage of daylight time spent by Ateles geoffroyi *in different activities*

Activities	% of daylight time
Feeding	10·84 ± 0·91
Resting	54·07 ± 2·80
Moving	27·61 ± 1·60
Interaction	6·97 ± 1·45
Vocalization	0·41 ± 0·15
Urination and defaecation	0·10 ± 0·24

Revised from Richard, 1970.

methods resulted in considerable larger sample of those periods of the day when feeding was least likely), and (c) the effects of the availability of artificial and introduced food.

As noted in the section on feeding, spider monkeys are capable of rapidly ingesting large quantities of fruit. Since the stones and seeds are usually swallowed as well as the pulp and juice, and the ratio of stone weight to pulp weight for most natural fruits was far greater than one to one (Bollard, 1970; Klein, 1972), significant increases in body weight may result from intensive feeding bouts. Carpenter (1935), for example, found in one animal's stomach and intestine the stones of 90 *Virola panamensis* (Hemsl.) Warb., each fruit about 4 cm diameter and collectively weighing at least 550 g (Hladik and Hladik, 1969). We have observed captive *Ateles belzebuth* of about 9 kg frequently eat more than 700 g of ripe fruit within a 10-min period. Although ingesting the pulp along with the indigestible seeds and stones may be both ultimately and proximally advantageous to spider monkeys (Klein, 1972), one of its most immediate effects is to load the gastrointestinal tract with large quantities of material which passes through separated from the digestible pulp but otherwise unaltered. The actions of the intestinal tract on hard, indigestible material of this sort ought to be rather rapid and require little expenditure of chemical energy or complex processes of fermentation (Chaney, 1960). However, the mass of the material ingested (about 10% of the animal's body weight) may tend to inhibit subsequent activity, at least until a portion of the indigestible material is eliminated. The behavioural results predicted would be a pattern in which periods of intensive eating were followed by relatively long rest periods, which terminated shortly after defaecation and signalled the onset of a new period of sustained activity. This does, in fact, correspond reasonably well to the cyclic pattern of activities which were observed to occur.

5. SOCIAL ORGANIZATION

5.1. Methods

Observations during our initial survey period at several locations in eastern Colombia between June and November 1967, and for the first several months at our study site, November 1967–January 1968, consistently revealed that the number of animals encountered at any one location, even on the same day, was extremely variable. We therefore adopted the following criteria for determining the number, sex and age of animals in presumed contact with one another at any given time.

(a) Counts were considered complete only when the animals were kept under observation for a minimum of 15 min.

(b) Counts were considered complete only if no additional spider monkeys were seen or heard moving nearby for the same minimum period of 15 min.

(c) No spider monkey vocalizations were heard from areas within 180 m not traceable to one of the animals under observation or already counted.

It was assumed that these counts included all those individuals potentially in constant or at least frequent intermittent visual and/or audible contact with one another. Spider monkeys so considered were also usually simultaneously engaged in similar or complementary activities, e.g. feeding, resting, grooming or moving.

Four-hundred and ninety-eight counts meeting the above criteria were made in an 11-month period between 4th December 1967 and 22nd November 1968. Visual contact with these units, hereafter referred to as subgroups, was maintained by one or both of the observers for an average of 66 min. Contact with any single subgroup was considered terminated if all members of the subgroup were lost to sight, or a new subgroup was formed either by merger or division which, in turn, persisted for a minimum of 15 min. As a consequence of extreme variability in facial pelage pattern and other identification marks (see Fig. 1), by February 1968 we were able to individually identify a substantial number of animals (approximately 25 adults and juveniles).

5.2. Results

The median subgroup encountered over the 11-month period was composed of 3·5 independently locomoting spider monkeys. Infants under one-year were not considered independent. Subgroups of two comprised 21% of the total number of subgroups, and was the modal size subgroup. Subgroups of four individuals represented 16% of the total, and isolated animals 15%. Subgroups of eight or more comprised about 23% of the subgroups (see Table VII).

Subgroups of most sizes as well as isolates were observed when the animals were engaged in all types of major activities. There was no indication that subgroups assembled into larger units or reassembled at specific "lodge" trees before nightfall for sleeping (cf. Carpenter, 1935; for greater detail see Klein, 1972 and Klein and Klein, 1975).

Seventy-five instances of isolated animals were recorded, constituting 15% of the total number of subgroups observed. Observer contact was maintained on the average for 55 min before the animal either encoun-

TABLE VII

The percentage of subgroups consisting of one to eight or more independently locomoting A. belzebuth

Subgroup size	Frequencies	% of total subgroups
1	75	15
2	105	21
3	72	14
4	78	16
5	36	7
6	36	7
7	20	4
8–22	76	15
Total:	498	99

tered others (22% of cases), or was lost to sight (78% of cases). Adult females without infants constituted 66·7% of the total number of isolates; females with infant, 10·7%; adult males, 22·7%. No juvenile or infant was ever observed to be isolated for longer than a few minutes. The maximum periods that animals were actually continuously observed and known to remain isolated were as follows: adult female, 8·5 daylight hr and then overnight; adult female with infant, 6 hr; adult male 40 min. Observations of these instances of isolated animals were terminated as a result of lost contact. It was concluded that temporary isolation of most adult spider monkeys for periods as long as 1 to 3 days was a regular occurrence. (For greater detail, see Klein, 1972.)

As a consequence of our ability to individually identify spider monkeys, it became clear that the same animals were at times both isolated and members of subgroups of all sizes and compositions, although subgroup membership over a period of a few days could be relatively stable. During the course of the study it also became clear that the spider monkeys encountered at the study site could be assigned to three mutually exclusive networks of animals, which usually interacted peacefully with one another, and agonistically toward members of other networks. Only animals of the same network formed subgroups with one another. The number, approximate age, and sex of the animals of two of these networks was fairly completely known by the end of the study. The larger was made up of 22 animals of 1-year or older (five adult males, 12 adult females and five juveniles), the smaller of 17 (three adult males, 11 adult females and three juveniles, Klein, 1972). The individuals of these mutually exclusive social networks utilized different but overlapping sectors of the study site.

Distances as great as half a mile (0·8 km) between different subgroups of the same social networks did not appear to be unusual. Estimates of this kind were based on several criteria including the persistent following by one observer of an individually recognizable animal or animals as it departed from the animals it had been moving and feeding with, while the other observer stayed and moved with the remaining spider monkeys. Spacing between members of the same subgroups varied with ongoing activity, but was rarely more than 180 m.

That aspect of the social organization of *Ateles belzebuth* which appeared to be most clearly related to feeding behaviour was the size and stability of subgroups. Intermonth variations in median subgroup size ranged from 2·2 to 5·6 animals (see Table VIII). In addition, the frequency with which animals were observed in very large subgroups (eight or more) ranged from 20% of all groups seen in some months to less than 10% in others. Although isolated adults of both sexes were recorded in each month of the study, at certain times they were especially frequent. And in at least one month (October) a recorded high frequency of isolates and very large subgroups coincided.

TABLE VIII

Intermonth variations in A. belzebuth *subgroup size*

Months	Median	Mode	Range	No. of encounters	% of encounters with isolated individuals	% of encounters with subgroups of 8 or larger
Jan.	2·9	3	1–17	64	17	2
Feb.	4·0	2	1–18	103	5	16
Mar.	4·3	4	1–10	48	4	12
Apr.	3·7	2	1–11	82	12	15
May	5·6	3	1–20	43	7	40
June–Aug.	2·7	1	1–6	19	32	0
Sept.	2·2	2	1–11	47	28	6
Oct.	5·2	1	1–22	44	21	43
Nov.	2·2	2	1–11	36	25	3
Dec.	1·5	1	1–4	12	50	0
Total over year	3·5	2	1–22	498	15	15

Changes in subgroup size and apparent stability corresponding to ripe fruit availability included the following. In those months (September, December and January) when small, widely dispersed trees bearing ripe fruit for lengthy periods were the most important source of food (accounting for as much as 30–50% of observed feeding time) subgroups were smallest and most stable. Isolated animals were observed frequently (28% of all subgroup encounters in September) and appeared to remain isolated for periods ranging from several hours to several days. Eighty per cent of the subgroups were composed of four or fewer animals, median size was 2·2 and subgroups were relatively stable (mean duration of observation time per subgroup was 90 min). The situation was probably similar in December, but fewer data were collected.

The feeding situation in October contrasted markedly with September, December and January. The most important food source (more than 60% of feeding time) was the rapidly ripening and falling fruit of several scattered groves of very large *Brosimum* sp. trees. Larger subgroups were considerably more frequent. Subgroups smaller than five accounted for less than 50% of all observations and groups of eight or more animals composed more than 40% of our encounters. These large subgroups were about as stable in their membership as the much smaller ones in the preceding and subsequent months.

The relationship between subgroup size and fruiting patterns was more complex when a greater variety of trees with differing patterns of dispersion and ripening characteristics were bearing mature fruit in quantity. For example, in February 1968, a greater variety of fruits than usual was available to spider monkeys, including large and small tree species of wide dispersion as well as species of large size and clumped dispersion. The size of subgroups during this period was not very different from the annual average, although they appeared to be more unstable in membership than in September or October. Median subgroup was four, subgroups of eight or more individuals accounted for 16% of subgroups encountered, isolates were infrequent (about 5% of observations) and mean duration of subgroup observation was about 70 min.

5.3. Discussion

Behavioural interactions reinforced the view that changes in food supply influenced subgroup size and cohesion. First, although supplantations and overt aggression were relatively infrequently observed between spider monkeys of the same social network (13 supplantations and 60 more intense episodes of intragroup agonistic interactions over 627 hr of observation) a relatively large percentage of those occurred (40% of the supplantations and 23% of the more intense agonistic interactions) when at least one of the participants was feeding (Klein, 1974). All but two of these episodes occurred when animals were feeding on trees with crowns smaller than 20 m on either fruit or wood restricted to an area less than 8 m diameter. Second, the number of spider monkeys that would simultaneously feed in a fruiting tree was limited and was frequently less than the number of animals in the subgroup itself. The maximum number of *Ateles belzebuth* observed feeding simultaneously in the same tree was ten, and numbers greater than eight were observed in exceptionally large trees on only a few occasions, and for only a few minutes. These maximum figures were smaller than the number observed resting in similarly sized trees and even in some cases the identical tree when it was not bearing fruit. Probably related was the fact that preferred daytime resting sites were usually tall trees with large limbs, but not those bearing ripe fruit at the time. Many of these same trees were intensively fed in when bearing ripe fruit, but were then not used for resting.

The characteristic flexible social spacing between spider monkeys of the same social network is readily interpretable as an adaptive response to fluctuating supplies, concentrations, and dispersal patterns of ripe fruit. In contrast, primates which can utilize either more varied or less seasonally variable products such as mature leaves, green fruit, and/or insects and arachnids may adapt to changes in food availability by varying food selection instead of grouping patterns (see Klein, 1972 and Klein and Klein, 1975).

6. SUMMARY

A 15-month observational study of the feral Colombian spider monkey, *Ateles belzebuth*, provided the basis for reported data on diet, activity patterns and social organization. Relative importance of specific items in the diet of *A. belzebuth* was assessed primarily on the basis of time and numbers of animals observed eating during periods of both 2 to 3 weeks and over an 11-month period.

The diet of *A. belzebuth* was composed of ripe fruit (82%), tree leaves and buds (5%), leaves and stems of epiphytic plants (2%), decaying wood (10%), immature fruit (1%) and flowers (0·1%). No vertebrates, invertebrates or eggs were observed to have been eaten. With two general exceptions, the height at which spider monkeys fed above the ground or water level depended upon the height of the tree in which they fed and the location of ripe fruit in it. The exceptions to the above were the fact that they were never observed either feeding on the ground or less than 8 m above it, even when small quantities of ripe fruit were available in these locations. Fruits eaten ranged in size from less than

3 mm in diameter to more than 50 mm. Adult spider monkeys usually swallowed the hard seeds of ripe fruits along with the softer pulp or flesh, but rejected the pericarp. Juvenile spider monkeys usually rejected both seeds and pericarp. The diversity of fruits eaten daily by spider monkeys averaged about four taxa over the year, but varied seasonally between two and nine taxa.

The temporal pattern of moving, feeding and resting activities, abstracted from 25 protocols averaging 7·5 hours in length, were compared with similar analyses reported by Eisenberg and Kuehn (1966) and Richard (1970). Some discrepancies were noted. *A. belzebuth* spent more time feeding between 5.00 and 7.00, and 15.00 and 18.00h, than at any other time of the day. During the day feeding and moving periodically alternated with resting. This pattern was interpreted as resulting from feeding on large quantities of ripe fruit.

Adult *A. belzebuth* spend between 15 and 25% of the daylight hours feeding, 5–20% of the daylight hours moving and 50–65% of the daylight hours resting (including all non-feeding stationary activities).

Ripening, dispersion, and crown diameter characteristics of fruiting trees had an important effect on the size and stability of the temporary subgroups of spider monkeys, feeding and resting patterns, and the frequency of agonistic interactions. *Ateles* appears to be limited in its ability to utilize substances other than ripe fruit. In other taxa, the ability to utilize either insects, arachnids, mature leaves or green fruit modified considerably the competitive effects of changing amounts and concentrations of ripe fruit and fruit tree dispersion. The considerable importance of sparse, widely dispersed ripe palm fruit in the diet of spider monkeys during periods in which other fruit was scarce strongly corresponded with minimal group size and maximal occurrence of isolated adult spider monkeys of both sexes.

ACKNOWLEDGEMENTS

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APPENDIX

The most important fruits utilized by A. belzebuth *at study site*

Family, genus	Time of year utilized	% of *A. belzebuth* diet at time of heaviest utilization	Estimated % of *A. belzebuth* diet over year	Relative abundance of fruit-bearing individuals of spp. at study site	Dispersion pattern of trees
Anacardiaceae					
Spondias mombin	1 Apr.–14 May	1–14 May 8%	> 1	Rare	Scattered
Annonaceae					
Xylopia sp.	1–13 Apr. and 16 Sept.–22 Oct.	2–14 Sept. 3%	> 1	Rare	Scattered
Burseraceae					
Protium sp. and/or* *Bursera* sp.	1 Feb.–13 Apr.	1–13 Apr. 11%	4	Uncommon	Scattered
Chrysobalanceae					
Licania sp.	1 Feb.–12 Mar.	1–12 Mar. 28%	5	Rare	Scattered
Euphorbiaceae					
Hyeronima sp.	1 Feb.–12 Mar.	1–14 Feb. 58%	19	Common	Clumped†
Flacourtiaceae					
Xylosma sp. or *Homalium* sp.	11–22 Nov.	11–22 Nov. 37%	> 2	Rare	Clumped
Guttiferae					
Calophyllum sp.	16 Sept.–14 Oct.	2–14 Oct. 8%	> 1	Uncommon	Clumped
Rheedia sp.	15 Feb.–27 May	18–30 Apr. 6%	> 1	Rare	Scattered
Lauraceae					
Licaria sp.	16 May–13 Sept.	18–24 June 31%	> 1	Rare	Scattered
Leguminosae					
Inga edulis	1–30 Apr.	18–30 Apr. 3%	> 1	Rare	Scattered
Inga latifolia	1–27 May	16–27 May 8%	> 1	Uncommon	Scattered
Inga sp.	1 Apr.–27 May	18–30 Apr. 1%	> 1	Rare	Scattered
Marcgraveaceae					
?	2 Oct.–30 Jan.	11–22 Nov. > 1%	> 1	Uncommon	Scattered

Moraceae					
Brosimum [v e] Brosimopsis] Sq?	5 Sept.–22 Oct.	2–22 Oct. 66%	7	Common	Clumped and dispersed
B. potabile	11–22 Nov.	11–22 Nov. 13%	> 1	Rare	Clumped
Ficus javensis ?	8 Jan.–14 Feb. and 15–22 Oct.	1–14 Feb. 7%	< 1	Uncommon	Clumped
F. sp. (LF)	15 Jan.–1 Feb. and 11–22 Nov.	11–22 Nov. 9%	> 1	Rare	Scattered
F. sp. (VLF)	1–29 Feb.	1–14 Feb. 7%	1	Rare	Scattered
F. sp. (Hig)	15–30 Jan. and 11–22 Nov.	11–22 Nov. 4%	> 1	Rare	Scattered
F. sp. (RF)	1–13 Apr.	1–13 Apr. 7%	> 1	Rare	Scattered
F. sp. (Sq)	18–30 Apr.	18–30 Apr. 8%	> 1	Rare	Scattered
Pseudolmedia sp. (RC)	15–29 Feb.	15–29 Feb. 5%	> 1	Rare	Scattered
P. sp. (B)	15 Feb–30 Apr.	15–29 Feb. 12%	3	Uncommon	Sometimes clustered
Myristicaceae					
Virola sp.	2 Feb–12 Mar.	1–14 Feb. 5%	1	Uncommon	Scattered
Virola sp.	1 Apr.–29 Sept.	1–13 Apr. 12%	3	Uncommon	Scattered
Olacaceae					
Heisteria sp.	15 Jan.–14 Feb.	1–14 Feb. 3%	> 1	Uncommon	Scattered
Palmaceae					
Euterpe sp.	1–12 Mar. and 16 May–22 Oct.	1–10 July 61% 5–13 Sept. 30%	1	Common	Scattered
Iriartea exorrhiza?	1–12 Mar. and 11–22 Nov.	11–22 Nov. > 1%	> 1	Rare	Scattered
I. ventricosa	2 Aug.–22 Nov.	5–13 Sept. 23%	2	Common	Scattered
Oenocarpus sp.	2 Aug.–29 Sept.	2–22 Aug. 22%	> 1	Rare	Scattered
Sapotaceae					
Chrysophyllum sp.	1 May–22 Aug.	1 July–10 Aug. *c.* 50%	< 3	Common	Clustered
Pouteria sp.	1 Apr.–24 June	18–30 Apr. 57%	18	Common	Clustered

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* Probably more than one species was treated by us as a single type.

† Tended to grow best at edge of tree falls or on well-drained banks of small streams.

7

Feeding, Ranging and Group Size in the Mangabey *Cercocebus albigena*

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1. INTRODUCTION

As data from more primate species have accumulated, exceptions to postulated correlations between social organization and habitat have frequently emerged (e.g. Struhsaker, 1969, 1975). Many of the shortcomings may result from the gross nature of the ecological categories within which species have been lumped; thus substantial differences between the niches of different forest-living primates have been obscured by lumping all as "forest omnivores" or "frugivore-omnivores". In the Kibale forest, in western Uganda, the mangabey, *Cercocebus albigena* (Fig. 1a), is sympatric with two species of *Colobus*, three of *Cercopithecus*, *Papio anubis* and *Pan troglodytes*. While six of these eight species would normally be classified as omnivorous, their group structure and ranging patterns have little in common; the small multimale groups and enormous home ranges of mangabeys are particularly distinctive (Waser and Floody, 1974; Waser, 1976). It seems of particular interest to delineate the foraging ecology of mangabeys in such a situation. In a framework of interspecific comparisons (see Oates, 1974; Struhsaker, 1974, 1975; Struhsaker and Oates, 1975), data on *C. albigena* feeding and ranging have been recorded during more than 2500 observation hours between May and June 1971, March 1972 and April 1973, and August and October 1974.

In the first major field study of this species, Chalmers observed that *C. albigena* in eastern Uganda ate "buds, shoots, and fruits of trees. In addition, they frequently peeled strips of bark from trees and ate objects from underneath" (Chalmers, 1968a, p. 257). Chalmers listed six tree species commonly utilized for fruits, six for shoots, and one for flowers. In the Bwamba forest, western Uganda, data from stomach contents (Haddow, pers. comm.) indicate feeding on seeds or fruits of three species and leaves of two, as well as on *Crematogaster* ants. Similar data from West Africa (Jones, 1970) suggest a higher proportion of leaves in the diet, but use of a broad range of items has been confirmed by the observations of Cashner (1972).

1.1. Methods

In this study, most data on feeding and ranging were collected during 5-min sampling periods centred on the quarter and three-quarter hours. Unless otherwise noted, all data reported here derive from one 15-member group[a] which was followed continuously, dawn to dusk, for a 10-day period at the beginning of each month. During the sampling periods, or "scans", the locations and activities of as many individual mangabeys as possible were recorded: when the activity was

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[a] Composed during 1972–73 of three adult males, two subadult males, six adult females, and three to five juveniles and infants.

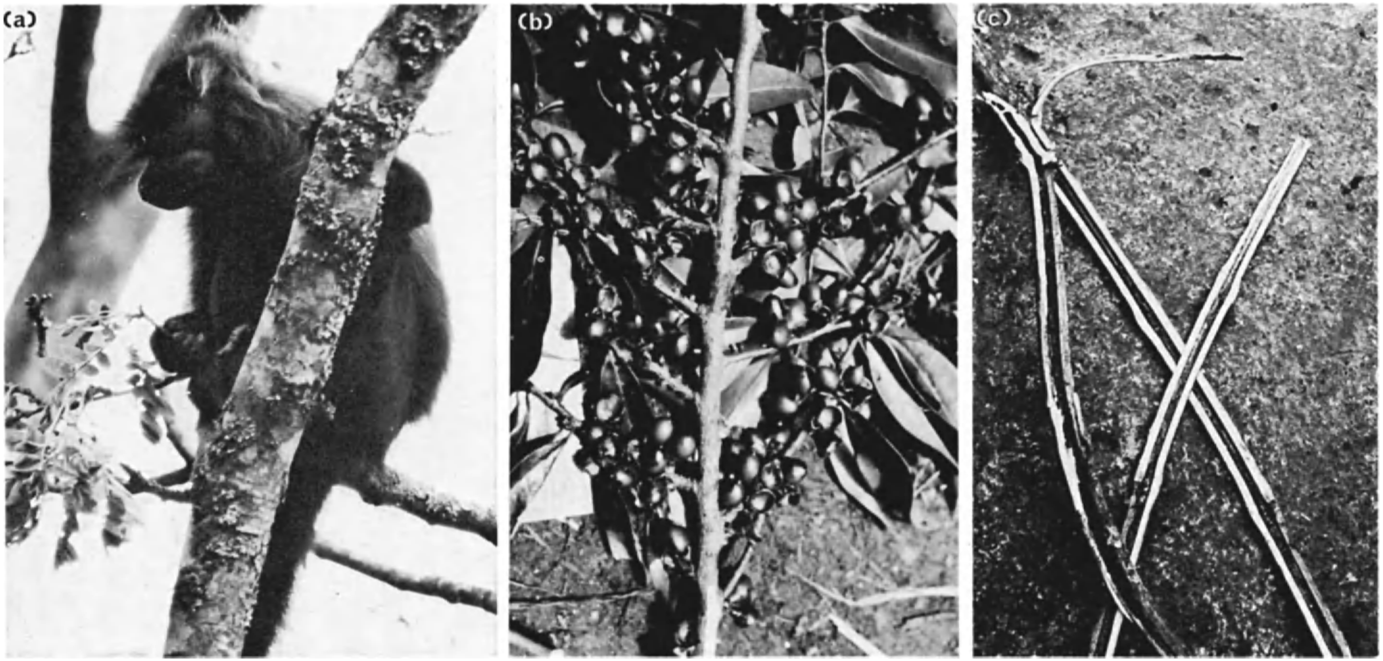

Fig. 1. (a) Adult female *Cercocebus albigena*, sitting in a *Milletia dura*. Note her distended cheek pouches. Young leaves and flowers of *M. dura* are commonly eaten. (b) *Diospyros abyssinica* branch dropped by feeding mangabeys. Note leathery epicarp caps where mangabeys have broken the fruit away, some covered with sticky pulp which has blackened on exposure to air. Fruit diameter is *c.* 0·5 cm. (c) Portions of a hollow-centred climber, split and dropped by mangabeys. Ants were found in the central chamber *c.* 2 mm in diameter.

feeding, the species and type of food (or, for invertebrate foraging, the substrate type and motor pattern) were also noted. Criteria used to define activity types were those of Struhsaker (1975) and Oates (1974); categories were mutually exclusive. "Feeding" was scored whenever the activities of reaching for, picking, manipulating or placing in the mouth of food items were continued for at least 5 sec. Chewing during periods of inactivity or locomotion could not be recorded reliably under prevailing observation conditions and was not included in the definition. An estimate of the percentage of scores spent chewing (while engaged in other activities) was derived from a smaller sample of records during which the animal's jaws were clearly visible.

Food types recognized were leaf buds, young leaves, mature leaves, flower buds, flowers, fruits, bark, pith and "probable invertebrates"; unidentifiable objects were scored as such. Size and degree of maturity of young leaves and fruits were noted when visible. During search for invertebrates, but not for other food items, periods of substrate manipulation without ingestion sometimes exceeded 5 sec; these occurrences were lumped with scores of invertebrate ingestion and scored as "invertebrate foraging" since the two were frequently indistinguishable under prevailing observation conditions. The percentage of foraging scores which included ingestion was estimated from a smaller sample of scores during which visibility was exceptionally good.

Individual records of age, sex, identity, spatial co-ordinates, activity, and food type and species, along with time and order of each record, were recorded in a form suitable for computer analysis. Between April 1972 and April 1973 these methods generated 18 118 records in 2474 scans of the main study group. This data base readily yields the relative amount of time spent by mangabeys foraging in different tree species or using various food types. For the investigation of potential sources of bias as well as for the sorts of analysis reported below, the advantages of machine manipulation are clear.

For tests of goodness of fit or independence, the log likelihood ratio or G test (Sokal and Rohlf, 1969) was used. When comparing data derived from scan samples, the assumption of independence was felt to be reasonable since (a) individuals were identifiable and thus scored only once per scan, and (b) individuals almost never continued a single activity, or fed on a single food source, for half-an-hour at a stretch. Thus, the activities scored during a given scan did not depend—at least not in these trivial ways—on those scored a half-hour previously.

Observations were scheduled systematically in time and without regard to the location, activity or identity of the animals involved, in order to minimize possible biases relative to these variables. Nevertheless, scan samples were potentially affected both by overall visibility conditions and by the differential visibility of different individuals or activities. For instance, the number of individuals seen during scans was substantially lower during the first and last hours of the day, although visibility did not vary for the rest of the day (Fig. 2).

A direct assessment of the degree of one possible kind of bias, that particular age/sex classes are more likely to be observed than others, can be obtained by comparing the numbers of observations of each age/sex class with the known composition of the group. Although on an average scan only half of the group was sampled ($\bar{x} = 7{\cdot}32$), and 26% of the individuals observed during scans were of unknown age and sex, the mean rates of observation of individuals of each age/sex class were remarkably similar (Waser, 1974). Sighting frequencies of adult males and adult females differ by less than 0·1%; the greatest deviations in sighting frequency from the mean (lumping all classes) are of juveniles, 13·5% less likely to be seen than the "average" individual; and of infants, 12·5% more likely to be seen than average.

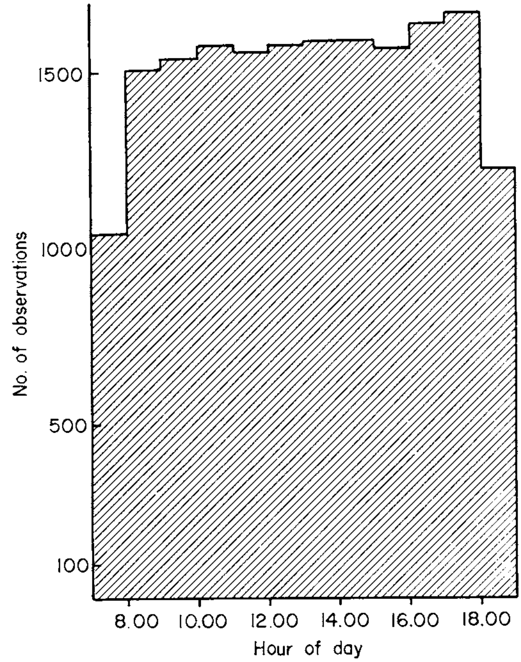

FIG. 2. Number of observations during scans as a function of time of day, May 1972–April 1973 inclusive.

Although no independent assessment of relative frequencies of different activities is available, the apparent constancy in visibility of individuals leads one to hope that visibility biases of this sort are small (see Waser, 1974, for further discussion of sampling methods).

It should be noted that the methods used here to record feeding data differ from those of Struhsaker (see Oates, this volume, for a description of those methods), in that they indicate relative time spent on species or items. Data were recorded by both methods during eight days of observation of mangabeys. While, in this sample, the methods of Struhsaker resulted in the recording of 33% more feeding observations representing 28% more species than did sampling only during scans, the results of his methods were strongly influenced by the abundance and spatial distribution of the food items concerned, and by the temporal pattern of individual feeding bouts. Thus relatively rare items (e.g. *Millettia* seeds), those fed on for only brief periods during any one sitting (*Premna* young leaves) and those which were widely scattered and present at low densities (insects), were recorded proportionally more frequently using Struhsaker's methods. Those items occurring in large concentrations and eaten continuously over prolonged periods (e.g. *Diospyros* fruit, *Ficus* fruits) were under-represented. The disparities increase if items between which mangabeys switched indiscriminately (such as leaf buds, small and large young leaves of *Premna*) are scored separately; such splitting of feeding or foraging categories can also substantially affect the calculated values of dietary diversity. On the other hand, unusual items are likely to be missed entirely using only data from scans. For this reason, novel dietary items observed outside scan periods were recorded in this study; however, over the year all but six such items were subsequently seen eaten during scans.

1.2. Study Area

The Kibale forest as a whole has been classified as "moist evergreen forest" (Langdale-Brown *et al.*, 1964) although the rainfall—165·8 cm between 1972 and April 1973—is near the lower limit generally characteristic of rain forest (Richards, 1966). Due to its relatively high altitude (*c.* 1500 m at the Kanyawara study area) affinities with montane forest also occur (Kingston, 1967; see also Wing and Buss, 1970 for a general description of the forest's vegetation and topography).

The main study area, approximately 4 km^2 near the Kanyawara forest station (0°34′ N, 30°22′ E), contains sections of swamp, secondary and colonizing forests as well as primary forest which has been without

FIG. 3. Mangabey's-eye-view of the Kanyawara study area. Photograph is taken horizontally through the canopy from *c.* 20 m above ground.

human interference during the last 50 years (see also Oates, this volume). In most areas, the canopy is 25–30 m high with some trees reaching 50 m in height (Fig. 3). A series of vegetational transects was run along compass bearings gridding the study area at roughly 200 m intervals. All trees more than 10 m in height and less than 2·5 m from the trail were recorded along 8685 m of transect. Including the data of Struhsaker (pers. comm.), 1667 trees on a total of 5·78 ha of transect were sampled (Table I, see p. 201).

The species composition of this sample included between 67 and 71 species (the number of unidentified species was not certain). Although only five species make up 50% of the sample, the species diversity is high ($H'_2 = 4{\cdot}37$). A large number of tree species occurs in very small numbers and, despite the size of the sample, several species important to mangabeys (including two large *Ficus* species) do not occur in it. Large-scale vegetational heterogeneity is marked, due in part to altitudinal relief and corresponding drainage patterns and to the presence of a variety of successional stages [compare the vegetational data of Oates (1974), Struhsaker (1975), and Waser and Floody (1974), recorded in different subsections of the study area].

2. FEEDING BEHAVIOUR

2.1. Activity Patterns

At any time of day, a substantial proportion of a mangabey group is likely to be feeding. Mangabeys in the main study group spent 42·5% of their time engaged in feeding or food manipulation, a figure which compares closely with that of Chalmers but which may vary both between groups and between months (Waser, 1975). Although this figure includes time spent scanning or manipulating the substrate in search of invertebrates (*c.* 10% of the total time budget) it does not include locomotion within (4·2%) or between (17·2%) trees. The former is particularly likely to be related to food collecting. Nor does it take into account the extensive use made of cheek pouches, for mangabeys generally retire in the evening and other inactive periods with pouches full. During half of the time that they were scored as inactive, and occasionally when they were moving, mangabeys were simultaneously chewing; chewing of cheek pouch contents may have taken place during as much as 15% of the activity records in addition to those spent in active feeding.

Although it appeared that mangabeys alternated several major bouts of feeding and resting during each day, the diurnal distribution of feeding records over the year is virtually flat (Fig. 4). At this latitude, dawn time varies by only half-an-hour over the year and thus has little effect on timing of activity patterns. Although regular activity patterns may shift between months due to weather or other factors, no cyclic patterns were apparent in any month's data. Even during the July sample period, during which no rain fell to disrupt behavioural cyclicity, diurnal deviations from the mean were not significant ($P > 0{\cdot}05$). It seems likely that diurnal activity patterns are dictated primarily by the irregular and changing distributions of food mangabeys encounter. These mask any regular physiological cycles, digestive or otherwise, which may occur. Species with more uniformly-distributed food might be expected to express underlying cycles more clearly; those utilizing relatively permanent resources, or able to visit all parts of small home ranges with relatively small outlays in energy or time, might similarly show a more striking diurnal activity pattern corresponding to some optimal pattern of utilization of known resources. Thus the study group of Chalmers (1968a), which (in striking contrast to Kibale mangabey groups) visited most parts of its small home range each day, also demonstrated more clearcut activity cycles (Fig. 4).

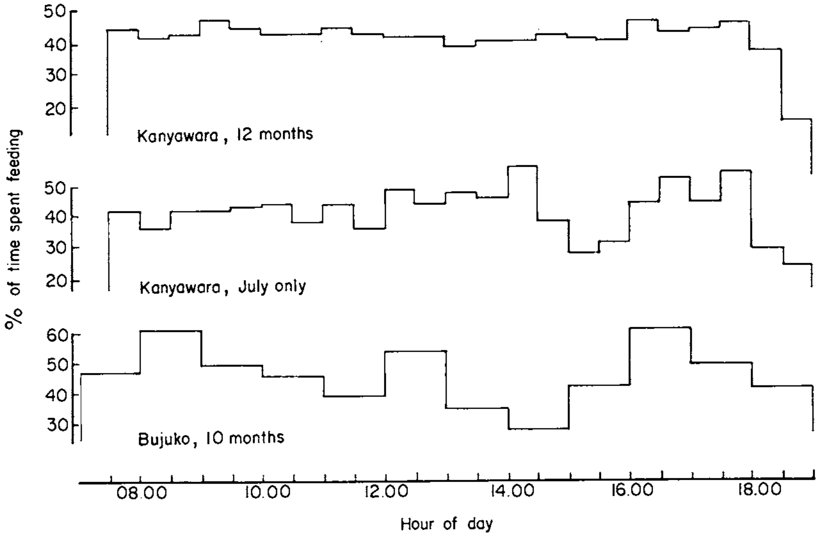

FIG. 4. Percentage of scan records during which activity was "feeding" as a function of time of day: (top) all observations, May 1972–April 1973, inclusive; (centre) all observations, 1–10 July 1972, a rainless sample period; (bottom) data from Chalmers' (1968a) Bujuko study area, March–December 1964.

2.2. Feeding Heights and Sites

Since data on feeding heights indicated no major shifts over the year, only those collected in May to June 1971 were analysed in detail. Feeding heights were normally distributed with a mean of *c.* 20 m; thus both middle and upper storeys of the forest were utilized (Fig. 5a). Mangabeys do not choose feeding trees randomly from those available: heights of trees used for feeding are significantly greater than those of trees in vegetational transects ($P \ll 0{\cdot}01$), even though the latter sample excludes trees lower than 10 m (Fig. 5b).

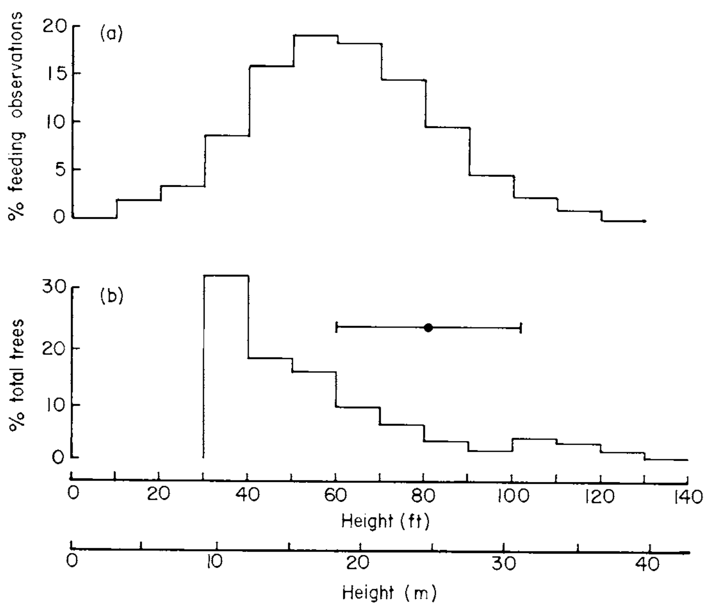

FIG. 5. Vertical distribution of mangabeys. (a) Distribution of estimated feeding heights, May–June 1971 ($n = 1011$ scan records). (b) Heights (mean and s.d.) of trees in which mangabeys were observed to feed, May–June 1971 ($n = 1011$ scan records); below, histogram of heights of all trees 30 ft and taller enumerated in transects within the area used by these mangabeys during May–June 1971 ($n = 313$ trees).

While the observed distribution of feeding heights is largely a function of the size of favoured tree species, there is also a slight tendency for mangabeys to remain lower in tall trees, and a clear one to stay higher in low trees, relative to expectation if all heights were used randomly (Waser and Floody, unpubl. data; cf. Chalmers, 1968a). Recording a mangabey's height as a function of the height of the tree it occupies also demonstrates these tendencies. The mean height of mangabeys in tall (30–40 m) trees was about 60% of the tree's height, but increased to 75% of the tree's height in lower (10–20 m) trees. A tendency to avoid areas near the ground is subjectively evident from the behaviour of animals feeding on low-stature plants (particularly *Millettia dura*, *Cyphomandra betacea* Sendtn., and a species of Acanthaceae).

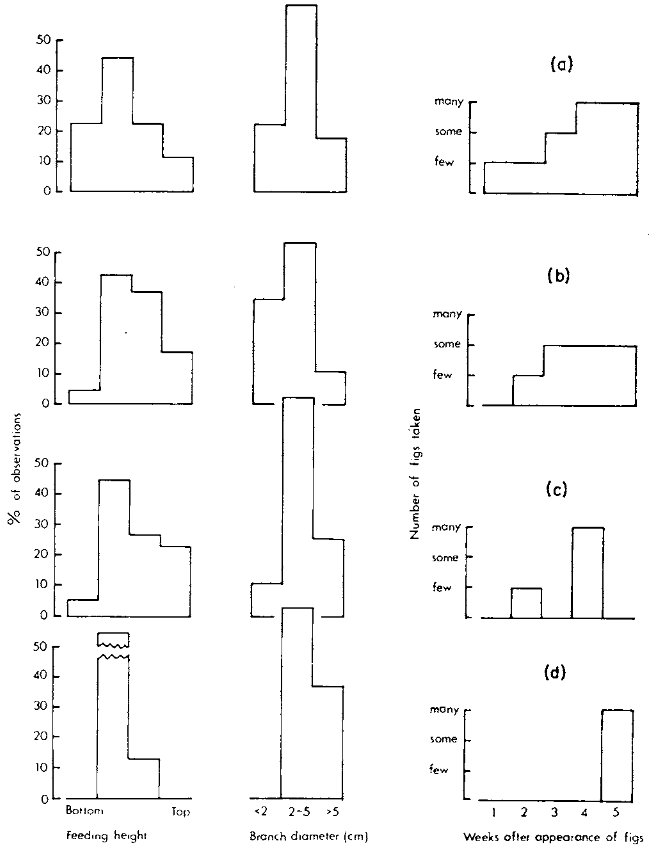

FIG. 6. Use of a single *Ficus brachylepis* by four primate species during one fruiting period in 1973: (a) *Cercopithecus ascanius*, (b) *Cercopithecus mitis*, (c) *Cercocebus albigena*, (d) *Pan troglodytes*. Data were recorded during half-hourly scans from a blind (see text). Numbers of scan feeding records: (a) 18, (b) 93, (c) 22, (d) 8. Left, percentage of scan records during which individuals fed in bottom, lower central, upper central and top quarters of tree canopy. Centre, percentage of scan records during which individuals took figs from small, medium and large branches. Right, number of figs taken (relative to total number taken by each species) during each of the last five weeks of fruit availability. Systematic observations began when spot-checks first revealed use of the tree by any frugivores. Note that many birds, squirrels, prosimians and viverrids also fed in this tree.

Animals were extremely hesitant when descending below 10 m and, if food was available only below this height, they did one of two things: (a) hung upside down, sometimes by the hind legs only, grabbing the uppermost branches of the feeding tree and pulling them up to their height; or (b) descended rapidly, broke off a food-laden branch, and reascended to eat it. As these observations indicate, some mangabey feeding (*c.* 5%) did occur below 10 m; on a few occasions individuals fed or foraged on fallen tree trunks or even on the ground.

Systematic data on feeding sites were recorded only during an investigation of the use of *Ficus brachylepis* by mangabeys and other species. Mangabeys took figs from small branches less than from larger branch sizes (*F. brachylepis* is cauliflorous) but used all branch sizes (Fig. 6c). They took fruit from the lowest segments of the tree less than from central segments, but fed at all heights and in both central and peripheral parts of the tree. These observations support subjective impressions that few sites are inaccessible to mangabeys. Mangabeys are quite capable of reaching the undersides of large branches (occasionally hanging quadrupedally beneath them); of climbing on fine branch tips (or recovering from falls if these break) or of bending or breaking small branches towards them. Branches were often carried to a more comfortable sitting spot or to a neighbouring tree when the feeding tree was crowded.

2.3. Feeding Types and Techniques

The tastes of *C. albigena* are catholic, ranging from orchids to snakes. As many as 41 species were seen to be used in a 10-day period, with monthly dietary indices of diversity of species (H'_2) varying between 2·83 and 3·88. Annual diet diversity was $H'_2 = 4{\cdot}21$. Most dietary items fell into three broad categories (see Waser, 1974, 1975 for a complete listing of species and parts utilized).

2.3.1. *Leaves and bark*

During this study, mangabeys devoted relatively little time to plant vegetative parts. Leaf buds formed 1·1% of the diet over the year, young leaves 3·4%, leaves of unspecified age (primarily large young leaves) 0·8%. Mature leaves were virtually non-existent in the diet. Leaf feeding was confined to a small number of species, and mangabeys fed on leaf buds and young leaves of all sizes in most of these. Leaves in earlier stages seemed generally to be preferred; this was particularly true of *Ficus* spp., in which almost no young leaf feeding was observed, and of *Monodora*, from which leaf buds, but never young leaves, were taken. This last may, however, be a special case, since the leaf buds enclose the developing flower buds and mangabeys almost certainly ingest these as well. Young leaves or leaflets are generally eaten completely, either with the petiole (*Erythrina*) or stripped from it by grasping the petiole and pulling off the leaf blade (*Premna*) or leaflets (*Millettia*) with the clenched hand. The leaves taken tasted mild or slightly bitter. In the case of the large, flat-leaved epiphyte *Platycerium elephantotis* Schweinf., mangabeys eat only the bases of the young leaves. These are spongy and succulent, and may represent a significant source of water (see also *Dracaena* feeding, below).

A striking aspect of mangabey feeding not observed in other Kibale forest primates is bark-stripping. Live bark is bitten and pried away from the underlying branch with the canines, and the broken strip of bark then ripped off with the mouth or hands. Strips several centimetres wide and up to a metre long may be removed in this way, generally from branches a few centimetres in diameter. In a less common variant of this type of feeding, twigs are broken off and chewed or the bark peeled back. *Celtis africana* accounted for nearly all bark-stripping, although several other species were occasionally used; bark of the more common *Celtis durandii* was very rarely stripped. *Celtis africana* bark is almost unique among mangabey foods in being quite sweet with no unpleasant aftertaste. In addition to bark, the pithy central core was eaten from twigs of one species (*Pseudospondias*). Bark-stripping accounted for 2·5% of mangabey feeding time.

2.3.2. *Flowers and fruits*

By far the largest proportion (62·2%) of mangabey feeding observations involved plant reproductive parts, generally the more advanced stages. Feeding on flowers and flower buds (3·4%) was confined to eight species, but in some cases (*Millettia*, *Erythrina*) flower predation was intensive enough that fruits were rarely formed; mangabeys were observed to virtually denude individual trees of flowers.

Mangabeys ate the whole flower [*Millettia*, *Erythrina*, the orchid *Tridactyle bicaudata* (Lindl.) Schltr., the hemiparasite *Loranthus aurantracus* Engl.] or sometimes concentrated on the ovary (*Symphonia*, *Mondora*). Most of these flowers are large and brightly coloured, and *Erythrina* and *Loranthus* in particular are said to contain abundant nectar (e.g. Faegri and van der Pijl, 1971). However, none of these flowers tasted noticeably sweet, but rather ranged from mildly bitter (*Erythrina*, *Millettia*) to highly astringent (*Symphonia*).

Fruits, in the botanical sense, comprise the largest single item in the mangabey diet. The main study group consumed the seeds or fruits of 54 species during 1972–73 (Waser, 1975). These ranged from the tiny capsules of *Acanthopale* sp. and the small (2 mm-diameter), bright red, grape-like fruits of the liana *Urera cameroonensis* Wedd., to the basketball-sized fruits of *Mondora myristica*. Most were figs or medium-sized (0·5–2 cm) drupes, with a fleshy pericarp surrounding the seed. Pods and capsules are less usual than drupes or figs in the mangabey diet, although this may reflect their relative abundances in the study area rather than any selectivity by mangabeys.

Fruits varied widely in their palatability to the observer; those of *Parinari* are said to be eaten by humans (Eggeling, 1952) and those of *Urera* are watery and bland. On the other hand, *Millettia* seeds and a number of other foods are mildly bitter, while fruits of *Diospyros* (Fig. 1b) and *Celtis durandii* are intensely so and leave a burning aftertaste.

Most fruits are eaten ripe, although just barely, as few fruits remain long on the tree once they show signs of ripeness. *Cyphomandra betaceae* ("bush tomato"), a fruit relished by human as well as non-human primates, is eaten when very green, perhaps as a result of intense interspecific competition. *Celtis durandii* fruits are often eaten green for the same reason; in other areas of the forest where ripe *Celtis durandii* fruits are more common, these are preferred. The considerable selectivity demonstrated with many species, involving feeling, sniffing or biting large green fruits, may be concerned with detecting the early stages of ripening. On the other hand, fruits of *Diospyros abyssinica* were eaten at all stages of ripeness, even when very small. In this case, another factor may be involved; the hard seeds, which are difficult to crack in the ripe fruit, are more easily eaten when younger.

Mangabeys eat *Diospyros* fruit, their favoured food, entire, discarding only the leathery epicarp. The sound of crunching *Diospyros* seeds is species-specific and serves to locate mangabeys at a considerable distance. However, seed-eating is not the rule. In many cases (e.g. *Ficus* spp., *Cyphomandra*, *Pancovia*, and probably others) the seeds pass through the gut intact; in others (*Celtis africana*, *Parinari*, *Uvariopsis*, often *Pancovia*) the seeds are separated from the fleshy parts and discarded. Although seed-eating involves a fairly large number of species, with the exception of *Diospyros* these are not common items in the diet.

Most fruit-eating involves little manipulation other than gathering the fruit with the mouth or fingers and possibly separating the seed, done with the teeth and lips. Fruits of *Diospyros*, *C. durandii* and *Pancovia* are sometimes rubbed on branches before eating, probably to break and separate the epicarp. Pods of *Millettia*, *Newtonia*, *Albizia*, *Funtumia*, *Spathodea*, *Erythrina* and several species of liana are broken open by hand or with the teeth, split, and the seeds bitten out; in the case of winged seeds [*Funtumia*, the liane *Reissantia parvifolia* (Oliv.) Halle, *Spathodea*] the seed is bitten away from the wing. Large fruits (*Tabernaemontana* and *Monodora*) require special treatment; the outer skin is first broken with the canines or incisors and the pulp and seeds then scooped or bitten out from inside. A single *Mondora* fruit, which only an adult male may be capable of opening, will often be fed on by a succession of individuals; the final juvenile may feed with his head entirely inside the fruit.

2.3.3. *Invertebrates*

The actual capture of invertebrates takes only a small fraction of the time expended by mangabeys in substrate manipulation and search. Of the 26·0% of scan feeding records scored as invertebrate foraging, only a third actually included one or more visible captures, and an almost negligible proportion of invertebrates are captured by mangabeys on open surfaces.

The items taken by mangabeys when foraging for insects and other invertebrates can rarely be identified, but the substrate and motor patterns used can be recorded and, during the substantial amount of time mangabeys spend in such activity, scattered observations under optimal visibility conditions can be used to build up a picture of the types of invertebrate involved. Substrates exploited by mangabeys fall into the following categories.

(a) *Moss and epiphytes.* The largest fraction of foraging time (13·0% of all feeding observations) occurs in this microhabitat. Substrate manipulation is extensive, including peeling strands or whole sheets of moss, epiphyte and lichen from branch surfaces, subsequently scanning either the newly exposed surface or the removed material. The mass of moss and epiphytes may be further picked apart with the hands or mouth, and eventually dropped. Vegetable matter was rarely seen to be ingested and, in most cases, this is probably incidental—for instance, filaments of moss are found intact in the faeces (cases in which leaves were clearly eaten were scored as such). Items are usually bitten or picked from the removed material, and picked, licked or bitten from the underlying surface. Lepidopteran larvae, cocoons, adult bugs or beetles, and (rarely) Orthoptera were found in this way.

(b) *Dead wood* (4·7% of all feeding observations). Dead branches up to 10 cm in diameter are broken off, cracked apart, and the broken ends investigated; smaller sections may then be bitten off or crushed with the jaws. Items are then bitten or licked from the exposed surfaces. Mangabeys may also break off larger chunks of rotten wood with their teeth, prying them apart or digging through them with their fingers or hands.

(c) *Dead bark* (1·7%). Dead bark is often split away, again usually with the teeth, and as with rotten wood, items may be picked, bitten or repeatedly licked from the wood removed or that exposed beneath. Ants, termites, adult stag beetles (Passalidae), coleopteran and other larvae were among the items taken from dead bark and wood.

(d) "*Sticks*" (2·3%) (Fig. 1c). Both dead sticks, live twigs and vines may be crushed and split with the teeth, items from within them being eaten. Use of this substrate is apparently peculiar to mangabeys, at least in the Kibale forest. This type of foraging is confined to a small number of plant species, particularly lianas, distinguished by having a soft, sometimes chambered, pithy core. Insects, sometimes small ants, can often be found within channels in the pith, and rapidly repeated licking is the feeding motor pattern most frequently observed. In Central America, trees of the genus *Cordia* have specialized chambers in the pith containing ant colonies (Bequart, 1922); it is of interest that *C. millenii* is the tree species in Kibale most intensively utilized for this type of foraging.

(e) *Leaf debris or dead leaves* (2·4%). The most common locations for this type of foraging were large, flat-leaved epiphytes, especially *Platycerium*. Dead leaves and sometimes live ones were removed and the interstices and surfaces examined; withered leaves were sometimes unrolled or picked apart. The unrolling of curled or withered leaves also took place when they were found in some tree species, especially *Celtis durandii* and *Markhamia*. A similar type of foraging was observed in accumulations of dead leaves such as those in tree crotches, hollow holes, and abandoned chimp nests. Items were generally picked with the fingers from these places, and included ants, larvae and pupae.

Another type of leaf foraging involves *Dracaena steudneri* Schweinf. This member of the family Agavaceae bears its leaves in a close-packed rosette at branch ends. Mangabeys pull the curled young leaves from the centres of these rosettes and unroll them, licking or biting at the fleshy bases. As these rosettes collect rain, this "feeding" may be a means of obtaining water; however, the possibility that the water may contain nutrients secreted by the plant, or in the form of debris or insects living in them, cannot be ruled out.

(f) *Live leaves* (1·5%). These are sometimes picked or pulled towards the mouth and something bitten from them, the leaf remaining substantially or completely intact. In some cases, the items taken were seen to be cocoons or, more usually, galls; leaves collected from those trees utilized extensively (primarily certain individuals of *Aphania*, *Celtis durandii* and *Diospyros*) were frequently gall-infested.

(g) *Bare surfaces* (0·4%). As previously mentioned, this was the least commonly observed type of insect foraging. However, it was also the most conspicuous, and the items taken most easily identifiable. Motor patterns included picking with one hand, biting, single or repeated licking. Rapid one-handed grabs were very rare, although winged ants and an orthopteran were taken in this way. A mangabey once captured a large flying dipteran between its hands, rising on its hind legs to reach it.

Crematogaster and other ant species, and several types of cocoons, were commonly taken from bare bark or lichen surfaces; aphids, caterpillars, and a large gryllacrid orthopteran were also eaten. This last was rubbed on the branch before being consumed, an action rarely seen among mangabeys. The taking of tent caterpillars and aerial webs, probably containing spiders or larvae, is included here; and on one occasion, an ant nest was broken apart and the resulting ants picked rapidly from the fur.

(h) *Other*. One additional type of insect foraging formed an undetermined proportion of the diet. In a number of tree species, fruits were found to be heavily infested with insect larvae. Fruit-dwelling insects were most noticeable in figs, occurring in all *Ficus* species used by mangabeys, but particularly *F. brachylepis*. The pollinating wasps (cf. Ramirez, 1970; German, 1972) were undoubtedly included in the array of larvae found in figs, and a great variety of braconid and chalcid wasps, parasitic both on the fig and on its inhabitants, were identified from casual collections of *F. brachylepis* fruit. In addition, some individual trees suffered virtually complete loss of their fruit crops due to larvae of a weevil, *Omophorus stomachosus* Boh. These weevils consumed the reproductive parts of their figs, the fruit never growing to more than half normal size and showing no signs of ripening. Samples of figs taken from *F. brachylepis* split individual trees into two subsets: those which (though containing a variety of small insect larvae) bore crops of normal ripe fruit, and those on which 80–90% of the figs were hard, latex-filled galls containing weevil larvae. Mangabeys fed on both types of tree; however, when both were available, longer periods were spent feeding in the latter. Further, although actual ingestion of larvae was impossible to observe, mangabeys dropped most of each fig they took but never dropped larvae. Inspection of fallen fig parts indicate that those dropped by mangabeys had a higher frequency of infestation (as evidenced by cavities or frass in the fruit) than did fruit otherwise fallen from the same tree ($P \ll 0.01$). Mangabeys may thus select insect-infested fruits both within and between trees.

Other types of food may also contain substantial numbers of insects. A type of mushroom avidly eaten by mangabeys contained a variety of small insects between the lamellae. Fruits of *Pancovia turbinata*, the major item in the mangabey diet in March 1973, were heavily infested with larvae, including those of a beetle, braconid wasps, eucosmid moths, and particularly the tephritid fly, *Pterandrus rosa* (Karsch). In a sample of 35 fruits taken from the tree, 33 contained larvae. Mangabeys ingest the pulp and presumably the larvae found in it, discarding the skin and usually the seeds. In such cases, fruit-eating by mangabeys may be viewed as a form of insectivory.

2.3.4. *Vertebrates*

Consumption of vertebrate prey is unusual, but it does occur. A subadult male once ate the eggs of a dove-sized bird, and, although I hardly ever found nests, mangabeys may be more successful. One suggestive indication is that mangabeys were sometimes mobbed by birds; extremely effective mobbing by a colombid was once seen. The monkey slipped while under attack and fell 20 m, subsequently remaining, cowering, in the understorey. A more spectacular case of vertebrate capture was that of a small (0·5 m) green snake by an adult female mangabey (M. S. Waser, pers. comm.). The female bit the head off the snake, which it gripped around the neck, and stuffed the writhing remains into her cheek pouches, grunting contentedly.

3. FEEDING SELECTIVITY

3.1. Degree of Selectivity

Chalmers (1968a, p. 256) states, "virtually every tree visited by the mangabeys provided some food for them". In this study as well, the list of species utilized by mangabeys closely approximates that of species enumerated in vegetational transects (Table I). However, the rank orders of those trees appearing both in the vegetation sample and in the mangabey diet are poorly correlated ($r = 0.21$), and several tree species used extensively by mangabeys were not represented at all in the vegetational sample. These and other uncommon trees were sometimes used so extensively when they did come into fruit that they dominated the movement patterns of mangabeys during this period (see below).

A small number of tree species was clearly avoided by mangabeys.

TABLE I

Tree enumeration, Kanyawara

Rank	Species	No. in total sample	No. per hectare	Rank in mangabey diet
1	*Markhamia platycalyx* (Bak.) Sprague	275	47·59	13
2	*Diospyros abyssinica* (Hiern) F. White	249	43·09	1
3	*Celtis durandii* Engl.	215	37·20	2
4	*Funtumia latifolia* (Stapf) Stapf ex Schltr.	113	19·55	28
5	*Teclea nobilis* Del.	110	19·03	24
6	*Uvariopsis congensis* Robyns & Chesquière	104	18·00	15
7	*Bosqueia phoberos* Baill.	69	11·94	43
8	*Strombosia scheffleri* Engl.	62	10·73	16
9	*Millettia dura* Dunn	30	5.19	12
10	*Strychnos mitis* S. Moore	29	5·02	44
11	*Celtis africana* Burm. f.	27	4.67	9
12	*Chaetacme aristata* Planch.	27	4.67	36
13	*Dombeya mukole* Sprague	26	4.50	—
14	*Parinari excelsa* Sabine	25	4·33	3
15	*Olea welwitschii* (Knobl.) Gilg & Schellenb.	19	3·29	8
16	*Linociera johnsonii* Bak.	17	2·94	31
17	*Premna angolensis* Guerke	16	2·77	7
18	*Lovoa swynnertonii* Bak. f.	15	2·60	47
19	*Pancovia turbinata* Radlk.	15	2·60	5
20	*Mimusops bagshawei* S. Moore	14	2·42	40
21	*Chrysophyllum gorungosanem* Engl.	13	2·25	34
22	*Aningeria altissima* (A. Chev.) Aubr. & Pellegr.	12	2·08	29
23	*Cassipourea ruwensorensis* (Engl.) Alston	12	2·08	45
24	*Trema orientalis* (L.) Bl.	12	2·08	50
25	*Neoboutonia macrocalyx* Pax	10	1·73	25
26	*Fagaropsis angolensis* (Engl.) Dale	8	1·38	32
27	*Ficus brachylepis* Welw. ex Hiern	8	1·38	4
28	*Aphania senegalensis* (Juss ex Bernh.)	7	1·21	21
29	*Cordia millenii* Bak.	6	1·04	17
30	*Ficus exasperata* Vahl	6	1·04	6
31	*Ritchiea albersii* Gilg	6	1·04	30
32	*Leptonychia mildbraedii* Engl.	5	0·87	—
33	*Monodora myristica* (Gaertn.) Dunal	5	0·87	23
34	*Newtonia buchanani* (Baker) Gilb. & Bout.	5	0·87	22
35	*Symphonia globulifera* Linn. f.	5	0·87	14
36	*Balanites wilsoniana* Dawe & Sprague	4	0·69	37
37	*Tabernaemontana holstii* K. Schum.	4	0·69	46
38	*Pterygota mildbraedii* Engl.	4	0·69	35
39	*Spathodea nilotica* Seem.	4	0·69	33
40	*Pseudospondias microcarpa* (A. Rich.)	3	0·52	26

(*continued*)

TABLE I (*continued*)

Rank	Species	No. in total sample	No. per hectare	Rank in mangabey diet
41	*Rauvolfia oxyphylla* Stapf	3	0·52	—
42	*Erythrina abyssinica* Baker	2	0·35	11
43	*Fagara angolensis* Engl.	2	0·35	—
44	*Harungana madagascensis* Lam.	2	0·35	52
45	*Macaranga schweinfurthii* Pax	2	0·35	—
46	*Mitragyna rubrostipulata* (K. Schum.) Harv.	2	0·35	—
47	*Sapium ellipticum* Pax	2	0·35	—
48	*Xymalos monospora* (Harv.) Baill.	2	0·35	—
49	*Apodytes dimidiata* E. Mey.	1	0·17	27
50	*Albizia grandibracteata* Taub.	1	0·17	49
51	*Ficus eriobotryoides* (Kanth & Bauche)	1	0·17	10
52	*Ficus natalensis* Hochst.	1	0·17	18
53	*Polyscias fulva* (Hiern) Harms	1	0·17	—
54	*Oxyanthus speciosus* D.C.	1	0·17	—
55	*Blighia unijugata* Bak.	1	0·17	20
56	*Ficus mucoso* Welw. ex Ficalho	1	0·17	—
57	*Randia urcelliformis* Hiern	1	0·17	—
58–71	sp. indet.*	45		

* 14 species could not be identified either by the author or by T. Struhsaker. It is possible that a total of fewer than 14 species is involved.

Fruits of *Balanites*, *Lovoa*, *Macaranga*, *Rauvolfia* and *Strychnos* were never eaten, although they were present and eaten by other animals. Similarly, a number of items (fruits of *Bosqueia*, *Cordia*, *Harungana*, *Pseudospondias* and *Strombosia*, and flowers of *Tabernaemontana*, *Markhamia* and *Spathodea*) were eaten only once or rarely by young animals and never by adults. Again, fruits of some relatively common species (e.g. *Teclea*) were eaten to a moderate extent but did not seem to be sought out by mangabeys.

Moreover, within a species mangabeys generally select only a single part. Of the 46 tree species used as sources of fruit, flowers, or leaves during 1972–73, mangabeys fed on all three phytophases of only three species. Fruits and flowers were used from four, fruits and leaves from seven, but fruits only from 30.

An indication of the degree of selectivity for different tree species can be derived from the relative number of observations of feeding on each species, divided by its relative abundance as estimated from tree enumerations. Similar calculations can be carried out for separate phytophases. These selection ratios may not, however, be directly comparable to those available for other primates (e.g. Clutton-Brock, 1972; Struhsaker, 1975) due to differences in methods of collecting feeding data and in sample sizes. In addition, they incorporate an important assumption: that the amount of food present per tree during the study period is similar between species. There are at least two reasons why this may not be true. (a) Size of fruit crop may vary between species. Data on canopy size are available for some species (Struhsaker, pers. comm.) and indicate that mean canopy height plus width for the largest species (e.g. *Ficus*, *Parinari*) is roughly twice that for the smaller (e.g. *Celtis durandii*, *Diospyros*). The density of food on a tree also differs substantially between species. Little information is available on this, and it may be a major cause of "selectivity". (b) Trees may fruit at widely varying intervals, and some of the enumerated trees may not be monoecious or reproductively mature. For this reason, selection ratios calculated for fruit are less satisfactory than those for more permanent items such as mature leaves or, possibly, insects. For instance, the Ebenaceae, probably including *Diospyros abyssinica*, are dioecious. In a sample of ten trees checked monthly over 50 months, only two regularly bore substantial fruit crops (Struhsaker, pers. comm.); in another sample monitored over 13 months, four out of ten trees fruited. If these samples are representative of the species as a whole, the selection ratio for *Diospyros* should be multiplied by as much as five—which would raise it to 8th rank (see below).

Nevertheless, these selection ratios provide an approach to understanding the factors underlying selectivity by eliminating the effects of one variable, differential species abundance; they confirm some, though not all, subjective impressions of the importance of various species (Table II).

Diospyros abyssinica, the top ranking tree species in the diet overall and during eight of the 13 months of observation, drops to 16th rank in terms of its selection ratio (but see above). Although the most used *Ficus* species ranks 4th in terms of feeding observations, four of the five most selected tree species are *Ficus*. Fig trees, eight species of which together provide the second largest species segment (14·7%) of the mangabey diet, have a communal selection ratio ten times as great as that of *Diospyros*, the only species eaten more frequently (23·4%). Other species with striking changes are *Celtis durandii*, falling from 2nd place in terms of time spent feeding to 21st in terms of selectivity; *Erythrina*, rising from 11th rank to 3rd; and *Blighia*, from 20th rank to 6th. Perhaps of equal interest is the degree of variation between selection ratios, which range over three orders of magnitude within these 25 species (Table II).

TABLE II

Selection ratios of most-commonly used 25 tree species

Rank by overall s.r.	Species	% of diet	Overall s.r.	Fruit s.r.	Insect s.r.
	All figs	14·7	52·46		
1	*Ficus congensis*	0·7		very high	
2	*Ficus eriobotryoides*	2·8	161·99	264·08	26·14
3	*Erythrina abyssinica*	2·6	75·72	0·64	26·14
4	*Ficus brachylepis*	6·4	46·05	74·99	5·81
5	*Ficus natalensis*	0·7	43·70	73·09	2·90
6	*Blighia unijugata*	0·7	39·18	66·66	—
7	*Ficus exasperata*	3·8	36·92	60·25	3·87
8	*Pancovia turbinata*	4·2	15·97	26·75	0·39
9	*Parinari excelsa*	6·8	15·67	5·28	45·07
10	*Symphonia globulifera*	1·3	15·07	—	4·65
11	*Premna angolenensis*	3·7	13·47	5·29	6·53
12	*Olea welwitschii*	3·6	11·14	15·79	7·03
13	*Cordia millenii*	0·8	7·53	0·21	22·75
14	*Celtis africana*	3·5	7·37	2·52	1·94
15	*Newtonia buchanani*	0·6	6·78	2·82	14·52
16	*Diospyros abyssinica*	23·4	5·38	8·94	0·30
17	*Aphania senegalensis*	0·7	5·06	0·55	16·59
18	*Monodora myristica*	0·4	4·82	0·26	4·07
19	*Millettia dura*	2·4	4·55	0·56	0·29
20	*Pseudospondias microcarpa*	0·2	3·77	0·43	2·90
21	*Celtis durandii*	7·9	2·12	2·90	1·40
22	*Strombosia scheffleri*	1·0	0·91	0·03	3·42
23	*Uvariopsis congensis*	1·1	0·62	1·04	0·03
24	*Markamia platycalyx*	1·4	0·28	0·18	0·59
25	*Teclea nobilis*	0·3	0·13	0·12	0·18

Selection ratios are calculated as follows:

$$\text{Overall s.r.} = \frac{\text{no. of feeding observations in species A/thousand feeding obs.}}{\text{no. of enumerated trees of species A/ha enumerated}}$$

$$\text{Fruit s.r.} = \frac{\text{no. of fruit-feeding obs. in species A/thousand fruit-feeding obs.}}{\text{no. of enumerated trees of species A/ha enumerated}}$$

$$\text{Insect s.r.} = \frac{\text{no. of insect-feeding obs. in species A/thousand insect-feeding obs.}}{\text{no. of enumerated trees of species A/ha enumerated}}$$

Where no. of ha enumerated = 5·78
no. of thousand feeding observations = 7·670
no. of thousand fruit-feeding obs. = 4·508
no. of thousand insect-feeding obs. = 1·990

3.2. Intraspecific Dietary Variation

3.2.1. *Differences between groups*

Among groups studied in the Kibale forest, substantial quantitative differences in the species composition of the diet occurred, but there is no evidence to suggest that these were not the consequences of local vegetational heterogeneity. However, there are some less easily explained differences between the mangabeys studied by Chalmers (1968a) and those discussed here. Chalmers mentions feeding on the flowers, shoots and fruit of *Sapium ellipticum*; although the tree is not uncommon in the Kibale study area, it was never seen to be used by mangabeys. Shoots of *Celtis durandii* and *Albizia grandibracteata*, used in eastern Uganda, were available but never eaten in Kibale; nor were cultivated crops. On the other hand, *Albizia* and especially *C. durandii* fruits, eaten in Kibale, are not listed as food items by Chalmers. Thus differences in diet between groups, linked to differences in inter- or intraspecific competition, to differences in the array of other foods available, or possibly to differences in local tradition, may occur.

Finally, there may be an interesting trend towards greater dependence on leaves (Jones, 1970) and lesser use of insects (Cashner, 1972; Jones, 1970; pers. obs.) in certain West African populations.

3.2.2. *Differences between age and sex classes*

Among mangabeys, substantial sexual dimorphism and a long developmental period potentially allow feeding specialization and niche differentiation between age/sex classes. Differences in diet may arise as consequences of differing nutritional requirements as well as of intraspecific competition; both factors are probably of importance to mangabeys. However, the continua along which diets have diverged appear not to include the height and location of feeding sites.

Data from May to June 1971 indicate no significant differences in feeding heights between sexes or ages ($P < 0{\cdot}05$ in all cases), while data on branch size use during *Ficus brachylepis* feeding support the impression that items available to juveniles who venture out onto small branches are equally available to adults who bend or break them off.

Motor patterns used by mangabeys are highly flexible, and none was seen to be exclusive to any age or sex class. Nevertheless, quantitative differences in feeding behaviour exist. On the most basic level, the amount of time spent feeding or foraging is not independent of age or sex. Adult females spend the highest percentage of time feeding, followed closely by subadult males, with adult males and juveniles spending considerably less (Table III). All combinations of juveniles, subadult males, adult males and females differ significantly in this respect (adult males/juveniles $P<0{\cdot}05$, other combinations $P\leqslant0{\cdot}01$) except subadult males and females ($P>0{\cdot}05$). A substantial degree of suckling may compensate for the low feeding time of juveniles; but sitting and lying replace feeding in the adult male's time budget.

TABLE III

Age/sex differences in feeding

	Adult ♂	Adult ♀	Juvenile
% Time spend feeding	41·0	48·9	37·5
% Feeding time on:			
leaves/leaf buds	5·4	5·2	5·8
bark/pith	3·9	3·3	3·7
flowers/flower buds	3·2	3·3	3·7
fruit	66·7	55·2	59·1
insects	17·1	29·9	25·4
(i) "epiphytes"	7·9	15·2	12·3
(ii) "dead wood"	3·6	5·5	3·2
(iii) "dead bark"	2·1	1·7	1·4
(iv) "sticks"	1·7	3·4	3·5
(v) "leaf debris"	1·2	1·7	1·4
(vi) "live leaves"	0·6	1·6	2·6
(vii) "bare surfaces"	0·4	0·4	0·5
Diospyros abyssinica	30·9	20·3	20·4
Celtis durandii	8·2	7·5	8·3
Parinari excelsa	5·6	7·4	6·5
Ficus brachylepis	5·0	7·0	6·3
Pancovia turbinata	3·9	4·2	4·8
Ficus exasperata	4·2	3·7	3·6
Premna angolensis	3·3	4·0	3·5
Olea welwitschii	4·2	3·6	2·8
Celtis africana	4·5	3·5	1·2
Ficus eriobotryoides	3·3	2·4	3·0

Age and sex classes also differ in the extent to which they utilize different food types. While juveniles, adult females, and adult males do not differ significantly in the proportion of leaves in their diet, both age- and sex-specific differences occur in fruit, flower, bark and insect feeding.

Among adult males, a greater proportion of "feeding" scan records involves fruit ($P\leqslant0{\cdot}01$—but note that as a proportion of total time budget, the amount of fruit-eating by males and females is similar) and bark ($P<0{\cdot}01$) and a lesser proportion involves insects ($P \leqslant 0{\cdot}01$), than among adult females. Flowers are eaten to similar extents. An important factor underlying some of these differences is probably the greater size and strength of males and particularly of male dentition. This interpretation is supported by the fact that, although female participation is greater in nearly all classes of insect foraging, differences are slight between the degree of foraging in dead wood and males actually forage in dead bark more often (Table III). Stripping live and dead bark are obviously strenuous activities, and these types of feeding involve extensive use of the heavy incisors and canines. The lower frequency of bark-stripping ($P<0{\cdot}01$) or of foraging in dead bark and especially wood ($P<0{\cdot}01$) by juveniles, as compared with adult females, underscores the importance of size and strength in these activities.

The more extensive foraging for insects by females, particularly among epiphytes and leaf interstices, may on the other hand be related to increased protein requirements. Juveniles, which might also be expected to require relatively high protein intake, also spend a higher proportion of feeding time than males in insect foraging ($P<0{\cdot}01$). Pregnant, lactating and acyclic females have not yet been compared directly in this respect.

Juveniles eat relatively more flowers than either females ($P<0{\cdot}01$) or males ($P<0{\cdot}05$); forage more by biting at leaves than either sex ($P<0{\cdot}05$, females; $P \leqslant 0{\cdot}01$, males); and crush lianas and sticks relatively more frequently ($P<0{\cdot}01$, males; n. s., females). In other aspects of feeding, juveniles are intermediate between adult males and females (Table III).

The relative frequencies with which individuals of different age/sex categories feed on the ten most frequently used tree species have been calculated (Table III). Juveniles differ only in feeding rarely on *Celtis africana*, a reflection of their infrequent bark-stripping. Males however, differ surprisingly in their use of several species. Males spend relatively more time eating *Ficus eriobotryoides* ($P<0{\cdot}05$) and *Parinari* ($P<0{\cdot}01$) than do females, but substantially less eating *Ficus brachylepis* ($P<0{\cdot}01$). Increased concentration by females on *F. brachylepis* could be a manifestation of the relatively greater importance of insects in their diets (see p. 199). Most striking are differences in feeding on *Diospyros*, the most intensively used species among all age and sex classes. *Diospyros* fruits accounted for 20·3% of adult female, 20·4% of juvenile, but 30·9% of adult male diets ($P \leqslant 0{\cdot}01$ for differences between males and both other classes). This major dietary difference might reflect either (i) differing nutritional requirements; (ii) a superior male capability of utilizing either hard *Diospyros* seeds or the extremely bitter *Diospyros* pericarp; or (iii) an ability of adult males to displace other mangabeys from a preferred food source. Direct supplantation was, however, rarely observed.

3.3. Characteristics of Favoured Trees

What traits do intensively utilized or highly selected trees share? Plausible answers can readily be proposed for species which are commonly used for insect foraging. The most highly selected of these trees, *Parinari*, is extremely large, with an extensive branch surface area bearing heavy loads of moss and epiphytes. *Newtonia*, some *Ficus* species and *Erythrina*, also with high selection ratios, are similar in possessing either large branch areas, dense epiphyte loads, or both. Common trees which are rarely used for insect foraging (e.g. *Diospyros*, *Celtis* spp.) are generally those which maintain their surfaces relatively epiphyte-free.

It is more difficult to generalize about trees used for leaves, flowers, or fruits (see Table III). These species do not cluster into any obvious taxonomic groups (except the figs). Forest edge (*Millettia*, *Erythrina*) as well as presumed climax species (*Parinari*) are used, as are trees occurring on dry ridgetops (*Diospyros*) and poorly drained lower slopes (*Symphonia*). Mangabeys do, however, tend to choose relatively concentrated food sources. Fruits less than 0·5 cm in diameter are rarely eaten unless they occur in bunches (e.g. *Urera*). Moreover, most of the highly selected tree species bear very dense fruit crops and are themselves large trees (*Blighia*, *Ficus*, *Parinari*), or spatially clumped (*Pancovia*, *Diospyros*, *Celtis durandii*) or both (*Ficus exasperata*) (Waser, unpublished data; Struhsaker, pers. comm.). Nearly all heavily-used tree species which are thinly-distributed are also large. Many such rare species, which form a substantial proportion of the mangabey diet (Table II), also fruit asynchronously or non-seasonally (Waser, 1974, 1975).

3.4. Possible Causes of Selectivity

Until considerably more information is available on the nutritional composition of foods in the Kibale forest, the nutritional requirements of mangabeys, and the physiological ability of mangabeys to utilize nutrients in their naturally occurring forms and combinations, only speculation concerning the ultimate causes of selectivity is possible. Concentration by mangabeys on reproductive rather than vegetative plant parts has obvious nutritional consequences. Is the high fruit content of the mangabey diet related to the energetic requirements of this mobile species? Age/sex classes must also differ in energy requirements, due to differences in the types of activity engaged in, or in metabolic or locomotory efficiency (e.g. between adults and juveniles). Are differences in the intake of different plant species and parts correlated with their content of sugars or carbohydrates? Again, the relative concentration on insect foraging by juveniles and females seems reasonable in terms of protein requirements, but to what extent are the high concentrations in insects of certain minerals, vitamins, or even water involved?

A mangabey's ability to acquire an optimal balance of nutrients is limited by at least two factors: interspecific competition, and its ability to find and harvest food items and to process them digestively. In the Kibale forest, competition is potentially intense, since nearly every plant part utilized by mangabeys is also taken by three or more other primate species, and many are taken by squirrels, bats, nocturnal prosimians and viverrids, turacos, hornbills, parrots and colombids. Similarly, insect foods are taken to some extent by many insectivorous birds (notably wood hoopoes), by all three *Cercopithecus* species, and by *Colobus badius*.

Nevertheless, primates in the Kibale forest have not generally responded by becoming extreme specialists. Half-hourly scans of feeding sites in a *Ficus brachylepis*, taken during 132 observation hours spanning the entire fruiting cycle, indicate slight differences between the four major primate species using this tree (Fig. 6). *Cercopithecus ascanius* tends to feed slightly lower in the tree, *C. mitis* and mangabeys slightly higher; chimps feed primarily on large branches and only on very ripe fruit. But none of these species was confined to a narrow range of feeding sites and the two most extensive users of the tree, *C. mitis* and *Cercocebus albigena*, did not differ significantly either in feeding height distribution ($P > 0{\cdot}05$) or branch size distribution ($P > 0{\cdot}05$). The situation in large *Ficus* trees seems not atypical. Although interspecific differences in selection of food species, types and sizes, feeding heights and locations clearly occur, most tolerances are broad and substantial interspecific overlap in these parameters results.

One of the few foraging techniques which appears to be exclusive to mangabeys is bark-stripping. While *Celtis africana* bark is quite sweet, and thus probably both usable and valuable to other species, none of them appears to be able to strip it. This may be a direct consequence of *C. albigena*'s heavy jaw musculature and strong dentition, suggested by Chalmers (1968a) and Haddow (1952) to be important in the use of several types of hard seeds elsewhere in Uganda, and it may allow mangabeys to take otherwise unutilized *Disopyros* seeds in Kibale. Again, fruits of *Mondora* can be opened by mangabeys, but *Cercopithecus ascanius* or *C. mitis* have not been observed to open them (Rudran, pers. comm.; Struhsaker, pers. comm.) yet these species eat from opened *Monodora* fruits and may wait nearby while mangabeys open and feed on them, taking the contents remaining after the mangabeys leave (pers. obs.). Finally, similar factors probably underlie the success of mangabeys in obtaining insects from dead wood or under dead bark, microhabitats here virtually unexploited by other insectivorous primates.

On the other hand, mangabeys may lack the ability or dexterity to capture certain classes of insects more readily taken by the smaller *Cercopithecus* species. The lower proportion of insects taken by mangabey adults from bare surfaces and leaves (Table III) is consistent with their more efficient utilization by smaller animals, either mangabey juveniles or other species.

Considering the wide range of fruits taken by mangabeys, it seems possible that those species specifically avoided may be toxic to them, a speculation supported by the fact that two of them, *Strychnos mitis* and *Rauvolfia oxyphylla*, belong to genera notable for the alkaloids occurring in other species (e.g. Palmer and Pitman, 1972). Nevertheless, other primates apparently have the ability to handle fruits of these species (pers. obs.) and the extreme bitterness of many favoured mangabey foods implies that mangabeys also are able to handle some potentially toxic compounds. The surprisingly large stomach, intestine and particularly caecum of *C. albigena* (Jones, 1970) is of interest in this regard. It is tempting to suggest that different cercopithecines might specialize in degrading or detoxifying different classes of chemically-related compounds. Such species-specific specializations would influence the stage of ripeness or development and the rate at which items could be taken, as well as accounting for the total absence of certain items from some species' diets.

Again, one may wonder how important species-specific differences in ability to find and recognize different food sources may be. Can mangabeys better remember the location of distant food sources or anticipate fruiting time for those fruiting at long intervals? Can they better interpret the cues provided by other animals or by the plants themselves which may indicate or predict the presence of food? Can they more quickly recognize fruits just reaching ripeness, or likely to contain insects? Can some primates more rapidly adapt to novel food sources and thus exploit rare and unusual ones? Has liana-splitting, presumably within the manipulative capabilities of the *Cercopithecus* species, never been learned by them? Such behavioural (and ultimately neural) factors may be as important as the more obvious morphological ones in determining what food types a species successfully utilizes.

Narrowing the range of items taken is one way, but not the only way, of escaping competition. Some of the behavioural abilities mentioned above, for instance, may reduce competition while *increasing* the range of items within which a species can switch. Finally, the dynamic pattern of food availability in tropical forests may allow certain species to coexist even when competition is intermittently intense. Such factors are probably of great importance to mangabeys (see p. 220).

4. TEMPORAL PATTERNING OF FOOD CHOICE

4.1. Short-term Patterning

A mangabey group generally feeds either when stationary, with its members scattered throughout one or several fruiting trees for periods of half an hour or more, or else in a foraging progression, during which members advance gradually on a broad front, feeding opportunistically on items in their path and spending only short periods in any given tree. These two patterns usually alternate, although occasionally movement between feeding trees takes the form of a rapid, single-file progression (see also below). It is rare for the group to feed more than an hour or two in any one tree, so that a whole flower or fruit crop is never depleted in one sitting.

Often, however, a group will revisit the same tree on succeeding days, and cases of nearly complete destruction of a tree's flower or fruit crop over a period of weeks were observed. The limited number of items reaching the proper stage of ripeness, rather than a limit on the amount of a single food item mangabeys can handle digestively, seems a primary reason for this. A group will often leave one tree after an hour to move to a nearby conspecific, continuing to feed on the same item. Occasionally, individuals interrupted bouts of feeding in a major food source for brief feeding excursions into neighbouring trees. The possibility that short-term diversity in diet is preferred or physiologically required cannot be ruled out; dietary diversity within days is as great as that over longer periods. In addition, I had the impression that certain foods tended to be eaten in combination, although this may have been due only to a tendency for the species involved to be spatially associated. No tendency to concentrate on different food sources on subsequent days was noticed; nor was there any tendency to feed on certain items at certain times of day, except for a high probability of retiring at night with fruit-filled cheek pouches.

4.2. Seasonal and Longer-term Patterning

Although food species changed over the year, seasonal trends were not apparent in the amount of time spent feeding, percentage of different food types in the diet, or other dietary indices (Waser, 1975). In large part, this is a consequence of the temporal pattern of fruiting of major food species. The importance of trees fruiting at long or irregular intervals (Waser, 1975) is underscored by several obvious characteristics of the mangabey diet. Few species or items are eaten to the same extent in successive seasons or years. For instance, *C. africana* bark formed 19% of the diet in May and June 1971, and a similar percentage in September 1974, but only 2·9% (with a maximum of 8% in any month) during 1972–73. Feeding on *Diospyros* reached a low during September to October 1973, months during which its use was extensive, and increased during 1974. *Fagaropsis* fruits formed the 3rd ranking dietary item (13·4%) during May and June 1971, but reached only 32nd rank (0·1%) during all of the 1972–73 study (see Waser, 1975, for other examples). In many cases, species or items may not be used at all for intervals of a year or possibly much longer. Feeding on *Platycerium* young leaves and *Celtis durandii* bark, for instance, was observed during 1971 but not again until August 1974. During August to October 1974, the main study group ate the fruits of six species (including three lianas, *Fagara angolensis* Engl., and *Ficus stipulifera* Hutch.) and young leaves of one (*Blighia unijugata*) from which these items had not been taken before. Seven new species were used as substrates for invertebrate foraging. This rate of acquisition of "new" species is only slightly lower than that observed during the main study. Thus, many additional food types, which were seldom or never used—or which, due to irregular fruiting patterns, were simply non-existent during the study periods—may nevertheless be of considerable importance on occasion.

5. RESOURCES AND RANGING PATTERNS

The rarity, large size (or spatial clumping), and asynchronous fruiting of many preferred mangabey food trees, combined with the fact that fruit persists on many of them for short periods and may be edible even more briefly, results in sequentially available and concentrated food sources which are likely to be separated by considerable distances. In their strategy of habitat usage, mangabeys must deal with at least the following aspects of their food supply: (a) large, temporary concentrations of food; (b) widely separated, relatively rare trees; and (c) long, variable, and possibly unpredictable intervals between fruit availability in any given location.

The importance of single, large, widely-scattered trees is reinforced by examination of the short-term ranging patterns of mangabeys. Areas of intensive use by mangabeys are scattered throughout their home range, rather than being concentrated in a central "core" area, and their locations correspond to those of large fruiting trees (Waser, 1974, 1976). Data on habitat use during two ten-day periods in 1972 (Figs 7 and 8) illustrate the short-term pattern of mangabey movements (see also Waser, 1975; Waser and Floody, 1974). Distribution of time in quadrats is strongly skewed during most months; for instance, one quadrat out of the 181 used accounted for 9% of the scan records in May, and one out of 129 accounted for 16% in September. The most heavily-used quadrat in each monthly sample period usually ranked first by a substantial margin and, in ten out of 12 months, could be traced to a single large fruiting tree (*Ficus brachylepis*, *F. exasperata*, *F. eriobotryoides*, *F. congensis*, *Blighia unijugata*, *Olea welwitschii*, *Diospyros abyssinica*). The exceptions were March 1973, during which time 44·8% of the diet was fruits of *Pancovia turbinata*, a small synchronously-fruiting understorey tree with a very clumped distribution; and December 1972, when no large fruiting trees were found by the group.

Subjectively, the mangabey movement pattern appears to be centred on a large fruiting tree, which the group repeatedly visits over periods of days or weeks while covering the surrounding areas much more evenly. In September, the group spent several hours each day in one *Ficus eriobotryoides*, supplemented by movements (still extensive) which resulted in rather systematic coverage of all the area within about 500 m of that tree (Fig. 7). In May (Fig. 8) the pattern was similar, with one long excursion out of the vicinity of the "focal" tree, looping back to it a day later. The area within several hundred metres of the focal tree generally contains a variety of the smaller, more common species in which mangabeys often took fruit, or foraged for invertebrates.

When food resources from one such tree were exhausted, and no others had been located nearby during this pattern of short-range excursions, the group often left the area entirely, searching widely over its home range until it found another similar tree. In December, for instance, the group circled virtually its entire home range in six days.

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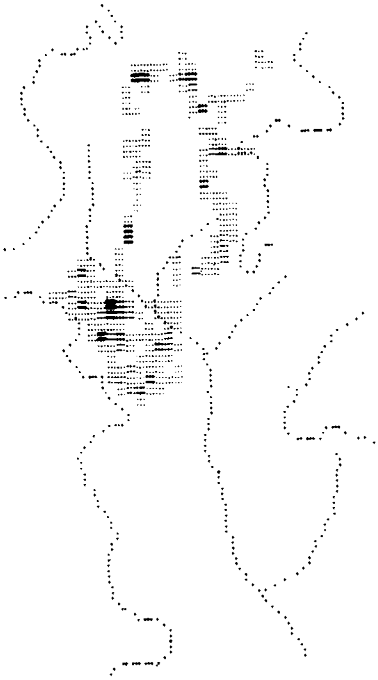

Fig. 7. Differential use of space by main study group, 1–10 Sept. 1972. Each block of six characters represents a 50 × 50 m quadrat, with optical density of characters proportional to the number of mangabeys sighted there during scans. Forest edge and streams are indicated by dotted lines.

Fig. 8. Differential use of space by main study group, 1–10 May 1972. Conventions as in Fig. 7.

This interpretation of mangabey ranging patterns, pieced together largely from observations during ten-day blocks, is supported by several unusual aspects of observed movements. First, if this picture is correct, we would expect the group's net straight-line displacement between subsequent days to be relatively small while it forages in a resource "patch", but on those rarer days while the group searches for or moves to a new patch, the displacement should be much longer. The expected bimodal distribution is indeed found (Fig. 9).

Second, a plot of cumulative home range size would be expected to level off quickly as mangabeys forage within a fig-centred patch, then to rapidly increase as a period of search for a new tree begins, levelling again after the new patch is found. Cumulative home range size measured over a period of 40 days in 1971–72 shows just such a step

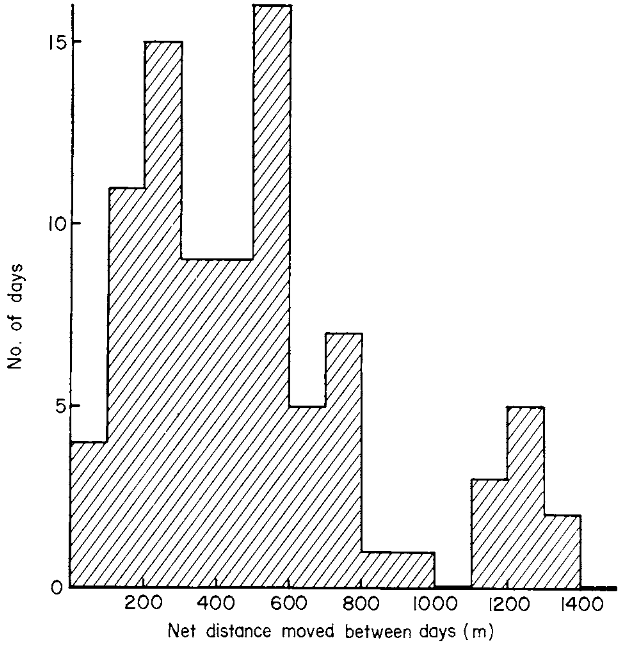

FIG. 9. Net straight-line displacements of the main study group over 24-hour periods, May 1972–April 1973.

pattern, including three separate steps each 1 to 2 weeks long (Waser and Floody, 1974). Over a longer period, such a pattern would explain the surprising finding that cumulative home range size continues to increase at a barely diminished rate even after a year's study (Waser, 1974, 1976).

Finally, this pattern explains the home range sizes found among mangabeys, which in the Kibale are enormous. The area of 4·1 km^2 used in 1972–73 (not 140 ha, as incorrectly published in Waser and Floody, 1974) is several times that of any other Kibale forest monkey or of most other forest primates.

In addition to forming an efficient strategy for the discovery and utilization of large fruiting trees, the mangabey pattern of movement lends itself well to the exploitation of sedentary invertebrates. Once a mangabey has peeled off the moss or dead bark or torn apart the rotten wood or epiphytes concealing such invertebrates, it seems unlikely that many of them have much chance for survival. Since few have any effective means of escape other than concealment, mangabeys probably take most of them; those which fall or are dropped by mangabeys probably have poor chances of making their way back to the microhabitats in which they can survive. Furthermore, the renewal rate of such insects is probably low, for several reasons. First, where mangabeys destroy the sites originally inhabited, these may not be readily replaced (until another hollow liana or layer of moss grows, or until another branch dies and rots). Some tropical epiphytes grow extremely slowly due to their nutrient-poor environment (Janzen, pers. comm.). Secondly, even when proper microhabitat exists, it may not be colonized rapidly, due to the poor dispersal capabilities of many of the relevant organisms and, possibly, their specialized habitat requirements. Thus there will be little point in covering the same area again until considerably later in time, and this is what mangabeys do.

6. RESOURCES, GROUP STRUCTURE AND GROUP SIZE

The spread of individuals within mangabey groups is usually high, and spatial subgroups are occasionally formed, possibly in response to the spatial distribution of food (Waser and Floody, 1974). For instance, subsets of the group can aggregate simultaneously at two or more fruiting trees, sometimes as much as 500 m apart; or they may be more evenly dispersed across 100–200 m when foraging for insects. The proximal forces maintaining these presumably adaptive patterns of interindividual spacing are likely to be social. Movement along a broad front, probably an efficient means of hunting both for thinly distributed insects and widely scattered fruiting trees, places little emphasis on leadership of the group by particular individuals, and this again may have social consequences. On the other hand, the occasional tendency for the group to follow certain individuals on long, rapid movements to new food sources, as well as the observation that these individuals sometimes wander extensively in areas far from the rest of the group (Waser, 1974; Waser and Floody, 1974) may be related to the finding of important but thinly-scattered resources. The retention in the group of individuals (of both sexes) past their reproductive prime (Waser, in prep.), as well as the unusually high level of many types of intragroup social interactions, may be favoured by the need to retain and transmit information concerning rare and seldom-available food plants. Aspects of the temporal and spatial distribution of resources have also been suggested to effect the pattern of intergroup spacing found in mangabeys (Waser, 1974, 1976).

Food may have a rather more direct effect on group size. For a uniform food distribution, doubling the size of a group will double the area over which it must move to feed itself. The energy required for foraging will thus be increased for individuals within a group, although individuals may minimize the increase by foraging in a dispersed array.

When resources are not uniform, however, an increase in group size need not necessarily carry energetic penalties. When food is clumped so that more is available in a small area than can be used by one animal, a second can join him there, and if such food aggregations are sequential and scattered in space, two individuals will have to cover the same distance as one to exploit them. Effects of group size on energetic costs of foraging in mangabeys can be empirically assessed by measuring the distances moved per day by different sized groups, or by measuring the percentage of time spent moving.

Data from six groups, ranging in size between six and 28 animals, are available. The assumption is made that these groups are exploiting food supplies of equivalent densities, which seems reasonable since the S and M group data are taken from movements in an area of range overlap, and the DS and SH ranges are also partly overlapping.

Though the data are based on a small sample of groups, it is clear that (a) distance moved per day increases with increasing group size, and (b) the relationship is not linear (Fig. 10). The data in Fig. 10 are echoed by figures for the M and S groups in 1974, when the larger M group moved an average of 150 m per day farther. Activity samples for these two groups in 1972 and 1974 indicate that the M group spent 5–10% more time moving during both years.

If the distance which had to be moved were directly proportional to the number of individuals in the group, addition of each new member to the M group would require it to move an extra 75 m per day. Data from the 28-member SH group indicate that increases in group size above 15 members may result in increases in daily movement of this order. For smaller groups, however, the relationship does not hold well, the 12-member DS group and particularly the six-member S group travelling farther than they should. Extrapolating back, we can see that a group of even one mangabey would have to move substantial distances during the day. A least squares fit to the six means gives a $y(1) \simeq 600$ m; including only the smaller five groups gives $y(1) \simeq 800$ m.

These figures indicate that up to a group size of 12 to 15 animals, the energetic costs to group members of adding a new member (and perhaps the costs to a non-member of joining) are relatively slight; above this size, the costs may become abruptly greater. Assuming that there are other benefits of sociality which can overcome the small energetic cost of foraging slightly longer distances, we might then

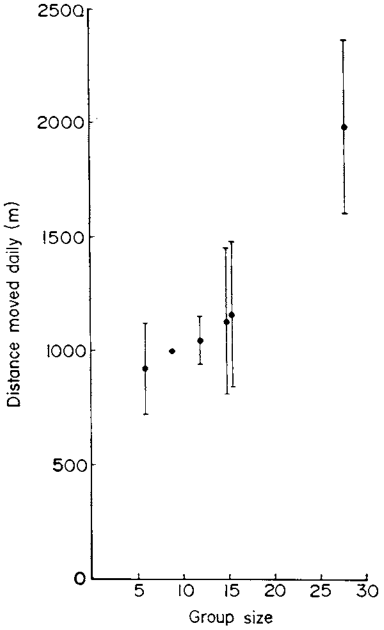

FIG. 10. Distance moved per day (daily range) as a function of group size (mean and s.d.). Groups involved, in order of increasing size, are: S (10 days' data); WR (1 day); DS (3 days); M, 1972–3 (107 days); M, 1971 (22 days); SH (5 days). See Waser (1974) for a description of the methods used in measuring these daily ranges.

expect a modal group size for the species to be about 15 animals. Larger groups would gain substantially by splitting. Although data are few, such a central tendency is apparent in the species as a whole (Cashner, 1972; Chalmers, 1968a; Jones and Sabater Pi, 1968; Struhsaker, 1969; Waser, unpublished data).

As has been argued, foraging in groups will not be costly so long as the size of group does not exceed the capacity of these food patches (Kummer, 1971). If the group exceeds this size, it will do better to split either temporarily or permanently. In mangabeys, a variety of tree sizes is used; in smaller trees, feeding parties may temporarily separate, and this separation is one factor responsible for high group spread. It might be argued that since small trees are usually common (e.g. *Diospyros*, *Celtis*) or clumped (*Pancovia*), the group as a whole is rarely required to move far to the next one, and foraging in a few more trees should not impose substantial costs. Nevertheless, data from the S and M groups show a clear tendency for increasing aggression in small food patches with increasing group size; the rate of observed chases or displacements in fruiting *Diospyros* trees was three times as high in the larger group. Moreover, the objection does not apply to large, scattered trees, of which more than one will not often be fruiting in close proximity. Although all members of the M group were sometimes seen to feed within a single *Ficus*, such was not the case with even the largest trees for the 28-member SH group. The need to visit larger numbers of such widely separated trees may account for the substantially longer distances moved by this group.

7. DISCUSSION

The home range of one mangabey group is estimated to contain 100 000 trees over 10 m high, only a very small number of which represent significant sources of food at any given time. A premium is obviously placed on means of acquiring, transmitting and retaining information concerning the location and timing of food concentrations, and on their efficient use.

Kibale forest mangabeys have become efficient followers of evanescent food superabundances, shifting erratically over several square kilometres of forest. Considerations of food distribution dominate their movement patterns and have ramifications for the temporal patterning of activities, the number and distribution of individuals in a group, and the nature of both intra- and intergroup social interactions.

In home range size, ranging patterns, and population density, mangabeys differ radically from sympatric omnivorous primates (e.g. Waser and Floody, 1974). How do these primates coexist while maintaining considerable overlap in diet, and why do they demonstrate such differences in ranging?

It is possible that, despite extensive feeding overlap, subtle differences such as the type of insects exploited allow mangabeys, *Cercopithecus mitis*, *C. ascanius* and *Pan troglodytes* to coexist. If the factors limiting populations of these species differ slightly, each species may exhibit competitive superiority in a small subset of resources, allowing coexistence despite the common use of most of them. For instance, at fig and other major fruiting trees, mangabeys are nearly always able to displace *Cercopithecus ascanius*, and usually *C. mitis*. This superiority at such sites allows them to arrive at fig trees later in the day than *Cercopithecus* species yet gain a significant proportion of the fruit (pers. obs.; Rudran, pers. comm.). Nevertheless, these species here maintain much higher population densities than do mangabeys (Waser, 1974; Struhsaker, 1975). They must, therefore, be competing more effectively for some types of resources—perhaps new leaves, thinly dispersed fruits, or certain types of insects. In areas where fewer primate competitors exist, mangabeys live at much higher population densities (Chalmers, 1968a). But as long as fig trees exist and act as a refuge for mangabeys, coexistence can continue despite considerable niche overlap. It may be inferred also that *Cercopithecus* species, by virtue of their superior ability to utilize other, neighbouring, resources, cannot be excluded from fig trees.

However, to search for static forms of niche separation may underemphasize the dynamic pattern of food availability in the Kibale forest. For instance, the "refuge" of fruiting fig trees is not continuously available even for mangabeys, yet as long as it is available at intervals, mangabeys may live through periods of potential competitive inferiority.

Moreover, the sudden appearances of food patches, especially those reaching spectacular, though temporary concentrations, opens several alternate routes to coexistence. For instance, mangabeys may be the first to utilize some infrequently occurring food types, thus behaving like fugitive species (Hutchinson, 1965). On the other hand, *Cercopithecus* species are likely to be the discoverers of a new fig crop within their limited home ranges (see Fig. 6) since they visit potential sites much more often. Thus, although mangabeys eventually displace these species, they obtain much of the fruit crop by being there first—a sequence repeated on a finer temporal scale on many mornings. In this case, *Cercopithecus* behaves as the fugitive species, being the first to exploit newly available resources.

Finally, some fruit crops may be large enough to saturate the resident *Cercopithecus* groups, and these primates' relatively exclusive home ranges leave the surplus available only to a new species. In fact, mangabeys may be one of a series of species exploiting very similar resources with varying degrees of opportunism, with chimpanzees representing a still further step in this direction. Mangabeys may thus be dependent for their existence on great variations in productivity within small areas and on spatial heterogeneity—in short, on the complexity of this tropical forest.

8. SUMMARY

1. *Cercocebus algibena*, generally classed as an arboreal omnivore, was observed in the Kibale forest, western Uganda, at intervals between May 1971 and October 1974. Most data on feeding and ranging come

from systematic monthly observation of one group between March 1972 and April 1973.

2. Mangabeys show no strong tendency to feed at particular times of day. While preferred trees are usually medium to large in size, mangabeys occasionally use low-stature trees and on rare occasions feed on the ground. The observed distribution of feeding heights is a consequence of the nature of preferred tree species combined with an avoidance of areas less than 10 m high.

Most mangabey feeding involves fruits, sometimes including seeds. Activities involving substantial substrate manipulation, of which bark-stripping is a striking example, are common. Flowers and young leaves take small fractions of foraging time, and mature leaves are almost never eaten. Foraging for invertebrates and occasional vertebrates is, on the other hand, an important activity. Most invertebrates taken by mangabeys are relatively sedentary, with lunges, rapid slaps and grabs being conspicuously absent among feeding motor patterns. In contrast, specialized behaviours aimed at exposing concealed insects are common.

3. Mangabeys demonstrate considerable selectivity among tree species and parts, with selection ratios ranging over three orders of magnitude. Males, females and juveniles show minor but significant differences in the proportions of different item and species in their diet, though no obvious differences in feeding height or site occur. Factors which may contribute to selectivity include morphological and nutritional aspects of the food, its temporal and spatial pattern of availability, and the behavioural flexibility of mangabeys.

4. Substantial but aseasonal differences in feeding occur between months, primarily stemming from the irregular availability of many food sources.

5. Mangabeys specialize on large but temporary food concentrations, which present them with an abundant but moving resource base. Movement patterns are well-adjusted to such a resource distribution, concentrating on single fruiting trees over periods of 1–2 weeks with concurrent forays into surrounding areas, allowing exploitation of less concentrated food and discovery of new resources.

6. Social variables, in addition to aspects of the movements and dispersion of individuals, can be explained in terms of resource distribution. Group size, in particular, may be constrained by the size and distribution of fruiting trees through the energetic costs of movements between them.

ACKNOWLEDGEMENTS

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8

Feeding Behaviour and Diet of Rhesus Monkeys *(Macaca mulatta)* in a Siwalik Forest in North India

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1. INTRODUCTION

Recent attempts to account for the diversity of primate social systems have been predicated on the hypothesis that they are functions of ecological variables. Discussion of these important relationships have proceeded with recourse to limited information on the overall survival strategies of the various species concerned. The major deficiencies have been a detailed analysis of habitats on the one hand, and insufficient attention to dietary preferences and patterns of feeding behaviour on the other. Nutritional analysis of diets and the energy costs of activities have only recently begun to figure in primate studies (e.g. Rodman, 1973a; Coelho, 1974). For the 12 or 13 species comprising the genus *Macaca*, detailed accounts of feeding behaviour have been published only for *Macaca sinica* (Hladik and Hladik, 1972) and *Macaca fuscata* (Suzuki, 1965).

This report presents an analysis of the foraging strategy of a forest-dwelling population of *Macaca mulatta* Zimmerman (Fig. 1). Much of the rhesus monkey population of present-day India is found in non-forested areas (Southwick *et al.*, 1961a, b), and this circumstance has led to frequent lumping of macaques with baboons as open country species. However, since the greater part of northern India was covered with forest within historic times (Randhawa, 1945), there is little doubt

FIG. 1. Adult male *Macaca mulatta*.

that adaptation of rhesus monkeys to open country habitats is a fairly recent phenomenon. Habitat–society relationships may therefore be best illuminated by studies based in a habitat which has characterized the species throughout most of its evolutionary history.

2. METHODS

The methods used in data collection have been described in detail elsewhere (Lindburg, 1971). I present here only the methodological details pertinent to the new information contained in this report and a description of analytical procedures which have been applied in order to elucidate certain aspects of foraging and related topics.

2.1. Recording of Behaviour

Most of the observations for this report were derived from two groups, numbering 35 and 80–85 individuals (the latter is hereafter referred to as the "main group"). The smaller group was observed in only the first two of the 12 months of this study. Total observation time equalled 527 hours, of which 41% falls between 5.00 and 12.00h, and the balance between 12.00 and 19.00h. Contact days with forest groups averaged 13 per month. From late September onward an Indian assistant was employed to map the location of the main group during periods when the author was absent. Our main procedure on each observation day was to attempt to maintain contact with the monkeys as long as circumstances permitted, and to make timed entries of behavioural activities as they were seen to occur. While this technique has certain advantages, it admittedly biases the results toward unequal representation of bolder, more approachable individuals. For this reason, precise comparative statements between age and sex classes are not attempted.

The identity of foods and portions consumed were collected on a daily basis. Distinctions between feeding and non-feeding periods were based on monitoring at approximate half-hour intervals the number of visible animals which were feeding. On each observation day we were able to distinguish between feeding periods in which a single food was being exploited as opposed to those in which feeding was more eclectic. This distinction was abetted by the tendency for groups to enter discrete stands of fruiting trees for variable periods of time, often extending over several hours in duration. Enumeration of these periods of whole-group feeding permitted a rough distinction between importance of different foods from the standpoint of time spent on each. The kinds of foods utilized at other periods were recorded, but no attempt at ranking was made. We did not attempt precise quantitative measures of intake and were not equipped to attempt nutritional analyses.

Day ranges were routinely plotted on Survey of India maps scaled to four inches to the mile. From these maps we obtained data on the length of day ranges and differential usage of portions of the total range.

2.2. Habitat Analysis and Description

The study area was located on the northern slopes of the Siwalik hills, at 30°20′ N and 78°0′ E. Siwalik forests are broadly classified as tropical moist deciduous (Champion, 1936). At our location the forest consisted of a long band running parallel to the Siwalik crest, averaging 6 to 7 km in width. Over this distance the elevation increased from approximately 400 to 1000 m, but the slopes were gentle until one approached the upper reaches. Most of the forest is government owned and managed. Cattle grazing and logging were permitted in designated areas, but the forest was otherwise closed to the public.

Monsoon rains descend upon the area about mid year and last approximately three months. Meteorological data provided by the Forest Research Institute (FRI) in Dehra Dun reveal that rainfall averaged 180 cm per year for the years 1963–65. Average daily temperatures for the same period ranged from 10·9° C in January to 27·7° C in June. Rainfall occurs periodically at other times of the year, but the combination of scanty rainfall and increasing temperatures results in increasingly dry conditions from February onward.

Forest Department records for that portion of the home range of our main group which fell within reserved forest (60%) indicate that approximately 6% of the land area was taken up by dry and heavily eroded stream beds (raos), grasslands, and mixed inferior forest (Nath, 1963). The remainder was covered with immature *Shorea robusta* Gaertn., or sal, a commercially exploited deciduous hardwood which varied in purity from region to region (Figs 2 and 3). According to Nath (1963), the mature sal in the Asarori forest was harvested more than 100 years ago. No equivalent breakdown for the portion of the range which lay within an adjoining private forest is available. However, the sal in the private portion was clearly of sapling and pole age, and areas taken up by raos and mixed inferior forest were substantially larger than in the reserved portion.

FIG. 2. Middle-aged *Shorea robusta* forest in the study area.

FIG. 3. Example of an eroded stream bed with fringe forest in the Asarori area.

In order to assess the composition of the vegetation in more detail, the author censused all trees and shrubs above 1 m in height in ten plots, each measuring 2024 m^2. Plots were spaced at 500 m intervals along a transect running NW–SE through the approximate centre of the range. In Table I, I present census results for the six most important

TABLE I

Distribution of primary food plants in ten sample plots at Asarori

	Plot number										
Food	1	2	3	4	5	6	7	8	9	10	Total (%)
Carissa	0	21	0	0	51	19	31	1	12	64	199 (8·1)
Ehretia	4	16	9	23	14	0	9	22	14	4	115 (4·7)
Grewia	0	11	15	3	0	1	0	25	1	0	56 (2·3)
Phoebe	0	0	0	0	0	0	0	0	0	0	0 (0·0)
Shorea	98	72	254	226	247	298	199	106	217	130	1847 (75·7)
Syzygium	3	2	0	0	32	41	68	27	0	51	244 (9·2)
Total	105	122	278	252	344	359	307	181	244	249	2441 (100·0)

food plants. Several conclusions may be drawn from these data: (a) the sampling provides an indication, albeit somewhat crudely, of the relative availability of the more important plant foods; (b) while varying in density from region to region, sal is clearly the dominant species (inclusion of non-food plants does not alter this conclusion), and has a virtually *continuous* distribution throughout the range; (c) other foods occur in *patches* (*Phoebe* did not occur in our sample, since it is found only in shaded ravines at higher elevations); (d) *Syzygium* and *Carissa* tend to occur together, but are temporally separated (discussed below).

We do not have data on the distribution of less important foods, such as climbers, herbs and grasses, but it is our impression that they were most abundant in the fringe forests along raos and in the least mature stands of sal. We attempted to measure their seasonal availability by use of a density board, described by DeVos and Mosby (1963). For our sampling, readings were taken from a distance of 15·2 m at 20 locations spaced at intervals of 200 m along two transects. Locations were carefully marked in order that readings could be repeated at different times of the year. Results of the ten readings per transect were pooled to obtain an average density at each reading. The results (Fig. 4) for both transects indicate a trend from medium density of undergrowth at the end of the rains to scarce conditions during the dry season. Given their location at or near ground level,

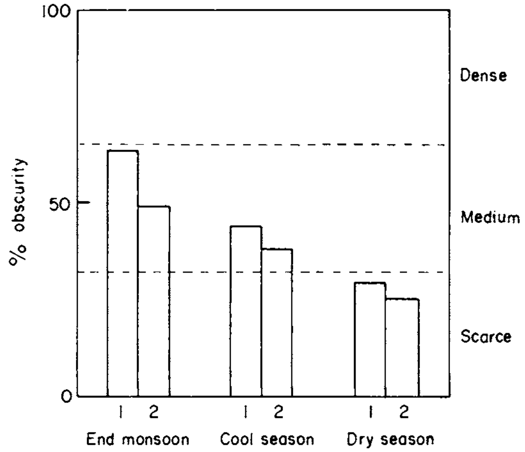

FIG. 4. Seasonal change in density of undergrowth. The columns for each season refer to two different transects.

it might be predicted that reduced availability of these items would lead to seasonally reduced frequency of terrestrial feeding.

In addition to the above, the observer routinely collected phenological data, such as season of flowering and fruiting, appearance of new growth, etc. Gupta's (1962) work on the flora of the region was consulted as the primary reference source for additional floristic details.

3. FEEDING BEHAVIOUR

3.1. The Nature of Feeding Bouts

Dispersion of group members for night resting roughly approximated dispersion during the last hours of feeding; hence, resumption of feeding on the next day could begin without relocating to feeding sites. Comparison of cool season foraging with the daily pattern at other times of the year reveals a marked seasonal effect (Fig. 5). Initial feeding was uniformly sporadic, intermixed with grooming, nursing, stretching and sunning. In the cool season this initial period was in the order of 1·5 to 2h in length, compared to a notable increase on the tempo of feeding within a half-hour of first activity during warmer periods. Given the delayed onset and shorter daylength in winter (maximum of four hours difference), the monkeys had fewer hours of daylight in which to feed. As a result, the midday rest period which

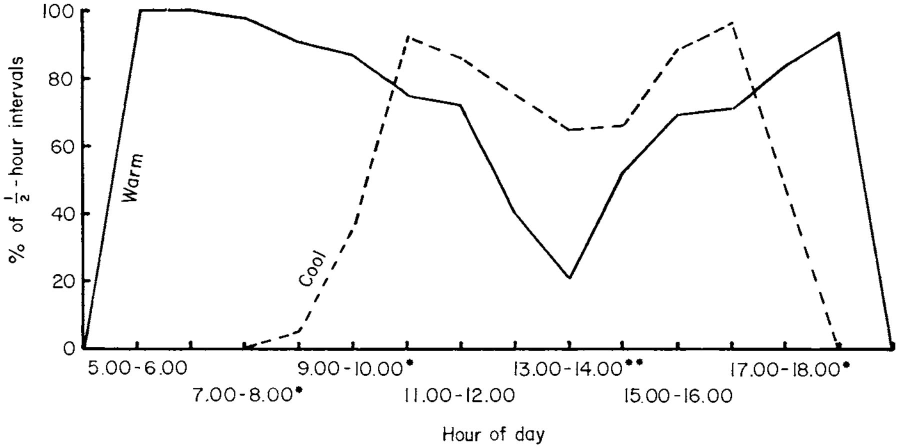

FIG. 5. A comparison of warm and cool season patterns of daily feeding activity, based on percentage of half hour observation periods in which a majority of visible monkeys was feeding.

was characteristic of the warmer parts of the year was less pronounced in the winter months. If we have accurately measured the feeding periods, the shape of the curves (Fig. 5) suggests that in winter food consumption was reduced, or else the rate of intake per unit of feeding time was increased. We are presently unable to state which of these is in fact the case. Except for the dry season, when our main group often lingered near permanent water, daytime resting and social activities, like night resting, took place at feeding sites.

Coincident with the onset of foraging was a shift from resting perches to nearby food items. Movement from item to item occurred in concert with slow, rather amoeba-like progression of the larger mass. When utilizing foods suitable for storage in cheek pouches, feeding continued during shifts between items as evidenced by chewing and by pausing in travel to nudge food from the pouches with the hand. On occasion we saw behaviour which suggested that cheek pouches enhanced safety during feeding. For example, when exploiting isolated fruit trees in open areas, the monkeys stored food in their pouches before retiring to the tree line for processing.

The density of the vegetation must have limited the reliance on vision in maintaining contact between foraging individuals. We believe contact was largely maintained by auditory stimuli, based on the periodic occurrence of "cooing" which elicited like-responses from all parts of the group. In the larger trees several monkeys could feed simultaneously, but except for mating pairs and mother–offspring clusters, they tended to avoid close contact. Terminal branches were exploited in two ways. Smaller individuals simply climbed out to the terminals, supporting their weight by clasping multiple branches with hands and feet. Adults seemed too heavy for this technique, but solved the problem by bending terminals inward and holding them in position with hand or foot while feeding. Sometimes branches were broken or bitten off and carried in the mouth to a more stable perch toward the centre of the tree. Other details of individual feeding have been described elsewhere (Lindburg, 1971).

3.2. Composition of Diet

The rhesus monkeys in the Asarori forest subsisted primarily on vegetable foods. Insects were consumed in small quantities in all months of the year. We saw no evidence of utilization of animal matter other than insects.

The vegetable diet included the products of a variety of trees, shrubs, herbs, grasses, climbers and fungi (Table II). In evaluating the relative importance of the different plant species, and of the portions consumed, we make the following distinctions:

(1) Primary food sources. Virtually whole group feeding for all or part of an observation day on one or two foods.

(2) Secondary food sources. Foods which typified periods when no single item was dominant, or which were supplemental foods during feeding on primary sources.

(3) Incidental foods. Foods infrequently consumed.

For the 92 different species on our list, six fall into category 1, 27 into category 2, and the remainder into category 3. Finer distinctions were attempted only for the primary foods, for which it was possible to make an assessment of usage on the basis of the duration of concentrated periods of feeding on each. By this measure, *Shorea robusta* represented the single most important food. The other primary foods, in descending order of usage, were *Syzygium cumini* (L.) Skeels, *Grewia elastica* Royle, *Phoebe lanceolata* Nees., *Ehretia laevis* Roxb. and *Carissa spinarum* A.DC. (For further discussion, see section on seasonality.)

At certain periods, feeding was limited to items in categories 2 and 3. It is possible that the cumulative total of certain of these items, used in small quantities on many days, exceeded that of the least used primary foods. They were rarely the object of extended feeding, however, perhaps because no single item occurred in patches of sufficient size to accommodate localized feeding of more than one or two individuals. Notable exceptions were short but concentrated periods of searching

TABLE II

Species totals for vegetation types and portions of plants used as food by rhesus monkeys in the Asarori forest

		Part consumed										
Type	No. of species	Shoot and stem	Seed	Flower	Leaf	Pith	Whole plant	Fruit	Bud	Bark	Root	Resin
Grasses	4	1	3									
Herbs	17	4	4	3	4	1	5					
Climbers	13	3	1		9	4		2		1	1	
Shrubs	21	2		2	15	2		9		1		
Trees	35	2	5	7	13	8		17	2			1
Fungi	2						2					
Totals	92	12	13	12	41	15	7	28	2	2	1	1

among the leaves at ground level for mushrooms (*Russula* sp.) and "puff-balls" (*Scleroderma* sp.).

We do not know the reasons for the occasional sampling of the many foods in category 3. Some were of limited abundance while others were thinly dispersed. We doubt if these factors alone accounted for their limited use, however, since those quantities immediately available at a feeding site did not appear to be exhausted. We suggest two other possibilities: (a) the incidental foods constituted a small but important source of essential nutrients, or (b) their infrequent use was a monitoring of reserves which could be tapped in times of food scarcity. In either case, the ability to utilize a wide range of plant foods was undoubtedly a crucial attribute for survival as the forests of India underwent degradation.

The amount of feeding on primary foods (all of which were fruits) in relation to total feeding time, plus the relative percentages of parts consumed for foods in category 2, indicates that the diet was in the order of 65 to 70% frugivorous. Leaves were the second most important item in the diet from the standpoint of quantity consumed.

Identity of insect foods could rarely be determined. Most of the observations consisted of monkeys snatching at insects in flight, or in examination of bark and leaf surfaces too far above ground for identification. Notable exceptions were a few occasions of grasshopper hunting during the monsoon season, occasional feeding on ant nests and the breaking open of termite mounds.

Clods of dirt and soil from termite mounds were nibbled upon in each month from September through May. Samples were found to be high in iron content, but had no other distinguishing characteristics.

3.3. Regional Differences in Diet

There is limited information on diet from other forest areas in India. We collected data on diet for a second population living on the grounds of the Forest Research Institute (FRI) near Dehra Dun, and found 24 foods (plants) which were used in both areas. An additional 45 plants were consumed at FRI, but many of these were exotics from a botanical garden. While much of the difference was the result of availability in the two areas, there is limited evidence of regional preferences among commonly available foods. For example, the monkeys at FRI made frequent use of *Lantana camara* Linn. and *Solanum hispidum* Pers., while those at Asarori did not. Similarly, sal, the most heavily used plant at Asarori, was available at FRI but hardly touched. In foothill forests near Mussoorie we noted monkeys feeding on oak (*Quercus incana*

Roxb.), barberry (*Berberis lycium* Royle) and *Rhododendron arboreum* Sm. Buds and seeds of *sheesham* (*Dalbergia sissoo* Roxb.) were the object of long hours of winter feeding during visits by the author to Corbett Park and South Kheri forests. For non-forested regions, the use of roadside trees and cultivated plants by rhesus monkeys has been amply described in other reports (Southwick, *et al.*, 1965; Neville, 1968).

3.4. Seasonal Variation in Food Choice

A schematic representation of food preferences on a monthly basis is presented in Fig. 6. The year may be divided into periods when feeding was predominantly on one or two wild fruits, and periods when the diet was more eclectic. The fruiting season for sal is roughly May and June. Flowers of this species were heavily exploited in March and April, while

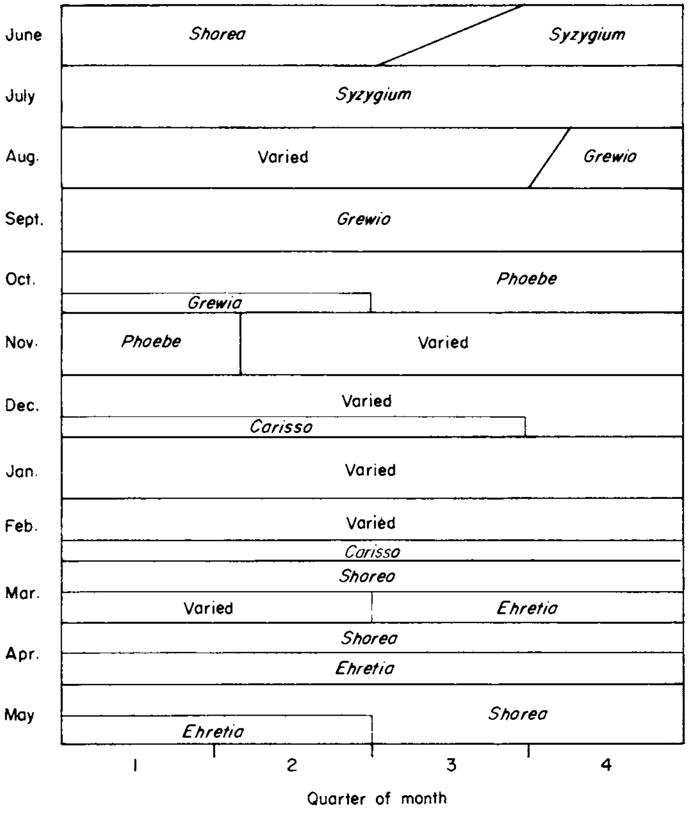

FIG. 6. Schematic representation of the most frequently used food plants on a monthly basis.

I

leaves of seedlings, buds and pith of terminal twigs were eaten in the cool season. Coincident with the use of sal from March through May was feeding on the ripening fruit of *Ehretia laevis*, a small, slender tree which was scattered thinly among the sal in shaded portions of the range.

In the latter half of June and throughout July the monkeys fed mainly on *jamun* berries (*Syzygium cumini*). Jamun is a moderate sized tree found mainly in areas fringing the erosion beds which dissected the range. August was a transitional period between jamun and the appearance of *Grewia elastica* in the latter part of the month. Wild mushrooms (reported also by Roonwal, 1956) and a variety of herbs, climbers, grasses and shrubs were exploited during this period. The fruit of *Grewia* dominated the diet from late August through September. The sounds of monkeys cracking the stones of this fruit between the teeth was an auditory aid to identification of food preferences during this period.

While *Grewia* is reported to be in fruit through November (Gupta, 1962), its limited occurrence in the Asarori forest may have been a factor in the monkeys' shift to the fruits of *Phoebe lanceolata* during October and early November. The rather limited stands of this small evergreen tree were concentrated in shady ravines at higher elevations, often extending to within 35 m or so of the Siwalik crest. For the remainder of the cool season the diet became noticeably more variable, consisting of foraging on the products of as many as ten to 15 different plants on a daily basis. The berries of a low shrub, *Carissa spinarum*, were the most important of these during December and February, and were periodically the object of concentrated feeding characteristic of fruits at other seasons.

3.5. Feeding Heights

In the rare stands of more mature sal, the upper canopy is light but fairly continuous. Understorey vegetation in these regions is scarce. The immature stands of sal and mixed fringe forests, by contrast, have a discontinuous upper canopy, but understorey growth ranging from moderate to dense.

The distance above ground at which primary foods occurred and the amount of time spent feeding on each provided a rough indication of feeding heights. Ignoring time on the ground for shifting between items, we estimated that feeding at heights greater than 10 m accounted for no more than 20% of foraging time. The majority of this high level feeding occurred during the dry season, when sal was in fruit and ground level vegetation was correspondingly scarce. Utilization of foods within

2–3 m of the ground accounted for about 41% of feeding time, and was more evident in the winter months than at other seasons, when the monkeys fed on thinly dispersed grasses, herbs, climbers and low shrubs.

4. RANGING BEHAVIOUR IN RELATION TO RESOURCE DISTRIBUTION

4.1. Essential Features of a Habitable Range

Southwick *et al.* (1961b) found zones of forest in the Siwaliks at Corbett Park which were devoid of rhesus monkeys during the dry season, and suggested that lack of water was the probable cause and that population densities are probably low in sal forests because of lack of sufficient food. The evidence from the Asarori forest shows that food would indeed be seasonally scarce in the purer stands of sal (Table I). However, such areas may constitute an important part of a larger niche, and habitability would therefore depend on their relationship to the total complex of essential resources on a year-round basis. In the sections which follow we will discuss the spatio-temporal availability of resources in the Asarori forest, and their effect on ranging behaviour.

As yet there exists very little information on the size of annual ranges for rhesus monkeys. The main group at Asarori utilized an area in the order of 15 km². Lindburg (1969, 1971) studied a population inhabiting a patch of forest at the Forest Research Institute near Dehra Dun, and found 115 individuals in five groups confining their activities to an area about 2·59 km². He concluded, however, that the FRI site bore the characteristics of a refuge area, and probably therefore supported a density much higher than occurs in undisturbed forest. On the basis of periodic sightings of recognizable groups, Neville (1968) estimated home ranges for four groups in forested areas near Haldwani as between approximately 1 and 3·1 km². We are certain that, with the possible exception of a group of nine, none of the groups at Asarori confined their activities to areas as small as Neville has reported. We are unable to state at this point whether a difference in methods or a difference in habitat quality, or some combination of these, accounts for the discrepancy in our findings.

Length of day ranges for the main group was reliably determined for 38 complete days, spread over the last nine months of the study. Mean travel distance for all 38 days was 1428 m. On a monthly basis, mean length of day journeys ranged from a low of 830 m in October to a maximum of 1895 m in March. Dry season ranges were, on the average, longer than those at other times of year, probably because of occasional long moves to and from water. Rhesus monkeys are certainly capable of much longer journeys, such as, for example, an occasion when they travelled 12 km in the last hours of the day.

The day ranges of rhesus monkeys lack the often circuitous pattern of daily movement which has been described for hamadryas (Kummer, 1968) and yellow baboons (DeVore and Hall, 1965; Altmann and Altmann, 1970). The baboon pattern is dictated by the need for safe sleeping sites which are in short supply. No such requirement exists for forest-dwelling rhesus monkeys, for which the usual pattern is to use the trees immediately at hand at the day's end. We believe that, except for travel to and from water and occasional shifts between food patches, daily travel patterns were determined primarily by the location of food items within the patch being exploited at a given time. The shortness of day journeys, compared to those reported for baboons (summarized by Altmann and Altmann, 1970), is consistent with this view.

4.2. Factors Affecting Ranging Patterns

4.2.1. *Sleeping sites*

In measuring usage of different portions of the total range we used the clearly marked boundaries of compartments established by the Indian Forest Department (Fig. 7). Records of night resting locations revealed that 28 of the 34 compartments entered during the study were used for sleeping. Nearly 50% of the night lodging sites were concentrated in five compartments (approximately 18% of the total range), but this pattern closely paralleled entry of these same areas for food and water. In the dry season the main group often withdrew from the immediate vicinity of water sources in late afternoon, but in none of the compartments could we detect a preference for particular sleeping trees. We conclude that sleeping sites by themselves had little or no effect on movement patterns.

4.2.2. *Location of food*

In Fig. 8 we show the distribution of the main vegetation types in the Asarori forest. Several of these areas probably qualify as food patches, defined by S. A. Altmann (1974) as "the most inclusive sets of food items that are situated in such a manner that it is possible for an animal to go from one to another without interrupting his feeding activities". We include among the patches the more important stands of wild fruit trees, and zones of mixed, somewhat scrubby forest which became the foci of feeding activity during a part of the cool season. Sal is the only one of the primary foods which had a nearly continuous distribution

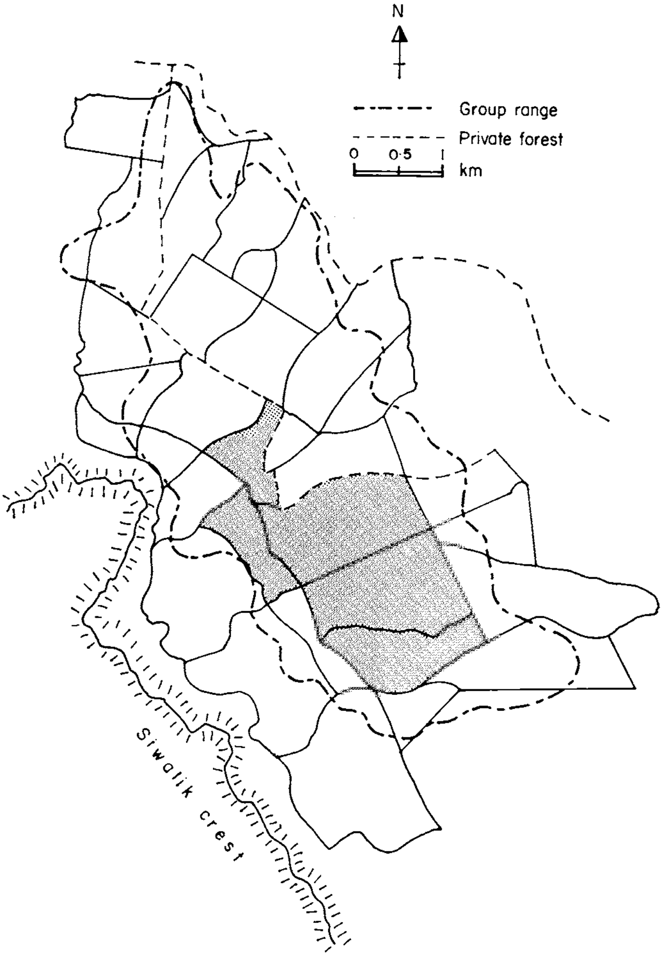

FIG. 7. Boundaries of the 34 compartments frequented by the main study group. Shaded compartments account for nearly 50% of sleeping locations.

spatially. It follows from our earlier description of seasonal availability of primary foods that for nearly two-thirds of the year ranging would conform to the location of these patches. Our records of daily movements reveal that for periods ranging from 13 to 58 days, day journeys were largely confined to movement within patches. The different patches were situated within an easy day's journey of one another, and there were periodic excursions of one to three days' duration into other parts of the range, possibly in order to monitor food availability in other patches.

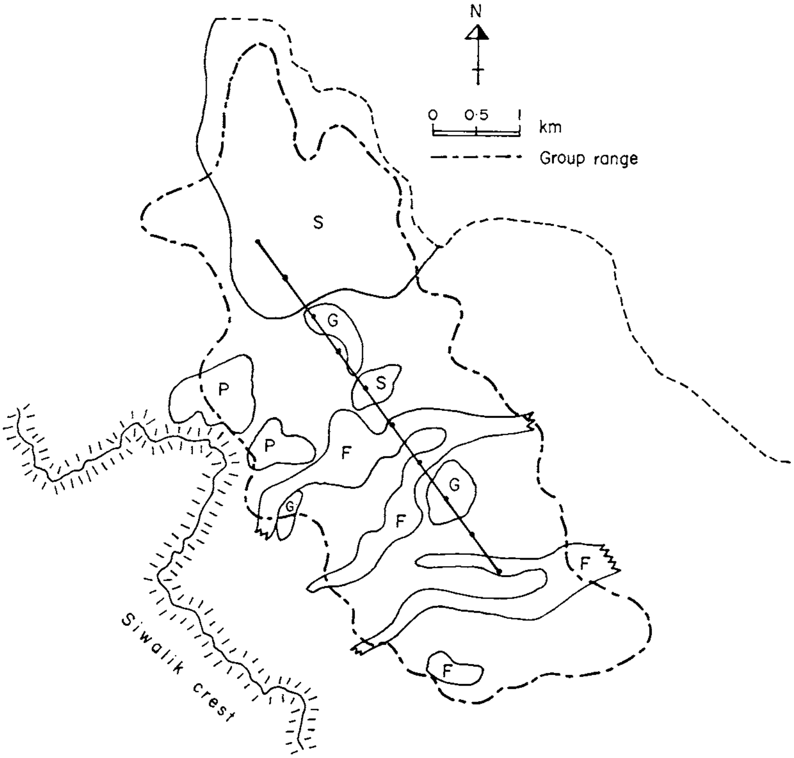

FIG. 8. Distribution of the more important food patches in the sal forest at Asarori. F: fringe forest containing *Carissa spinarum* and *Syzygium cumini*; G: *Grewia elastica*; P: *Phoebe lanceolata*; S: predominantly scrub forest; •—• transect along which vegetation was censused.

4.2.3. *Water*

Given its nearly continuous distribution, when sal became the primary food, the monkeys could theoretically range in a less constrained pattern. Availability of sal occurred during the dry season, however, and at this time the location of water replaced food as a factor limiting group movement. As the dry season progressed, permanent water could be found only in two pools at the south-eastern limit of the range. Beginning in March, the monkeys shifted to this area and remained there for most of the dry season.

In Table III we present data which show that on five of six occasions our study group left the vicinity of water on the day of, or within one to three days of, the occurrence of rain. For variable periods following rainfall water could be found in small depressions, in tree hollows, or in

TABLE III

Relationship between occurrence of rainfall and visits by one group of rhesus monkey to permanent water source

Date of rain	Amount (mm)	Date group leaves water	Date group next seeks water	Days since last rain
Mar. 5	4·6	—	Mar. 18	13
Mar. 19	23·8	Mar. 22	—	—
Mar. 27	2·2	—	Apr. 4	8
Apr. 7	2·6	Apr. 7	Apr. 12	5
Apr. 14	0·2	Apr. 14	Apr. 16	2
Apr. 23	0·1	Apr. 23	Apr. 25	2
Apr. 26	0·8	—	—	—
May 10–12	33·8	May 11	May 29	18

curled, dry leaves on the forest floor. The importance of water to group movement patterns seems to be indicated, furthermore, by a relationship between amount of rainfall and number of days which passed before the group has to again seek water, i.e. the heavier the rain, the longer moisture could be found away from permanent water. But, since food was abundantly available in the vicinity of the water source, why did our group leave the area at all? There are two possible reasons. A water source which was available near the centre of the range in the previous dry season dried up entirely in 1965, probably as a result of an unusually light monsoon in 1964. It is possible that the need for water in 1965 therefore forced the group beyond the limits of its normal range. This notion draws support from the fact that the monkeys did not frequent this part of the range at any other time of year. The second possibility relates to reduction of the frequency of contact with another group of rhesus monkeys and a group of *Presbytis entellus* which shared the same water source. Typically, such periods of contact were tense, as evidenced by branch-shaking and long-distance threats on the part of the macaques. However, the tendency to linger near water on a given day and hence to prolong the periods of intergroup contact leads us to conclude that the first explanation is the more plausible.

4.2.4. *Predators*

Potential predators in the Asarori forest were the leopard (*Panthera pardus*), tiger (*Panthera tigris*), jackal (*Canis aureus*) and several species of raptorial birds. Contacts with wild cats by the main study group were observed on five occasions. Four of these occurred in an area of scrub forest frequented by the monkeys in the winter months. This winter range was near the edge of the forest and, according to villagers, was an area where cats occasionally preyed on their cattle. The first known contact was a case of successful preying upon a fully adult male rhesus by a young tigress. This event occurred at about 7.45h on the morning of 26th November. The kill took place in an area where the monkeys had spent the night and prior to the onset of foraging. Between this event and 21st December there were at least three additional contacts with tigers in this same area. The last of these, as reported by my Indian assistant, involved a mature tiger approaching a water hole as the rhesus group was drinking. The monkeys initially withdrew but, as the tiger finished drinking, responded in a manner which we interpreted as mobbing behaviour. Despite the apparent high predator risk in their winter range, the monkeys did not forsake the area until the day following the encounter at the water hole.

In early February, in another part of the range, the study group rapidly shifted a distance of about 12 km in response to roaring by a nearby tiger. They did not return to that area until a month later.

One unsuccessful attempt by a raptor to snatch a small juvenile from the top of a feeding tree was seen. On ten occasions we heard alarm barks which were precipitated by an unknown stimulus. It is not certain that these were provoked by predators since, on other occasions, the monkeys responded with alarm to such events as a peafowl flapping its wings. None of these events resulted in subsequent migration from, or avoidance of, the area where they occurred.

On the basis of our admittedly limited data, we can confirm only one unequivocal case of relocation in response to predator danger. Surprisingly, the one part of the range holding the greatest predator risk did not produce immediate avoidance of the area. We suspect that feeding requirements during a time of relative scarcity of food may have been an overriding factor.

4.2.5. *Intergroup competition*

Substantial portions of the range of our main group were shared by other rhesus groups. We documented 48 instances of encroachment, seven of which resulted in direct contact. (A small group of nine monkeys has been excluded from this tabulation, since it appeared to be continuously within the larger range of the main group.) We estimated the area of overlap to include a minimum of 40 to 50% of the range of the main group. It is possible of course that other areas were encroached upon at times when the observer was not present. Although we could not evaluate all parts of the range equally, at least

67% of the observed encroachments involved resources of limited distribution (i.e. food patches, water). Five of the seven contacts with our main group occurred at a dry season water source. Typically, the main group arrived at water before midday and lingered nearby until foraging resumed in the late afternoon. Drinking is an activity which can be consummated in a matter of minutes; it is therefore difficult to understand the tendency to linger near water, particularly when it resulted in several hours of tense contact with another group. We offer as a speculation the possibility that the combination of high ambient temperatures and the burden of a crop of new infants had a generally depressing effect on group mobility at this time of year. Such an hypothesis is not necessarily at odds with the observation that occasional long journeys away from water, coincident with rainfall, occurred at this season. For any activity, the costs in terms of energy expenditure must be weighed against the gains to be realized by its performance.

5. FEEDING BEHAVIOUR AND SOCIAL BEHAVIOUR

5.1. General Characteristics of Rhesus Monkey Social Organization

In the refined terminology of Eisenberg *et al.* (1972), rhesus monkeys have a multimale group structure. Long-term studies on a captive population have revealed that individual groups consist of a number of genealogical units, each headed by a founding female (Sade, 1965). Males apparently lose their genealogical identity with approaching adulthood through a somewhat different process of socialization than that of females (Altmann, 1968; Lindburg, 1974). In both captive (but free-ranging) and natural contexts males may transfer to other groups, whereas females live out their lives in the natal group (Koford, 1966; Lindburg, 1969; Boelkins and Wilson, 1972). Although census data are limited, a size of about 25 to 30 individuals is probably typical for forest populations (Dolhinow and Lindburg, in prep.). Changes in group size result from mortality and recruitment through birth. Fission has been noted to occur, but information on this phenomenon exists presently only for artificially maintained groups (Koford, 1963). The probable net effect of male shifts is a redistribution of males without appreciable size change for any one group.

In species which maintain long-term, cohesive groupings of several adults of both sexes, the causes of sociality are to be sought in phenomena other than mate location and parental care (Eisenberg, 1966). In rhesus monkeys, adult males rarely engage in care-giving behaviour.

Although the basis of mate selection is complex (Lindburg, 1975), the occurrence of mating on a seasonal basis would require only that bisexual associations be of a seasonal occurrence. Year-round cohesiveness in order to derive a seasonal benefit would, in terms of energy expenditure, be a most inefficient reproductive strategy. While there are undoubtedly a number of other factors, such as the benefits of group rearing of offspring (Eisenberg, 1966), which favour mixed sex groups that are more or less permanent, enhanced predator detection and avoidance is probably the most important advantage realized from group living.

For rhesus monkeys, then, the foraging unit is the year-round group. We will argue that a modal group size of 25 to 30 individuals for forest populations represents a compromise between forces selecting for optimal foraging unit and for safety from predators. The smaller group size of arboreal monkeys, in contrast to certain terrestrial, especially non-forest, species, is believed to be a result of reduced predator pressure and more uniform spatio-temporal distribution of food resources (Aldrich-Blake, 1970b; Crook, 1970). [The term "forest" seems to have been used to refer to tropical rain forest as opposed to woodland savannah or temperate zone deciduous forest, but the diversity of forest types as well as the varied econiches within any one, as shown for example by Rodman (1973a), points up the difficulty which arises in trying to relate social organization to broadly defined habitats.] We have shown that the forest habitat of our rhesus population is both spatially and temporally diverse in terms of food distribution. The size of individual food patches at the season of least abundance, and their frequency of occurrence, probably places an upper limit on group size. Theoretically, smaller groups could exploit the food in habitats with these characteristics equally well, but with greater risk of predation. Numerous authors have pointed out the advantages of large group size for predator detection. In a forest habitat the area which any one individual can monitor is limited by the vegetation. The combined alertness of many individuals therefore increases the overall size of the total area which can be monitored. Whether or not the risks of predation are significant for forest rhesus cannot yet be determined, but even infrequent predation for mammals with low reproductive rates may occur at substantial cost to the population (Conaway, 1971). Predator pressure may therefore have selected for group size as large as can be supported by a habitat with uneven distribution of food.

5.2. Social Roles and Co-ordination of Foraging Behaviour

Co-ordination of foraging becomes important where social units utilize relatively large ranges with discontinuous distribution of resources. In an earlier report on group movement patterns in rhesus monkeys, we made the following observations:

> Typically, it was an adult of low rank that showed the first signs of stirring in a resting group. Upon coming to the ground, such an individual sat, looked around, scratched itself, plucked and ate a handful of leaves, groomed itself, and then perhaps wandered off a short distance and repeated many of the same behaviors . . . The alpha male often slept on through the initial stirrings and seemed to join the move only as increasing numbers of animals left the resting trees. The initiators, having moved off a short distance, looked back as if to note whether or not the main body was following, or sat and groomed as if waiting for the balance of the group to join them. There is a suggestion, then, that group moves did not really start until the alpha male and possibly certain of the females had arrived (Lindburg, 1971, p. 27).

This pattern bears a resemblance to group movement in hamadryas baboons, for which Kummer (1971) identified individuals who functioned as "proposers" and "deciders". Other evidence consistent with a "decider" role for adult male rhesus is the observation that, in crossing open areas, they were more often than not in the approximate centre of the progression column, probably as a result of their late start relative to that of the "proposers".

If other group members are in fact co-ordinating their travel to that of certain adult males, what advantage is realized from this differentiation of roles? One line of reasoning is that males are repositories of knowledge on where food and water are located, and perhaps also where risks of predation are greatest. This is essentially the conclusion which Kummer (1971) draws for hamadryas, in which the "decider" role was typically assumed by the older males in the population. Crook (1970) gives even greater weight to male "experience of the habitat" in suggesting that, in at least some primate societies, it is the basis of the males' association with "mother–litter families". These views seem to require either that males have better memories than females, or that males acquire superior knowledge as a consequence of greater longevity. Since both are unlikely, there is no compelling reason for believing that knowledge of the range becomes differentiated on the basis of sex.

Substantial evidence exists to show that individuals can assume controlling roles independently of status, but in our sample there does appear to be a correlation with high male rank. However, this is not to say that assertion of status is the basis on which following during the course of foraging is induced (Rowell, 1972).

Alternatively, we propose that the regulation of daily foraging by rhesus males is made possible simply by the attraction which they hold for the females, and that this attraction stems primarily from their role as protector of the group. Attraction of one sex for the other in bisexual groupings need not be equal. For rhesus monkeys there is substantial evidence showing that females contribute more to the maintenance of group cohesion than males. Lindburg (1974) found, for example, that adult females performed far greater amounts of social grooming than males, and Bernstein and Sharpe (1966) concluded from a captive study that adult and juvenile females had the highest approach scores and tended to remain in proximity with other group members more than males. Other evidence consistent with a sex difference in attraction is the fact that males will forsake their natal unit to join other groups or to assume a solitary existence, whereas these tendencies are either rare or non-existent for females. (It is of interest to note that all studies of male transfer indicate a higher incidence during the mating season when male attraction for females should be at its highest.)

The "safety-in-numbers" argument discussed above was based on the observation that vigilance is exercised on the part of all but the very young. Warning calls, similarly, are emitted by juveniles and adults of either sex, and of course male and female benefit equally from this system of combined vigilance. Other observations indicate, however, that certain protective functions are largely the prerogative of adult males. We note the following:

(a) Adult males sometimes climbed trees and scanned the area in response to mildly alarming stimuli. At times they subsequently moved off in the direction of the stimulus, as if to investigate.

(b) Only adult males positioned themselves in clear view between the observer and the group in the early stages of habituation.

(c) In 57 protective episodes, adult males participated in 65% and were exclusively involved in 49%. The lesser involvement of females appeared to depend on their proximity to incidents and on the identity of the threatened individual. (These data were derived from our FRI population, where humans and domestic dogs were the principal causes for alarm.)

(d) Mobbing responses toward potential predators were seen on two occasions (again, in the FRI population). Mobbing is by definition a group response, and the importance of males to the success of such events is obvious.

The composite picture is of a substantial though not exclusive dependence on males for protection. Bisexual grouping on a year-round basis is probably the basic antipredator strategy, but there are additional protective benefits which accrue to females and young by their association with males, and it is these benefits which account for male control of foraging.

5.3. Foraging in Relation to Energy Requirements

If the foregoing is correct, how then do adult males "decide" where a group will range on a given day? The proximate determinants probably relate to such factors as the recency with which food source in the range have been visited, or to recency and location of contacts with conspecific groups. While all individuals possess this information, the dependence on males for protection would allow their "choices" to prevail.

The question of immediate causation aside, how does a system favouring male co-ordination of foraging relate to the different food requirements of group members? While little specific information on energy costs is available, differences in body size, reproductive state, growth requirements, and individual levels of activity are characteristics which affect energy expenditure. As noted previously, males contribute minimally to the rearing of young. It may be erroneous to assume that their expenditures for reproduction are negligible, however. We had the impression that males lost weight during the mating season, probably due in part to reduced food intake, since mating time must be subtracted from time devoted to other activities. However, the confinement of mating to three to four months of the year, plus the multiple copulation pattern which characterizes a sexual pairing and the unequal sex ratios of adults, means that the energy expenditure per individual male is seasonally prodigious.

Other roles characteristic of males, in addition to the protective functions discussed above, are the policing of intragroup quarrels and the maintenance of intergroup spacing. The latter is accomplished primarily by the branch-shaking display, and in our forest population 100% of the displaying in this context was performed by adult males. Nevertheless, these activities are infrequent compared to the day-to-day burdens of offspring production borne by females. An indication of reproductive costs for females is provided by Coelho's (1974) study of captive Sykes' monkeys, *Cercopithecus albogularis*, in which he notes that lactation and pregnancy increase metabolic rates by factors of 1·5 and 1·25 respectively. Although smaller by about 30% than males (Crook, 1972), sex differences in the net costs of locomotion are probably insignificant, given the predominantly horizontal dimension of travel, and the fact that foraging as a group requires equal amounts of travel for all individuals. It must also be borne in mind that the smaller females have almost total responsibility for transport of the young. Compared with the adult males, and with immature members whose greatest expenditures are for growth and long bouts of play, adult females probably have the highest net energy expenditures on a year-round basis.

If this assumption is correct, a female's foraging strategy entails finding sufficient food while remaining within the protective sphere of the adult males. We have earlier established that the primary constraint on group movement is the location of food. This being the case, resting and social activities occur at feeding sites. Since the males do not forsake the feeding areas for these activities, it is theoretically possible that individual differences in time required for feeding could be accommodated without loss of male protection. Preliminary evidence in support of this contention is Clutton-Brock's (1974) finding that in red colobus monkeys (*Colobus badius*) females feed for longer periods than males, and the finding by Bernstein and Sharpe (1966) that in captive colonies adult male rhesus had the highest resting scores. Further verification of these points requires the documentation of individual differences in activity patterns and their respective costs in terms of energy expenditure.

6. SUMMARY

1. The study of forest-dwelling populations of rhesus monkeys provides an opportunity for further exploration of habitat-society relationships.
2. This study took place in a tropical moist deciduous forest in which primary foods are shown to be inconstant in space and time for the greater part of the annual cycle.
3. Rhesus monkeys feed primarily on wild fruits, but supplement their diet with a variety of leaves, stems, flowers, shoots and insects. There is marked seasonal variation in the availability of foods, and in the daily cycle of foraging behaviour. Most feeding occurs at heights less than 10 m above ground.
4. Day ranges reflect the movement of groups in exploiting food patches and in shifting between patches. Sleeping sites and predator avoidance are of little consequence for feeding locations. The spatio-temporal distribution of food and limited water supply in the dry season are the two primary constraints upon ranging behaviour.

5. In rhesus monkeys the year-round group and the foraging unit are equivalent. Foraging as a group affords protection from predators, but an upper limit on group size is imposed by the patchy distribution of primary foods. Daily foraging is co-ordinated by adult males, who are attractive to other group members as a result of the protection which they provide. Females probably require more food than males, and the tendency for non-feeding activities to occur at feeding sites provides a protective zone in which their greater energy needs can be fulfilled.

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Feeding Ecology of Gelada Baboons: a Preliminary Report

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1. INTRODUCTION

The gelada baboon, *Theropithecus gelada* Rüppell, is the sole surviving species of a genus which in Pleistocene times was found throughout the grasslands of sub-Saharan Africa (C. J. Jolly, 1972). Today, the gelada are confined to the Amhara plateau in Ethiopia, an area of volcanic uplift lying at approximately 1500–4500 m altitude which is dissected by the extensive gorge systems of the Blue Nile and Taccazze rivers. In their almost treeless habitat the gelada are dependent on these gorges for safe refuges and sleeping sites; consequently, they rarely stray more than 1–2 km inland from the gorge rim (Crook, 1966). This unusual baboon is of particular interest from the ecological point of view since, as an exclusive graminivore, it is one of the most specialized of the primates. It is the only member of the order which is a true grazer capable of competing with ungulates on the open grasslands. Furthermore, the species has long been put forward as a prime example of the interrelationship between ecology and social structure. Crook and Gartlan (1966), for instance, argued that the species' social organization (one-male groups and all-male groups that were capable of forming large herds) reflected an adaptation to a seasonally arid environment.

Although our 1971–72 field study was mainly concerned with social organization and behaviour, we were able to obtain enough information for a preliminary assessment of the species' ecology to be made. This paper constitutes an interim report pending the results of a more detailed study of gelada feeding ecology currently being carried out by R. W. Wrangham.

2. METHODS

2.1. Data-Recording Methods

The main sampling procedure used to obtain quantitative information on gelada diet and activity patterns was scan sampling (J. Altmann, 1974). In the present case, the samples were carried out at 20-min intervals. For each sample, a sweep would be made from one side of the herd to the other recording what each visible animal (except infants) was doing in as near an instantaneous sample as possible. Depending on the number of animals visible at any one time, the samples took 2–7 min to complete. Although as many as 350 animals might be present, many would be out of the observer's field of view. The median number of animals recorded in samples was 65 (range 1–233). Samples were generally smallest in the first and last hours of the day when the gelada were on the sleeping cliffs below the observer.

For the purposes of the samples, five categories of activity were distinguished: rest, feed, move, social and other. In the present context, only two of these require definition. An animal was said to be *feeding* if it was harvesting, passing to the mouth or biting any item; however, eating things picked from the fur during grooming was scored as grooming rather than feeding (see Sparks, 1967). An animal was said to be *moving* if it was in quadrupedal locomotion, providing it was not engaged in any form of social activity. Shuffling forwards on the haunches while feeding was scored as feeding since it was usually carried out at the same time as one or more of the activities defined as feeding.

The samples were carried out during two different seasons: July to August in the middle of the wet season, and January to February at the height of the dry season. Each sample was carried out over a period of about two weeks.

The wet season samples were taken whenever the animals were under observation, and no attempt was made to ensure an even distribution of records across the hours of the day. A total of 7319 animal-records was taken, with a median of 768 records per hour (range 375–901). Since most observation time was concentrated in the morning and evening hours, records for the middle of the day might be biased by the fact that the time at which the morning observation period was terminated may have depended on what the animals were doing (see Altmann and Altmann, 1970). The observers might have stayed with the animals longer, for instance, if something of behavioural interest was going on than if the animals were feeding quietly. Hence, records for these hours might show peaks of social activity, for example, which are in fact artefacts of the sampling procedure.

In view of this, a more determined effort was made during the dry season sample to ensure that the times at which sampling started and finished were independent of what the animals were doing. Rather than sampling continuously from dawn till dusk, the day was divided into three periods, 7.00–10.59h, 11.00–14.59h and 15.00–17.59h. On successive days the morning and evening periods were alternated with the midday period. A total of 13 863 records was taken during the two-week sample period, with a median of 1281 records per hour (range 554–2133). However, due to the fact that varying numbers of animals were visible during each sample, samples were still not evenly distributed across all hours. Table I shows the number of records obtained during each hour of the day for the two seasons.

"Instantaneous" scan sampling was chosen as the most appropriate recording strategy since it is easy to use, permits a large quantity of data to be collected in a short period of time and gives an exact estimate of the proportion of time animals spend in a given behavioural state (J. Altmann, 1974). The underlying assumption with this strategy is that animals which are visible to the observer at any given time are a random sample of the animals in the population. The organization of the gelada herd into one-male units and all-male groups tended to result in a

TABLE I

Number of records obtained from scan samples at 20-min intervals for each hourly block during the wet and dry season samples

	Number of records											
	7.00	8.00	9.00	10.00	11.00	12.00	13.00	14.00	15.00	16.00	17.00	Total
	(hour of day)											
Wet season	428	703	768	826	775	750	901	449	792	834	375	7319
Dry season	709	1508	1544	1281	2133	1543	1569	998	939	1085	554	13 863

more or less random sample of each age/sex class within the observer's field of view. Except, perhaps, for the subadult males of all-male groups, there was no tendency for the various age/sex classes to be found in different parts of the herd. Furthermore, the excellent observation conditions (see Fig. 1) meant that both the animals and their activities were clearly visible.

To determine what the animals were feeding on, we recorded the species and part being eaten by feeding animals whenever possible during the scan samples. Animals more than 100 m from the observer were discounted since they were too far away for an accurate identification to be made. However, even at closer quarters it was often easier to identify some plants than others. To avoid biasing the data against plants which were more difficult to identify, generalized categories such as "herb" and "small plant" were used in cases where a positive species identification could not be made.

In addition to the wet and dry season samples, a random sample of 231 feeding records was taken over a number of days during November in order to obtain an estimate of what the animals were feeding on at this time of year.

Finally, a crude estimate of the vegetational structure of the habitat was obtained by sampling the amount of cover in 60 one-metre square plots spaced 15 m apart along a single transect placed across the centre of the main study band's home range. In each sample, the proportion of ground level (0–30 cm) cover was estimated by eye, the proportions of grass and herbage and of green cover being distinguished. In addition, it was noted whether or not the plot had any bush (30–600 cm) or tree (more than 6 m) cover. Transects were carried out in the wet and the dry seasons separately.

Statistical comparisons were carried out using the Wilcoxon matched-pairs signed-ranks test and the Mann-Whitney U test (Siegel, 1956). In all cases, the *P* values quoted are two-tailed. It is perhaps worth noting that chi-squared tests on the pooled data for the whole sample give identical results in almost all cases except that the significant levels are generally higher.

2.2. Study Areas

The main study was carried out in the Sankaber area of the Simien Mountains National Park, Ethiopia, between July 1971 and March 1972. Comparative data were obtained from the Bole valley some 500 km to the south between May and October 1972. These two areas lay on the northern and southern limits of the species' geographical range, and were also close to the limits of the species' altitudinal range.

The Sankaber study area (13°15′ N, 38°00′ E; altitude 3300 m) consisted of a narrow ridge bounded on one side by the 1500 m escarpment face of the Simien mountains and on the other by the 600 m deep gorge of the Khabau river. The vegetation was afro-alpine in character, consisting predominantly of *Erica arborea* L. forest and dense thickets of *Hypericum revolutum* Forssk., *Rosa abyssinica* R. Br., *Solanum* sp. and other bushes interspersed by areas of more open grassland. Figure 1 illustrates part of the more open area on the ridge top and shows scattered *Hypericum* and *Erica* bushes along the cliff edge in the background. Although this photograph clearly illustrates the excellent observation conditions, much of the habitat had considerably more bush cover than is indicated here. More than 50% of the one-metre square plots sampled on the gorge side and escarpment face had some bush and/or tree cover, while about 35% of the plots on the ridge top did so (see Table V).

FIG. 1. Part of a gelada herd feeding on the ridge top at Sankaber, Simien Mountains National Park.

The Bole valley (9°25′ N, 38°33′ E; altitude 2300 m), a box canyon some 600 m deep, formed part of the Blue Nile drainage system. The habitat was similar to that in the Simien except that the *Erica* and *Hypericum* were replaced by *Acacia* spp. and *Olea africana* Mill, while *Carissa edulis* (Forssk.) Vahl. was a common bush in addition to *Rosa* and *Solanum*.

Climatically the two areas were similar although the Simien, being higher, was more extreme. The main rains last from July to early September, with short rains in March or April. However, some rain is to be expected in most months of the year, and the annual rainfall may be as much as 1500 mm. Heavy mists are common during the wet season, usually accompanied by thunderstorms and hail. Ground frost occurs nightly throughout the dry season in the Simien, but is less common at lower altitudes.

3. FEEDING BEHAVIOUR

3.1. Feeding Techniques

The gelada are almost exclusively graminivorous, and their feeding techniques reflect this extreme specialization. Feeding is generally carried out in a sitting position (Fig. 2), items being collected from immediately in front of the sitting animal. From time to time, the animal shuffles forwards a few paces on its haunches to begin harvesting a new area (Crook and Aldrich-Blake, 1968; Dunbar and Dunbar,

FIG. 2. Adult female digging for grass roots.

1974a). However, the hand actions used depend on which part of the plant is being eaten.

Grass blades are collected by alternate rotary motions of the hands, snipping off the leaves between the thumb and index finger. The blades are gathered into the palm of the hand, and when a handful has been collected the bundle is transferred to the mouth. Feeding is generally a continuous operation in which the animal masticates the previous handful of grass while gathering the next.

Grass seeds are collected either by pulling the stems through the teeth one at a time, or by stripping standing stems between the thumb and index finger. In the latter case, the seeds are again gathered into the palm of the hand as when feeding on leaves. The action used depends on the type of grass seed.

When feeding on grass rhizomes, the hands are held flexed at right angles to the forearm and the earth is removed with rapid alternate digging movements (Fig. 2). The exposed rhizomes are then transferred to the mouth. This technique is extremely efficient for obtaining both the trailing, subterranean root systems of the grasses and the roots and bulbs of small plants.

These feeding actions are highly skilled, and permit the gelada to feed on grasses at a much faster rate than other baboons (Dunbar and Dunbar, 1974a). They are made possible by two specializations in the anatomy of the gelada hand. In the first place, gelada have the highest opposability index of all the catarrhine primates (Napier and Napier, 1967), permitting them to pick individual grass blades. This is especially important in the dry season when green blades are to be found only here and there among the nutritionally useless dry leaves. Secondly, the short, robust phalanges provide a strong appendage for digging. These adaptations are of particular importance since they permit the gelada to exploit a grassland habitat much more efficiently than other primates.

When feeding on the flowers or fruits of small plants and bushes, the gelada generally pick individual items and place them in the mouth one at a time, much as other baboons do. Usually both hands are used alternately, although when the animals have to climb into bushes (as in the case of *Rosa abyssinica* or *Hypericum*), they may use only one hand while holding onto the bush with the other.

3.2. Feeding Heights

Since grasses constitute the bulk of the gelada's diet, most feeding takes place at ground level. Only 15 of the 3051 animals recorded as feeding during the wet season samples (0·5%) were not on the ground. All these records were of animals climbing into *Rosa abyssinica* bushes to reach fruits. Often, however, these could be reached from the ground: the 15 records accounted for only 16·7% of the records of animals feeding on this species. Out of the total feeding records for this period, only 3% of the items being eaten were classed as bushes, while during the dry season, less than 0·4% of the items were classed as bushes (see Table III below).

3.3. Diurnal Pattern of Feeding

The daily cycle of activity can be summarized as follows. Approximately 1 hr after dawn, the animals move up to the cliff top from the sleeping ledges below. There they settle and spend some 2 hr engaged in social activity. Between 9.00 and 10.00h, feeding begins to replace social behaviour as the predominant activity and at the same time a gradual drift along the cliff edge gets under way. Feeding continues to predominate right through the middle of the day until late in the afternoon. At the same time, movement is continual but slow, the entire herd generally advancing on a broad front as animals shift their feeding places (see Crook, 1966). This gradual drift may sometimes be punctuated by true progressions, during which the herd may move 0·5 to 1 km in a rapid march. The timing of such bouts of fast travel varies from day to day, and indeed may sometimes not occur at all. As a result, there is little indication of a peak in movement to or from sleeping sites, as has been recorded in other baboons (Kummer, 1968; Altmann and Altmann, 1970). By 16.00h, the animals have usually arrived at one of their sleeping cliffs; movement and feeding decline in frequency and a small peak in social activity is observed before the animals descend to their sleeping ledges around 18.00h. Since most movement is accounted for by slow foraging, the distance travelled in any one day is low compared with other open country species. The day range (the distance travelled by the herd during the day as measured "round-the-curve") seldom exceeds 3 km, and normally averages around 2·5 km (median 2·25 km, range 1·5–3·5 km, $n = 29$).

Estimates of both the proportion of time spent feeding and the diurnal cycle of feeding were obtained from the scan samples of activity. The distribution of feeding records over the day during the wet and dry seasons is shown in Table II. Between 10.00 and 16.00h, feeding accounted for some 50–60% of the animal's time. Averaged over the whole day (7.00–17.00h inclusive) gelada spent around 45% of their time feeding. Two estimates of the exact proportion of time spent feeding can be obtained from the data: (a) by taking an average of the hourly percentages and (b) by converting the summed raw feeding records to a percentage of the total number of samples. Both procedures give remarkably close estimates for the two seasons despite the variation in the number of records for each hour of the day: 40·6 and 43·1% respectively for the wet season, and 47·1 and 47·3% for the dry season. This difference between the wet and dry seasons is just significant ($t=10$, $P<0{\cdot}05$, $n=11$).

Consideration of the data in Table II shows that there are a number of differences between the two seasons in the distribution of feeding over the day. Firstly, in the dry season the animals tended to begin feeding earlier and continue later in the day. There is a significant difference in the amount of time spent feeding at 7.00h ($P<0{\cdot}01$), although the differences at 8.00 and 17.00h are not significant ($P>0{\cdot}10$; $P>0{\cdot}05$ respectively). (Analysis based on pooled samples for individual days.) The reason for this difference seems to lie in the spatial distribution of preferred food items (see below). Secondly, the animals spent less time feeding around midday during the wet season than during the dry season, although the difference here is not significant ($P>0{\cdot}05$, at 12.00h). This can in part be attributed to a small peak in social activity at this time of day during the wet season which might be an artefact of the wet season sampling procedure (see Section 2.1). However, it probably also reflects the fact that thunderstorms are most common around midday during the wet season. During heavy storms, the animals tended to sit in huddles and a marked drop in the proportion of feeding and moving is recorded (Dunbar and Dunbar, 1975).

TABLE II

Proportion of animals recorded as feeding during each hour of the day in the wet and dry seasons

	% of records										
	7.00	8.00	9.00	10.00	11.00	12.00	13.00	14.00	15.00	16.00	17.00
						(hour of day)					
Wet season	5.1	12.5	41·2	39·1	58·8	41·3	48·9	57·0	51·6	55·0	36·0
Dry season	19·6	22·5	40·1	55·7	53·3	51·8	50·6	54·0	59·2	57·9	53·8

3.4. Diet

More than 90% of the gelada's diet consists of grass. The remaining 10% is accounted for by a variety of tubers, fruits (mainly *Rosa abyssinica*), leaves and flowers of bushes and small plants (including

Hypericum revolutum, *Echinops* spp. and other thistles, *Cotula cryptocephala* A. Rich., *Trifolium* spp., *Salvia* sp. and *Kniphofia foliosa* Hochst.) and a few insects.

Although grasses accounted for more than 90% of the gelada's diet throughout the year, there was considerable seasonal variation in the part eaten. Likewise, the other plants eaten depended on seasonal availability. Table III gives the percentage breakdown of the animal's diet for three periods of the year: July/August during the wet season; November; and January/February during the height of the dry season. [It should be noted that, owing to the structure of the sampling procedure, the data presented here on diet reflect the proportion of time which the animals spent feeding (in the sense defined on p. 252) on the different plant types. They do not *necessarily* reflect either the proportion of time spent ingesting the various items or the quantities ingested by weight or calorific value.]

TABLE III

Percentage breakdown of diet during three periods of the year

		% of records		
Plant type	Part eaten	Jul.–Aug.	November	Jan.–Feb.
Grasses	Leaves	93·0	17·3	24·7
	Rhizomes	—	6·5	66·9
	Seeds	—	69·7	—
Herbs, plants	Leaves, stems	0·2	0·4	2·7
	Roots, tubers	3·3	0·9	—
	Flowers	0·2	3·0	0·1
	Seeds	—	1·3	5·2
Thistles	Leaves	0·1	0·8	0·1
Bushes	Leaves	0·2	—	0·2
	Flowers	—	—	0·1
	Fruits	2·9	—	—
Insects	—	0·1	—	0·1
No. of records		3051	231	3291

The data show a marked change in the proportion of time spent feeding on grass leaves, seeds and roots in response to the latter's seasonal availability. During the wet season, fresh green grass was abundant everywhere and the gelada consumed little else. By November, the grasses had gone to seed, and seeds accounted for a substantial proportion of their diet at this time. By the middle of the dry season in February, much of the grass cover had withered, although green leaves continued to be plentiful wherever bush cover provided shade from the direct rays of the sun. At this time of year, the gelada spent 67% of the time feeding on grass rhizomes and about 25% of the time harvesting blades.

Similar seasonal changes can be observed in those items which made up the remainder of their diet. The fruits of *Rosa abyssinica* accounted for about 3% of their diet during the rains when this species was in fruit. At this time of year, they also dug up the roots of a variety of tuberous plants such as *Merendera abyssinica* A. Rich. and *Moraea* sp. During the dry season, the seeds of *Trifolium arvense* L. and the leaves and roots of *Cotula cryptocephala* (a small herb which proliferated in well-watered areas) provided the bulk of the non-grass diet.

The gelada appear to make maximum use of the resources available to them. Their preferred food appears to be grass leaves, but during the dry season, when these are in limited supply and more nutrition is available below the ground, they concentrate more heavily on roots and rhizomes.

3.5. Dietetic Diversity and Selectivity

Compared with other baboons, the gelada are exceptionally specialized with regard to diet. This specialization apparently appears early in the genus' history, since all known theropithecine species show the same dental adaptations to a small item diet (large, hypsodont molars for crushing, with reduced incisors: C. J. Jolly, 1972). The theropithecines are thus primarily grassland animals adapted to occupying habitats where grasses constitute the bulk of the primary production. This extreme dietetic specialization is likely to make the gelada particularly susceptible to the effects of food resource availability on population size and dispersion (see below).

While grasses make up the bulk of their diet, the gelada are selective both with regard to the species and the quality of grass they will eat. Coarse, reedy grasses are never eaten, and areas which consist predominantly of these types of grasses are rarely entered. This was especially noticeable in our secondary study area in the Bole valley: the gelada there seldom entered the forest in the river bed or the heavily bushed lower slopes of the valley where the grass cover was predominantly of the tall, coarse types such as *Cymbopogon vallidus* Burtt-Davy and *Setaria chevalieri* Stapf & Hubb (Dunbar and Dunbar, 1974a; see also Crook and Aldrich-Blake, 1968). Furthermore, even during the dry season, when much of the grass cover was dry and brown, they fed only on green leaves.

This extreme specialization raises a number of issues. In the first place, the gelada are extremely efficient at handling the high cellulose content of the grass blades. Although fibre can be discerned in their faeces, undigested blades are rare. In contrast, the faeces of *Papio anubis* J. P. Fischer are commonly full of undigested blades after extensive feeding on new grass growth (pers. obs.). Since the digestive tract of *T. gelada* does not apparently differ from that of the *Papio* baboons (Hill, 1970), this suggests that they have evolved some unique adaptation designed to handle this problem. One possibility might be that they have acquired a specialized internal flora: however, this aspect of gelada biology has yet to be investigated. Another possibility is that the large, hypsodont cheek teeth of the gelada permit grass blades to be thoroughly pulverized prior to ingestion so that their nutritional content can be extracted. Jolly (1972) has suggested that this dental specialization has been specifically evolved to handle a small item diet. While seeds and roots also require considerable chewing, it is clear that some means of rendering grass blades digestible must have been at a special evolutionary premium in a graminivorous species lacking the specialized digestive tract of the other leaf-eating primates.

In the second place, the gelada's ability to utilize all parts of the grasses so efficiently explains why they are able to exist at such high densities in what has hitherto been thought of as a seasonally arid environment (Crook, 1966). In both study areas, the population density was around 75–80 animals per km^2 in the ranging area and around 30–40 animals per km^2 if areas not normally utilized are included (Dunbar and Dunbar, 1974a, 1975). Such densities are unusually high for a large, terrestrial primate and contrast markedly with the densities achieved by other baboons. The highest density so far recorded for *Papio* baboons is 34 animals per km^2 (Aldrich-Blake *et al.*, 1971), although overall densities are often much lower than this, generally being in the region of 5–15 animals per km^2. On the other hand, the only truly arid-country baboon, *Papio hamadryas* L., is able to exist at overall densities of around only two animals per km^2 (Kummer, 1968). At least part of the reason for this is that typical gelada habitat is actually very rich from the animal's point of view. This can be illustrated in the case of the Bole valley where a given section of gorge side was able to support three times as many gelada as *Papio anubis* baboons, largely due to the fact that grasses constituted the bulk of the primary production (Dunbar and Dunbar, 1974a).

This successful exploitation of a grassland habitat depends on the gelada's ability to utilize both the leaves and roots of grasses efficiently. The latter food source is particularly important during the dry season when green blades are in short supply. Thus, despite the obvious desiccation of the habitat during the dry season (the amount of green ground level cover fell from 86% in August to 35% in February), the gelada probably experienced only minimal food shortage at this time of year. As Struhsaker (1967b) has pointed out, grass rhizomes are a highly nutritious and plentiful source of food in grassland habitats during the dry season. At this time of year when the plants are dormant, most of their nutritional content is stored in the root systems. Grass rhizomes, of course, have virtually the same distribution in the dry season as green blades do during the wet season. Consequently, although the habitat looks impoverished to the *observer*, it is questionable as to just how poor it is from the *gelada*'s point of view. In this respect, the fact that the gelada spend slightly more time feeding during the dry season than during the wet season might reflect the fact that rhizomes take slightly longer to harvest than blades per unit calorific value. It should not, of itself, necessarily be taken to imply that the animals experience severe seasonal food shortage. Indeed, a difference of five percentage points may well be within the day-to-day variation in the amount of time spent feeding and might reflect the small number of days sampled in each case.

4. TEMPORAL AND SPATIAL VARIATION IN FOOD CHOICE

Little diurnal variation in diet can be detected during the wet season when the animals concentrated almost entirely on the new grass growth. However, the dry season data reveal some striking differences in the food items being eaten over the day. Table IV gives the percentages of the various items being eaten during each hour of the day at this time of year. It can be seen that the relative proportion of grass leaves to roots is lower during the middle of the day than during the morning and evening.

TABLE IV

Percentage of items being eaten during each hour of the day in the dry season

	% of records										
	7.00	8.00	9.00	10.00	11.00	12.00	13.00	14.00	15.00	16.00	17.00
	(hour of day)										
Grass leaves	44·3	32·9	17·4	9·3	17·5	23·2	19·3	38·5	42·9	32·2	59·5
Grass roots	47·5	44·5	79·6	88·1	72·9	72·0	77·3	59·0	54·2	46·0	38·0
Other	8·2	22·6	3·0	2·6	9·7	4·9	3·3	2·5	2·9	21·8	2·4
Number of records	61	146	436	344	656	371	331	200	310	261	121

This can be explained relatively simply by the fact that much of the bush cover in the habitat is to be found on and immediately above the main cliff face. Since this cover protects the grass from desiccation during the dry season, green blades are most plentifully available in this section of the habitat. This can be seen from Table V which shows the relevant dry season vegetational data for the three main sections of the habitat (escarpment face, ridge top and gorge side). The mean percentage of ground level cover (grasses and herbs), the mean percentage of green ground level cover and the proportion of plots with some bush or tree cover are given for each area. On the escarpment face, where some 70% of plots had bush or tree cover, all the ground-level vegetation was green. In contrast, on the ridge top where bush cover was least common, only about 15% of the available ground cover was still green, while on the Khabau gorge, which fell between these two in the proportion of bush cover, approximately 32% of the available ground cover was green.

TABLE V

Vegetational cover in three sections of the Sankaber habitat during the dry season, based on m² plots sampled at 15 m intervals

Section of habitat	% ground level cover (mean of all plots)	% green ground cover (mean of all plots)	% plots with bush/tree cover	No. of plots sampled
Escarpment	86·4	86·4	70·0	10
Ridge top	86·3	13·0	37·0	27
Khabau gorge	52·0	16·5	56·5	23

Hence, so long as the gelada remained on or near the cliffs, they could feed on grass leaves. Once they had moved away on the day's march along the ridge top, however, they were forced to feed more or less exclusively on the roots and rhizomes which were more plentiful there. Thus, the apparent diurnal cyclicity of diet can be attributed to variations in the spatial distribution of these food items and the temporal structure of the gelada's day range.

Furthermore, this very probably accounts for the fact that the gelada began to feed earlier and continued later in the day during the dry season than they did in the wet season (Table II). Their preference for grass leaves over other forms of edible matter apparently tends to result in their making as much use as possible of the leaves still available along the cliff edge before having to concentrate on roots and rhizomes.

5. SEX DIFFERENCES IN FEEDING BEHAVIOUR

During the dry season scan samples, we distinguished records for adult males and females. The data show that 829 of the 1975 records for males (42·0%) were for feeding compared with 1341 of the 2951 (45·4%) records for females. (Means of hourly percentages gave figures of 41·6 and 44·6% respectively.) This difference is not statistically significant ($t=18$, $P>0{\cdot}01$, $n=10$, there being one tie). Since adult males weigh approximately twice as much as adult females, the lack of any difference in the proportion of time spent feeding is striking. We were unable to distinguish any qualitative differences between males and females either in feeding behaviour or items eaten. Hence, females must consume proportionately more per unit body weight than do males (in fact, almost exactly twice as much). This can probably be attributed to the nutritional requirements of gestation and lactation.

6. INTERPOPULATION VARIATION

A comparable analysis of gelada diet in the Bole valley (see Dunbar and Dunbar, 1974a) revealed few differences from the Sankaber population. More than 96% of the items recorded as being eaten in scan samples were grasses. Of the remaining 4%, some minor differences were noted which can be attributed to differences in botanical composition between the two study areas. Likewise, 98·5% of the animals recorded as feeding at Bole were doing so on the ground. Observations made by us in the Geech area of the Simien mountains, by Crook (1966) in other areas in Simien and by Crook and Aldrich-Blake (1968) at Debra Libanos in the south, indicate that grasses are the main food source of gelada in all habitats.

Some quantitative differences were, however, detected between the Bole valley and Simien populations in other aspects of feeding and ranging behaviour. Scan samples taken at 10-min intervals at Bole revealed that the gelada there spent an average of only 36·2% of the time feeding. Since the Bole valley data cover both the wet and dry seasons, it is necessary to pool the two sets of Simien data before a more direct comparison between the two areas can be made. If the two sets of data for each hour are averaged, the gelada spent 43·9% of the time feeding in the Simien. The resulting difference is not statistically significant ($t=18{\cdot}5$, $P>0{\cdot}05$, $n=11$). The difference might, however, reflect the small size of the Bole valley sample and the consequently greater risk of small sample bias. Alternatively, it is possible that the small size of the foraging units at Bole and the greater dispersion of the animals resulted in less interference from other animals during feeding. In the large, compact herds of 200–400 animals found in Simien, displacements from feeding places were relatively common. On the other hand, at Debra Libanos (some 50 km north of the Bole valley) where foraging units were only slightly larger than those at Bole, Crook and Aldrich-Blake (1968) found that gelada spent approximately 47·9% of the time feeding during the wet season, a figure comparable to that for the Simien gelada during the dry season. Although there seems to be some variation in the amount of time the animals spent feeding in different areas, the diurnal pattern of activity was qualitatively similar in all three localities. On balance, gelada seem to spend around 40% of their time feeding, a figure which is generally higher than that reported for *Papio* baboons (usually around 25–30%). This probably reflects the fact that gelada diet is relatively unnutritious and requires a larger intake by weight than that required by the more frugivorous diet of *Papio* baboons.

The mean day range for the Bole valley groups was about one-quarter of the distance covered by herds in the Simien (0·6 km as against 2·5 km), although the proportion of time spent moving did not differ (17·1% at Bole as against an average of 20·5% in Simien; $t = 15$, $P > 0{\cdot}05$, $n = 11$). The difference in day range lengths can be attributed to the fact that at Bole one-male units tended to forage separately rather than in large herds as in the Simien. Hence, the distance an animal had to move to find an unoccupied patch of grass at Bole was less than in Simien where the ground was literally covered with animals. The day range figures, of course, represent only the distance covered by the group *as a whole* during the day, and do not take into account the fact that individual animals may move back and forth several times over the area occupied by the group while the unit itself does not progress a significant distance forwards. This may well have been the case at Bole, whereas in Simien units had to move to the edge of the herd to find unoccupied ground with the result that the herd as a whole progressed slowly forwards (see Crook, 1966). It is consequently likely that the actual distance covered by *individual animals* during the course of the day did not differ between the two areas, as suggested by the fact that the animals spent about the same proportion of time moving. Indeed, on the few occasions that individual units foraged alone in Simien, they tended to have much shorter day ranges than was typical of the large herds there.

7. FEEDING AND RANGING BEHAVIOUR

This aspect of the gelada's ecology is discussed in more detail elsewhere (Dunbar and Dunbar, 1975). In this paper, the results will be summarized without presenting the data on which they are based.

7.1. Food Availability, Band Size and Herd Size

The basic population unit of the gelada is the *band*. Each band consists of a number of reproductive and all-male groups and occupies a home range which overlaps to varying extents with the ranges of neighbouring bands. The band itself, however, does not necessarily constitute a foraging unit. The foraging unit, or herd, may consist of all or only some of the units of the band, and in areas of home range overlap may even consist of the units of two or more bands. However, the gelada's dependence on grass as a food source makes it likely that the size of both kinds of population unit will be affected by the local conditions of food resource availability.

It seems likely, for instance, that there will be a close relationship between the amount of grass cover available in the band's range and the size of the band. As a preliminary examination of this hypothesis we estimated the area of grass cover available for five bands, three at Sankaber and two in the Bole valley. Since home ranges (that is, the area in which each band ranged during the course of a year) overlapped extensively at Sankaber, we took into account only that area which the band used most of the time. For this purpose, the area which accounted for 75% of the band's movements was chosen. The proportion of each area covered by grass during the dry season was then estimated from the appropriate sections of the botanical transects carried out in each study area. From these two figures a crude estimate of the area of grass cover available in each home range was obtained.

This estimate of available grass was found to correlate well with the number of animals in each band, with four of the five bands having between 240 and 270 animals per km^2 of grass available. Bearing in mind the crudeness of the quantitative approach, this is a remarkably close fit and suggests that an upper limit may be imposed on the absolute densities of animals, which is of the order of about 250 animals per km^2 of grass cover available during the dry season.

It seems likely that herd size, likewise, will depend on food resource dispersion. Crook (1966), for instance, observed that herd sizes in different areas appeared to be correlated with the richness of the local habitat, irrespective of the season. Some evidence supporting this was obtained during the course of the present study. The units of the main study band on the relatively rich ridge top at Sankaber almost always foraged as a single herd of 260 or more animals. On the other hand, the band of 140 animals which ranged on the poorer habitat on the Khabau gorge side spent significantly more time doing so in two or more herds, while at Bole, likewise a poor habitat, the units foraged alone most of the time. A comparison of the distances between adult males and their three nearest neighbours in Simien and the Bole valley showed that the animals were spaced significantly farther apart at Bole. With grass cover averaging only 37% of the ground surface at Bole compared with 50% on the ridge top in Simien, it seems plausible to argue that individuals in poorer habitats may be forced to forage farther apart due to the lower density of grass cover. A natural tendency for individuals of the same unit to stay together may lead to the spatial separation of units. It might likewise lead to the spatial clumping of units which have particularly close ties, thus resulting in the band foraging in two or more spatially discrete herds.

7.2. Seasonal Variations in Ranging Behaviour

The main study band at Sankaber showed some striking variations in ranging patterns during the course of the year. In the first place, the animals made differential use of their home range during the dry season when green grass blades were more patchily distributed. Secondly, two major shifts in the locus of their ranging into areas outside their normal home range took place, one in the wet season and one in the dry season.

In the first case, the gelada tended to enter the *Erica*-covered escarpment slopes earlier in the evening and leave them later in the morning during the dry season than during the wet season. This largely reflects the continued abundance of green grass blades beneath the bush and tree cover on the escarpment face during the dry season (Table V). There was consequently a tendency for the animals to begin the day by feeding rather than socializing (see Table II) with the result that the social period tended to occur later in the morning. As a result, the period of foraging travel tended to be delayed. This can be seen from Table VI which gives the percentage of animals recorded as moving during activity samples for the two seasons. During the wet season, movement began around 11.00h and continued until around 15.00h. (The marked drop in the number of animals recorded as moving at 13.00h can, again, probably be attributed to the midday thunder-

TABLE VI

Proportion of animals recorded as moving during each hour of the day in the wet and dry seasons

	% of records 7·00	8·00	9·00	10·00	11·00	12·00 (hour of day)	13·00	14·00	15·00	16·00	17·00
Wet season	8·6	8·8	7·3	15·6	24·1	26·4	12·2	29·8	36·0	19·9	21·5
Dry season	15·0	6·5	11·2	11·5	15·4	32·1	35·1	34·6	25·8	21·8	30·0

storms.) During the dry season, on the other hand, movement did not begin until around 12.00h and continued to occur at a significant level until as late as 17.00h. (The slightly higher rate of movement early in the morning during the dry season can be attributed to the early morning bout of feeding.) However, the animals did not spend more time moving during the dry season than during the wet season (21·7% as against 19·1% respectively: $t = 25$, $P > 0{\cdot}10$, $n = 11$), suggesting that their day range is probably about the same during the two seasons.

In the second case, the major shifts of ranging locus into areas outside the band's normal home range were apparently due to climatic conditions in one case and to the local availability of a preferred food source in the other. During the study period, the main band ranged over an area of 3·4 km^2 on the ridge top and the upper slopes of the main escarpment face and the Khabau gorge. During the wet season in July and August, this part of the habitat was frequently enveloped in thick mist with the result that visibility was reduced to as little as 20 m for much of the day. During such times, activity tended to cease and the animals sat huddled in their social groups until breaks in the mist permitted the resumption of feeding. Heavy rain and hail storms which commonly accompanied the mists had a similar effect on activity. These factors must have a considerable effect on the feeding efficiency of the gelada in that they reduce the amount of time the animals can spend feeding during any one day.

The band's solution to this problem was to move onto the Khabau gorge side beyond the western limit of their normal range for periods of a few days to a week at a time. This part of the habitat was relatively sheltered since the mists were forced up by the higher ground to the north, and the area consequently remained free of mist on most days. These shifts of ranging locus onto the gorge side continued until November, the last month in which mists were recorded.

Shifts of this kind are probably exceptional since most gelada bands range along a single cliff-line and do not have the benefit of a second line of cliffs sufficiently close at hand to be accessible. However, the gelada in the Bole valley appeared to make *vertical* shifts in their ranging, utilizing the lower slopes of the gorge more during the wet season than during the dry season (Dunbar, in press). In general, mists were most severe on the upper slopes and this may constitute a comparable strategy aimed at avoiding excessive loss of feeding time.

The second major shift occurred during the dry season when the amount of green graze available in their home range was considerably reduced. Around the middle of December, the band moved west along the escarpment line more than 2 km beyond their normal range. After a few days, they moved rapidly back through their own range and out about 2–3 km on the eastern side into a set of barley fields which were at the time being harvested. From the beginning of January until March, the band oscillated between this area and their own home range, spending anything from a few days to a few weeks in each area. In the barley fields, the animals seemed to be feeding partly on fresh shoots growing amongst the stubble and partly on fallen grain, though they also dug for roots. They did not, however, attempt to plunder as yet unharvested fields, and they showed no interest in the fields before harvesting started late in December.

It seems likely that they had learned that a new source of food becomes available around this time of year. For some time before they moved into the barley fields they had made several trips to the eastern end of their range from where they had a clear view across to the barley fields to the east. Their foray beyond the western limit of their range may perhaps have been for a similar purpose, since they went as far as the village of Michibi before turning back. Although the villagers had extensively cultivated this part of the habitat in previous years, they had not done so in the 1971–72 season.

Gelada are known to congregate on threshing floors during the dry season to gather up the fallen grain (Crook, 1966). Observations by Crook on the southern face of the Amba Ras ridge in Simien during the 1965 dry season also indicated that considerable shifts in ranging locus took place, with large herds building up on abandoned threshing floors during the later part of the dry season, only to disperse again once the short rains in March and April brought on a flush of new growth. In areas under intensive agricultural use, such as those localities where Crook worked, the dry season may impose considerable strain on the gelada. With the bush cover removed and most of the grass cover destroyed by ploughing, the ground bakes hard and little grass is available in any form. Inevitably, the animals are forced to congregate on the few resources available in unusually large numbers (see Crook, 1966, p. 240). Comparable effects may be observed when the first showers of the small rains bring an extremely localized flush of new growth (Crook, 1966, p. 241). These patterns of dispersion and movement can be attributed primarily to extensive habitat destruction as a result of intensive cultivation. In undisturbed areas where grass is plentifully available, such large-scale movements are less likely to occur. Crook (1966), for instance, noted that on the Geech plateau, where agriculture was limited to a small section at one end, comparable large-scale movements were not observed.

It is not entirely clear why the main band at Sankaber should have made this particular change in ranging behaviour, since they had more grass cover available per animal in their range than any other band (see Dunbar and Dunbar, 1975). The data thus suggest that they were under little pressure during the dry season. It may, however, reflect a preference for a particular type of food (e.g. barley grain) which is seasonally available.

8. SUMMARY

1, 2. This paper presents data on the feeding ecology of *Theropithecus gelada* Rüppell, a grassland baboon endemic to the Ethiopian plateau. A scan sampling technique was used as the main quantitative procedure for obtaining information on both the diurnal activity patterns and the diet of gelada in two localities which lay on the limits of the species' geographical and altitudinal ranges.

3, 4. Feeding is carried out in a seated position and the hand actions used are primarily related to harvesting the leaves, seeds and rhizomes of grasses. Almost all feeding is therefore carried out on the ground. Gelada spend approximately 40–45% of their time feeding. A small difference was found in the amount of time spent feeding between the wet and dry seasons. Some 90–95% of the items eaten by gelada are grasses. However, the relative proportions of leaves, seeds and rhizomes being eaten depend on seasonal availability, although grass leaves appear to be preferred at all times. During the dry season, the proportion of grass leaves to rhizomes being eaten decreases during the middle of the day because green grass is more abundant close to the sleeping cliffs than on the ridge top. Unlike *Papio* baboons, gelada are able to digest grass leaves efficiently. Furthermore, their ability to utilize all parts of the grasses probably accounts for the fact that they are able to maintain much higher population densities than other open country species.

5. There is no significant difference in the proportion of time males and females spend feeding, despite the marked sexual dimorphism in size and weight. This is attributed to the fact that females require a larger intake of food per unit body weight than males due to the requirements of their reproductive activities.

6. Comparisons with other populations reveal few differences in diet or the proportions of time spent feeding and moving. A shorter day range in the Bole valley compared with the Simien was probably a product of differences in the size of foraging groups.

7. Band size correlates with the area of grass available in its home range. The data suggest that 1 km^2 of grass cover available in the dry season can support approximately 250 animals. Bands living in habitats with a low density of grass cover tend to forage in two or more herds more often than those living in areas with a high density of grass cover, probably due to the fact that animals have to forage farther apart as the proportion of grass cover decreases. Differential use of the home range was observed between the two seasons due to the fact that green grass is more patchily distributed during the dry season. In addition, two major shifts in the locus of ranging into areas outside the normal home range were observed. These shifts, which probably occur regularly each year, were apparently due respectively to climatic conditions and to the local availability of a preferred food source.

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The Guereza and Its Food

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1. INTRODUCTION AND METHODS

1.1. Introduction

A field study of the guereza (*Colobus guereza* Rüppell 1835), one of the black colobus monkeys, was conducted in East Africa from October 1970 to March 1972 and was followed by observations in Uganda in October–November 1973, and in Kenya and Uganda in July–September 1974. Previously, a number of workers had made field observations on the same species (see particularly Ullrich, 1961; Schenkel and Schenkel-Hulliger, 1967; Marler, 1969, 1972; Leskes and Acheson, 1971; Kingston, 1971; Clutton-Brock, 1972, 1975a). However, these studies had been of relatively brief duration and only Clutton-Brock had collected any detailed, quantitative data on feeding behaviour. Concurrently with my own study, Dunbar and Dunbar (1974b) collected quantitative information on guereza feeding in the Bole valley, Ethiopia, during 192 observation hours.

The primary aim of my study was to obtain detailed information on the ecology and social organization of the guereza (over a period of at least one year in one locality) that could be directly compared with data collected by T. T. Struhsaker on the red colobus monkey. Details of methods used in the guereza study, and their results, have been presented elsewhere (Oates, 1974) and a summary comparison has been made between the two colobus species by Struhsaker and Oates (1975).

1.2. Study Areas

The majority of guereza observations were made in the Kanyawara area of the Kibale forest, western Uganda, and comparative data were obtained from other parts of the forest and from elsewhere in Uganda, Kenya and Tanzania. In particular, detailed data were collected at Chobe in the Murchison Falls (now Kabalega) National Park, western Uganda. The Kanyawara and Chobe study areas have been described at length, and other localities tabulated, by Oates (1974). The Kibale Forest Reserve has also been described by Wing and Buss (1970) and the Chobe area by, amongst others, Gartlan and Brain (1968).

FIG. 1. *Colobus guereza* in an *Acacia sieberana* at Chobe.

The Kanyawara study area comprised about 0·4 km^2 of compartments 14 and 30 in the northern part of Kibale forest, close to the Kanyawara Forest Station (0°34′ N, 30°21′ E; 1500 m a.s.l.). The vegetation in most of compartment 30 was a moist high forest that had been largely untouched by man, apart from a small amount of felling by pit sawyers, since the reserve was gazetted in 1932. Compartment 14 (together with a small segment of compartment 30 within the guereza study area) had been selectively felled under Forest Department supervision in 1969, with the removal of large, commercially-valuable trees.

In the study area the ground rose nearly 100 m from a valley-bottom to a ridge crest, and this produced vegetational heterogeneity additional to that resulting from felling. The middle slopes between the extremes

FIG. 2. Kanyawara study area. Swamp vegetation in the valley-bottom, with forest on the ridges behind.

supported a forest containing a great variety of evergreen and deciduous tree species, with an upper discontinuous canopy layer at 25–30 m (Fig. 2). Langdale-Brown *et al.* (1964) have described the natural vegetation of northern Kibale as evergreen *Parinari* forest. But although *Parinari excelsa* was present in the study area it was outnumbered, amongst large trees, by *Strombosia scheffleri*, *Mimusops bagshawei*, *Celtis africana*, *Ficus exasperata* and *Olea welwitschii*. Other important large trees were *Pterygota mildbraedii*, *Aningeria altissima*, *Chrysophyllum gorungosanum* and *Newtonia buchananii*. *Celtis durandii* and *Markhamia platycalyx* were the most abundant middle-storey trees. Where felling had taken place it had mostly affected this middle slope forest, replacing the high growth with a dense tangle of secondary species which rarely reached above 6 m. Occasional groves of medium-sized trees and a scattering of large, commercially "undesirable" trees remained.

On the highest ridge in the study area most trees reached to only

6–12 m and the variety of trees was small, with *Diospyros abyssinica* and *Chaetacme aristata* common. In the permanently waterlogged valley-bottom, low dense swamp vegetation flourished; *Pennisetum* grass, shrubs and large herbs were dominant, but there were also scattered small trees. The study area was flanked by once-grassy high ground, now planted with exotic conifers by the Forest Department.

Due to Kanyawara's position close to the equator, the only climatic factor which showed obvious seasonality was rainfall, which totalled 1376 mm in 1971. There was some rain in every month, but peaks occurred in March–May and August–November. There was little monthly variation in temperature but considerable diurnal fluctuation. During periods of intensive guereza observation the highest maximum (day-time) temperature at Kanyawara was 31·2° C on 5th March 1971 and the lowest minimum (night-time) temperature was 10·8° C on 31st January 1971. These weather records were taken in the open at the Forest Station (data from Uganda Forest Department). Temperature fluctuations were probably smaller inside the forest. Sunrise in 1971 varied between 6.40h (local time) and 7.10h, and sunset between 18.47h and 19.17h (Astronomical Ephemeris).

The natural vegetation at Chobe (2°15′ N, 32°09′ E; 945 m a.s.l.), on the north bank of the Victoria Nile at the eastern edge of Kabalega Park, has been classified by Langdale-Brown *et al.* (1964) as *Terminalia* woodland. In fact, immediately by the Nile bank, where the guerezas lived, the vegetation (Fig. 3) was a degenerate riparian forest containing groves of *Markhamia platycalyx*, *Kigelia aethiopum* and *Margaritaria discoidea* (together with a few *Spathodea nilotica* and *Ficus brachypoda*) reaching to between 9 and 21 m in height. Beneath these trees grew a dense scrub of *Markhamia platycalyx* and *Teclea nobilis* bushes, mostly kept below a height of 3 m by large herbivore browsing. Between 50 and 100 m from the river the bank rose steeply and above this rise the forest gave way to a tree savannah with widely-scattered *Acacia sieberana* and *Kigelia aethiopum*. In 1970, rainfall at Karuma Falls Hydromet. Station (12 km east of Chobe) totalled 1176 mm, distributed as at Kanyawara but with no rain at all in July (rainfall in 1970 at Kanyawara totalled 1610 mm). With lower elevation and precipitation, temperatures were higher at Chobe than at Kanyawara. At Gulu, 40 km north of Chobe, the highest maximum temperature in 1971 was 35·6° C in March and the lowest minimum was 12·0° C in January (data from East African Meteorological Department). Sunrise during studies at Chobe in 1971 varied between 6.35h and 6.47h and sunset between 18.37h and 19.02h.

At Kanyawara, the guereza shared its habitat with five other monkey

FIG. 3. Chobe study area. Guerezas inhabited the Nile bank in the foreground (the trees are *Markhamia platycalyx*) and the island in the background.

TABLE I

Composition of guereza groups in Kanyawara and Chobe† study areas*

		Age/sex category‡														
Locality	Group no.	A♂	A♀	A prob. ♀	A/SA u	LSA♂	SA♂	SA♀	SA u	SA/J u	J♂	J♀	Ju	BWI	WI	Total
Kanyawara	2	1	3			1	1	1						2		9
	3	5	3			1	2	1						1	(?1)	13–14
	4	1	5				3									9
	6	1	3			2	3						1	2		12
	8	1	3	1		1	1	1				1		1		10
	13	2	2		3							1	2		2	12
	15	1	3	1				1		1			1	2		10
Chobe	1	1	4			1					1			1		8
	2	1	2						1			1		1		6

* In February/March 1972.
† In October 1971.
‡ A: adult; SA: subadult; J: juvenile; BWI: black-and-white infant; WI: white infant; u: sex undetermined.

species (*Colobus badius*, *Cercocebus albigena* and three *Cercopithecus* spp.). Baboons (*Papio anubis*) and vervet monkeys (*Cercopithecus aethiops*) slept in the riparian forest at Chobe and obtained some of their food there, while patas (*Erythrocebus patas*) inhabited the savannah.

1.3. Guereza Social Structure

Guerezas live in relatively small groups. In East Africa, I found a modal group size of nine monkeys in large forest blocks, with smaller groups in riparian forest and small forest patches (modal size: seven). The composition of groups in the Kanyawara and Chobe study areas is shown in Table I.

The structure, composition and dynamics of guereza social groups are discussed in detail elsewhere (Oates, 1974, and in press). Groups were found to be highly cohesive. Most contained a single adult male, while several adult females formed a "friendly nucleus" and frequently groomed one another. Aggressive interactions occurred relatively rarely within the group, as noted by Leskes and Acheson (1971).

1.4. Methods, Sample Sizes and Sample Distributions

1.4.1. *Study groups and observation time*

One guereza group at Kanyawara, group 4, was habituated to the close presence of the observer and was followed from dawn to dusk for a five-day period at the beginning of each month from January 1971 through to January 1972. Group 4, and other groups, were observed to a lesser extent on other days. Most Chobe observations were also concentrated on a single group, group 1, to which two five-day observation periods were devoted (in June and October 1971). The distribution of observation time amongst East African black colobus populations is shown in Table II.

TABLE II

Time in field and in contact with black colobus

	Kanyawara			Chobe	Other parts of E. Africa	Total
	1970–72	1973	1974		(1970–74)	
Hours in field	2110	92	130	152	348	2832
Hours in contact with colobus	1265	50	84	132	96*	1627
Individual days in field	306	15	23	18	55	417

* Including 13 hours *Colobus angolensis* contact.

1.4.2. *Trail system*

A system of trails, mostly on a 50-m grid, was cut through the vegetation in the Kanyawara study area. This allowed animals to be approached without undue disturbance and acted as a spatial reference against which animal ranging patterns and vegetation could be examined. A trail system was not required through the open vegetation at Chobe and the majority of observations there were made from inside, or close to, a Land-Rover vehicle.

1.4.3. *Ranging patterns*

During the 13 five-day observation periods at Kanyawara the movements of group 4 were plotted onto prepared maps of the study area. These ranging data were subsequently analysed by means of an accurate 50-m grid superimposed on the field maps. Chobe ranging patterns were analysed in terms of a 100-m grid, since the accuracy of mapping was less good than at Kanyawara.

1.4.4. *Distribution of activities*

Since prolonged observation of individual animals was impossible in the Kanyawara vegetation, a form of scan sampling (J. Altmann, 1974) was used to assess both the amount of time devoted by animals to different activities and the distribution of these activities through the day. Activities were categorized as below.

Feeding, when an animal reached for potential food items, picked them, transferred them to the mouth or chewed them. This did not include movements between feeding sites nor periods of apparent inactivity during a feeding session.

Inactive exposed, when an animal was not obviously engaged in any active behaviour and its body was so positioned that the majority of its upper surface was unshielded by vegetation from the prevailing weather conditions.

Inactive sheltered, when an animal was inactive with the majority of its upper surface shielded from the prevailing weather conditions. Both inactive categories excluded infants clinging to other animals.

Moving, when an animal was engaged in locomotion. This excluded young animals moving in play.

Social grooming, *self-cleaning*, *playing*, *clinging* or *other*. These are defined Oates (1974).

Sampling was conducted during the five-day observation periods on the main study group. In 10-min periods, centred on half-hourly intervals from 7.00 to 19.00h, the group was scanned and the first activities seen to be sustained for at least 5 sec by the first four or five clearly visible monkeys were recorded. Twenty such "individual activity observations" were collected by this method for each half-hourly time period in each month, giving a total of 500 observations each month.

When activity samples were taken, the heights of the sampled animals above the ground were also estimated, according to 1·5 m blocks. As a check on accuracy, T. T. Struhsaker and I each estimated the height of a sample of 40 trees at Kanyawara, whose heights were then measured with a Blume-Leiss optical height-finder. No significant difference was found between the two estimators or between Struhsaker's estimates and the height-finder.

At Chobe, 500 activity observations were also obtained, using the same method, in each monthly sample. These were taken from 7.00–19.00h in June, but from 6.30–18.30h in October (when sunrise was at 6.35h). October data have been combined with those collected one half-hour later in June.

1.4.5. *Diet*

A frequency method, similar to that employed by Leuthold (1970) on gerenuk in Tsavo Park, was used to estimate the relative consumption of different food items. An item was one part of one plant species, and the following major plant parts were distinguished: leaf buds, young leaves, mature leaves, floral buds, flowers, fruits, leaf petioles, bark, wood and whole plants. When one individual monkey ate one part (e.g. mature leaves) from one individual of one plant species (usually a tree), a single score for this item was recorded. Further feeding on this particular item was not scored unless it was eaten by a different individual, or by the same monkey from a different individual plant, or by the original monkey from the same plant after the elapse of one hour. Therefore, two monkeys feeding on the same part of the same tree at the same time scored two records. If one monkey changed to eating a different part in the same tree, or changed to a new food species, this constituted a new record. Where relevant, the size and colour of parts consumed were noted.

In 1970–72, the majority of feeding records at Kanyawara were obtained from group 4 during the five-day observation periods, although some records came from other groups and other days (Table III). The aim was to obtain at least 100 records each month. Altogether, 2715 feeding records were collected in the main Kanyawara study area. At Chobe, most feeding records were taken from group 1; here, 148 feeding records spread over eight days were obtained in June and 122

TABLE III

The distribution of gereza feeding records at Kanyawara

				1971				
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.
No. feeding records	171	156	237	183	180	184	176	184
% from group 4	*c.* 65	*c.* 95	86·1	96·7	84·4	96·7	94·3	94·6
				1972				
	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	
	210	219	168	214	255	130	48	
	98·1	94·1	96·4	99·1	92·9	70·8	77·1	

spread over six days in October 1971. In East Africa as a whole, 3084 *Colobus guereza* feeding records were obtained in 1970–72. At Kanyawara, a further 94 records were collected in October–November 1973 and 299 records in August 1974.

There was no evidence of strong bias towards particular age or sex classes in the feeding data. In a subsample of 372 feeding records collected from group 4 between 1st January and 7th March 1972, the only evident departures from expectation were in the adult male and infant categories (Table IV). Infants were recorded less often than expected because suckling (not usually visible) was not scored as feeding. The adult male was recorded more often than expected, perhaps because he was the most easily observable group member, and one of the most easy to identify. However, such possible bias is small enough to have had a negligible effect on the results.

TABLE IV

*Distribution of a sub-sample of guereza feeding records according to age/sex categories**

			Age/sex category				
	A♂	A♀	SA♂	J/SA♂	I	Undet.	Total
No. of records	42	119	49	31	4	127	372
% (of identified animals)	17·1	48·6	20·0	12·7	1·6	—	—
% composition of group	10·1	50·5	20·2	10·1	9·0	—	—
Expected no. of records	25	124	49	25	22	(127)	(372)

* Data from Kanyawara group 4, 1 January–7 March 1972.

1.4.6. *Social behaviour*

Overt social interactions were infrequent and observation conditions were usually difficult, so an attempt was made to record all observed interactions (*ad libitum* sampling of J. Altmann, 1974). However, interanimal distance was sampled systematically and a "grooming pair" was temporally defined to allow quantification of social grooming (Oates, 1974).

1.4.7. *Food availability*

Tree density and dispersion at Kanyawara were examined by a series of sample plots distributed through the area used by guereza group 4. Most of these plots were circular, had a 10-m radius and were centred, where possible, on trail grid intersections. Eighty-five such circular plots were taken, together with two strip plots (in which trees within 2 m of one 270 m length of trail and within 10 m of another 460 m length were enumerated). This is a total area of 3·7 ha (0·037 km^2). All trees with a greater than 50 cm trunk girth at breast height were recorded, giving a total sample of 789 trees. Such a selective sample saved time, while it included the majority of trees reaching to the height above which guerezas spent over 90% of their day (Oates, 1974).

To examine phenology at Kanyawara, a sample of 63 marked trees was examined near the end of each month from December 1970 until February 1972 (see Table V). The species represented in the sample either formed a large proportion of guereza diet or were abundant vegetational elements in the main study area. Sample trees were taken from right across the range of the main study group (to avoid any bias from local differences) and were not chosen because of their appearance. However, very small trees were excluded.

During the monthly examination, the crown of each tree was scanned with field glasses and the quantities of vegetative and reproductive parts present estimated. Parts were categorized as leaf buds, young leaves, mature leaves, floral buds, flowers or fruits. Young leaves were distinguished from mature leaves on the basis of colour and texture. Quantity was judged using a five-point scale, geared to the maximum potential abundance of a particular part on a particular species, and was recorded as: "none", "very few" (1 point), "few", "some" or "many". Actual counts of structures were not usually feasible. "Very few" would generally mean ten or fewer of the structure, "few" would be from around ten to around one-quarter of the likely maximum, "some" would be from one-quarter to one-half, and "many" from one-half upwards. A note was made on the size and colour of structures—

TABLE V

Composition of Kanyawara tree phenology sample

Species	Rank order in diet*	Rank order in tree enumeration sample	No. individuals in sample	Period of sample
Balanites wilsoniana Dawe & Sprague	8	>20	5	Feb. 71–Feb. 72
Bosqueia phoberos Baill.	>20	8	5	Dec. 70–Feb. 72
Celtis africana Burm. f.	4	11	5	Feb. 71–Feb. 72
Celtis durandii Engl.	1	2	15	12: Dec. 70–Feb. 72 2: Feb. 71–Feb. 72 1: Feb. 71–Sep. 71†
Dombeya mukole Sprague	18	7	5	4: Dec. 70–Feb. 72 1: Dec. 70–Feb. 71‡
Ficus exasperata Vahl	3	>20	5	Feb. 71–Feb. 72
Funtumia latifolia (Stapf) Stapf ex Schltr.	N.e.	10	5	Dec. 70–Feb. 72
Markhamia platycalyx (Bak.) Sprague	2	1	5	Dec. 70–Feb. 72
Olea welwitschii (Knobl.) Gilg & Schellenb.	5	17	5	Dec. 70–Feb. 72
Spathodea nilotica Seem.	7	>20	3	1: Dec. 70–Feb. 72 2: Feb. 71–Feb. 72
Teclea nobilis Del.	N.e.	6	5	Dec. 70–Feb. 72

* From sample of 2366 guereza feeding records in period February 1971–January 1972.

† Fell. ‡ Died. N.e. = not eaten.

this was particularly important in describing young leaves, for which the quantity of different sizes present was also recorded. Although the subjectivity of this method was a drawback, it provided a practical way of monitoring phenological changes in the small proportion of the study time that could be made available.

No information was obtained on the density or seasonal behaviour of aquatic and climbing plants consumed by guerezas. Notes were made on the vegetation at Chobe and the distribution of the few trees was mapped in gross terms, but detailed enumeration and phenological studies were not conducted.

2. FEEDING BEHAVIOUR

When feeding in trees, guerezas commonly sat at one site for several minutes, exploiting food within arm's reach. Generally, a monkey would make a three-point support with the ischial callosities and two feet, and use one or both hands to obtain food. Sometimes one hand grasped a branch around shoulder level to give extra support. The tail provided balance during feeding, and from its movements seemed to be especially important as a balancing organ when an animal fed on slender branches.

Food-gathering was influenced by the lack of a precision hand-grip resulting from the great reduction of the thumb in *Colobus*. Large or medium-sized leaves were usually torn off a branch with one hand (often in bunches). On several occasions, adult males were observed to run a clenched hand along a twig towards its tip, stripping off all the foliage. Sometimes, small branches would be bent towards the animal and a bunch of leaves bitten off from the branch apex. Large leaves were occasionally bitten off at the petiole. In all these cases the leaves, after picking, were held in one hand and consumed from there in a series of mouthfuls. Some large leaves were not picked at all but eaten in a series of bites from the blade. Medium-sized fruits and large flowers and floral buds were also commonly picked with the hands, then held and eaten in several bites.

Small items (such as buds and small fruits) were generally bitten off whole and eaten without being held in the hand, although the hands were sometimes used to pull the branches bearing the food towards the mouth. When the monkeys fed on leaf buds of *Acacia sieberana* at Chobe, thorns prevented food-picking with the mouth and the hands were instead used to pick the buds carefully (and rather slowly) from between the thorns.

Very large fruits (for instance, of *Kigelia aethiopum* at Chobe and *Sterculia dawei* at Budongo) were often not picked off the branch at all but left attached and attacked with the hands and mouth.

In specialized aquatic feeding at Kanyawara, guerezas sat on the banks of small pools, or stood in the water, pulling up rooted plants with the hands or using the hands as scoops to gather small floating plants.

Group members were usually closely co-ordinated in the timing of their feeding, although during a feeding period different individuals would often eat different items, especially if the group was dispersed through several trees. Individuals were tolerant of other animals feeding close by; for instance, I have observed simultaneous feeding by two animals on the same *Millettia dura* compound leaf. Large males would, however, supplant other animals from feeding sites—especially when a group first entered a feeding tree.

3. DISTRIBUTION OF FEEDING THROUGH HEIGHT AND TIME

3.1. Height of Feeding

An analysis of the heights of different activities at Kanyawara is displayed in Fig. 4. This is based on 3166 individual height observations from 32 days when group 4 occupied only the unfelled forest sector, and 1276 observations from 13 days when the group occupied the felled and hill-top sector. The observations were collected between March 1971 and January 1972. The data have been segregated because of the marked differences in the vertical distribution of vegetation between the two areas. Lumping observations makes comparison difficult with data collected on other species occupying only one of the forest types.

Feeding and moving took place at lower forest levels than inactivity ("exposed" and "sheltered" records combined). In both sectors, over 70% of feeding observations were recorded below an estimated height of 18 m, and there was a concentration of records at 10·5–13·5 m. Over 50% of inactivity observations came from above 18 m in both sectors. Kolmogirov-Smirnov two-sample, two-tailed tests (Siegel, 1956) showed that inactivity and moving took place at significantly different heights ($P<0{\cdot}001$) in the two sectors. It is clear from Fig. 4 that the differences arose because both these behaviours occurred more frequently at lower heights in the felled forest. However, there was no significant difference in the height of feeding between the two sectors ($P>0{\cdot}1$).

The major guereza food species were small to medium-sized trees that were typical of the middle storey and forest edge and were common in both sectors. These trees had been little affected by felling, which probably accounts for the feeding height similarity between the two sectors.

3.2. Time Spent Feeding and Diurnal Activity Pattern

In the analysis of Kanyawara activity observations, data from the 12-month period February 1971 to January 1972 were combined, giving a total of 6000 observations (240 for each half-hourly period). Feeding occupied 19·9% of these observations and showed marked diurnal variation, as did inactivity (57·4% of observations: 35·9% exposed and 21·5% sheltered) and moving (5·4%) (see Fig. 5). Chi-squared one-sample tests showed that interhour variations in these

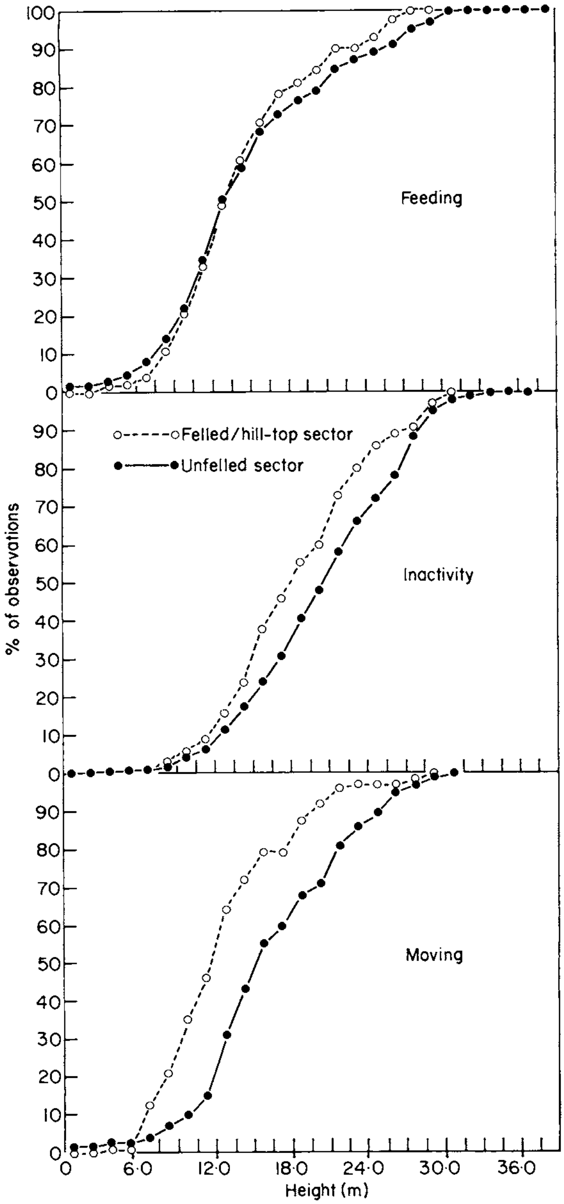

FIG. 4. Cumulative percentage distribution, according to height, of guereza activity observations in two forest sectors at Kanyawara.

activities were highly significant ($P<0{\cdot}001$). Social grooming (6·2% of observations) also showed significant interhour variation, but there was little variation in self-cleaning (0·7%), playing (4·6%) or clinging (5·7%).

At Kanyawara, a typical guereza group's day consisted of about five periods of movement and feeding, punctuated by long rest periods. In the late afternoon feeding was prolonged, but at other times a feeding bout commonly lasted for less than 30 minutes. Although the precise timing of different activities varied from day-to-day (so that combining many days' data obscures individual daily patterns), activities which commonly occurred at a similar time of day still produce peaks on a graph, as shown in Fig. 5.

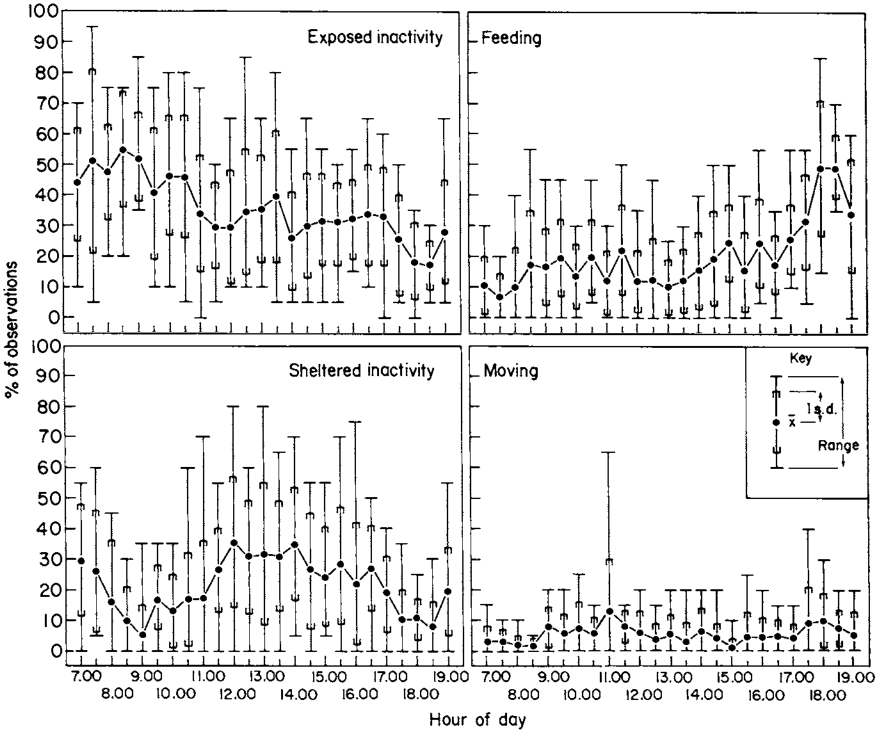

FIG. 5. Diurnal variations in the percentage importance of different guereza activity states at Kanyawara.

An obvious peak level of feeding occurred in the late afternoon and evening. The lowest scores for feeding coincided with a high level of exposed inactivity in the early morning (when there was sun-bathing) and a high level of sheltered inactivity at midday (resting in the shade). Although the scores for the same time periods in different months were highly variable (hence the large ranges and standard deviations in Fig. 5), the relatively low ranges which apply to the highest and lowest feeding scores indicate that such peaks and troughs were fairly regular temporal phenomena.

4. DIET COMPOSITION

4.1. Frequency of Consumption of Different Foods

The 3084 *Colobus guereza* feeding records obtained throughout East Africa in 1970–72 were distributed across 63 plant species (including two lichens). The 2715 Kanyawara records included 43 species, to which only one certainly new species was added by the 393 records collected in 1973 and 1974.[a]

Results presented in this section are based on data collected at Kanyawara during the 12-month period for which activity and ranging data are also presented: February 1971 to January 1972 (note that the 12-month period for which feeding data were analysed in Oates, 1974, was January–December 1971). A 12-month period has been selected to avoid bias introduced by seasonal changes in feeding behaviour.

During this period, 2366 individual feeding records were made which were distributed across 30 tree species (including a strangling fig), nine climbers and two aquatic herbs. In addition, lichens growing on two different tree species were eaten. No animal material was definitely seen to be consumed, and 126 records relating to unidentified parts were almost certainly plant parts. However, small animals (especially insects) may well have been ingested along with plant parts. This would apply particularly to fig consumption, as these fruits often contain huge numbers of pollinating and parasitic wasps and parasitic beetles.

The distribution of these feeding records between plant species and parts is shown in Tables VI and VII. The preponderance in the diet of one medium-sized tree species (*Celtis durandii*) and of young leaves is striking. Leaf parts as a whole (leaves of all ages, leaf buds and petioles) formed 76·9% of records. Only three species scored more than 5% of all records and these three formed 69·0% of the total. The guerezas ate many different parts of the common food species: young and mature leaves, leaf buds, floral buds and fruits of *C. durandii* were eaten.

Although the importance of different foods varied between months,

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[a] Unquantified observations were made of feeding on two additional tree species at Kanyawara.

TABLE VI

The top 20 guereza food species at Kanyawara in the period February 1971 to January 1972 and, for trees, their density and selection ratio

Plant species	Growth form when mature*	No. of feeding records†	% of feeding records	No./km^2§	Selection ratio‡
Celtis durandii Engl.	M, D	1185	50·1	3360	35·3
Markhamia platycalyx (Bak.) Sprague	S/M, E	310	13·1	4110	7·5
Ficus exasperata Vahl	L, D	138	5·8	80	172·5
Olea welwitschii (Knobl.) Gilg & Schellenb.	L, E	84	3·6	220	38·2
Ficus brachylepis Welw. ex Hiern	L, D	77	3·3	140	55·0
Spathodea nilotica Seem.	M, D	73	3·1	30	243·3
Premna angolensis Guerke	S/M, D	72	3·0	140	51·4
Celtis africana Burm. f.	L, D?	70	3·0	490	14·3
Balanites wilsoniana Dawe & Sprague	L, D	53	2·2	50	106·0
Mimusops bagshawei S. Moore	L, E	29	1·2	380	7·6
Rauvolfia oxyphylla Stapf	M, D?	23	1·0	30	76·7
Hippocratea plumbea Blakelock & Wilczek	C	21	0·9	—	—
Oncinotis sp.	C	21	0·9	—	—
Cardiospermum grandiflorum Sw.	C	19	0·8	—	—
Schrebera arborea Chev.	M, D	17	0·7	50	34·0
Dombeya mukole Sprague	S, D	15	0·6	920	1·6
Strombosia scheffleri Engl.	L, E	15	0·6	950	1·6
Dioscorea sp.	C	14	0·6	—	—
Prunus africana (Hook. f.) Kalkm.	L, E?	14	0·6	0	—
Strychnos mitis S. Moore	L, E	14	0·6	380	3·7

* S: small tree; M: medium-sized tree; L: large tree; C: climber; D: deciduous; E: evergreen.
† Total no. records = 2366. ‡ See text section 5.1.
§ Sampled area = 0·037 km^2, sample size = 789 trees.

C. durandii accounted for the majority of feeding records in all months of the study except August 1974 when *M. platycalyx* slightly exceeded it. In the case of plant parts, young leaves accounted for most records in all months except August and September 1971. Of specific food items, *C. durandii* young leaves accounted for the majority of records in every month except January, August and September 1971 and August 1974. In November 1971, when this item was abundantly available, it made up 60·7% of feeding records (it made up 70·8% of March 1972 records, but the total feeding sample was only 48 records in that month).

TABLE VII

The distribution according to plant parts and food items of 2366 guereza feeding records collected at Kanyawara from February 1971 to January 1972

	No. records	%
A. PLANT PARTS		
Young leaves	1369	57·7
Fruits	324	13·6
Mature leaves	294	12·4
Leaf buds	91	4·0
Undetermined age leaves	60	2·5
Flowers and floral buds	49	2·1
Wood and bark	25	1·1
Whole water plants	14	0·6
Leaf petioles, climber stem, foliaceous bracts	10	0·4
Lichens	4	0·2
Undetermined	126	5·3
B. FOOD ITEMS		
Celtis durandii young leaves	829	35·0
Markhamia platycalyx young leaves	211	8·9
Celtis durandii whole fruits	156	6·6
Ficus exasperata whole fruits	129	5·5
Celtis durandii mature leaves	124	5·2
Celtis africana young leaves	59	2·5
Markhamia platycalyx leaf buds	52	2·2
Olea welwitschii mature leaves	47	2·0
Ficus brachylepis young leaves	45	1·9
Premna angolensis young leaves	43	1·8
Spathodea nilotica young leaves	31	1·3
Balanites wilsonia young leaves	24	1·0
Balanites wilsonia mature leaves	23	1·0
Mimusops bagshawei fruits (probably seeds only)	23	1·0
Rauvolfia oxyphylla mature leaves	21	0·9
All other items	549	23·2

4.2. Dietetic Diversity

The heavy concentration by *C. guereza* on a few foods gave it a much less diverse diet than *C. badius* in the same area. To compare dietetic diversity between months, localities and species, indices were calculated using Shannon's formula (Pielou, 1966; Sager and Hasler, 1969):

$$H' = -\sum_{i=1}^{s} p_i \log p_i$$

where s is the number of species consumed, p_i is the relative abundance in the diet of each species, and $\log p_i$ is the log of p_i to the base of natural logarithms. The greater the diversity in a group of observations, the greater is H'.

For the 12-month period February 1971 to January 1972, the overall diversity (H') of guereza diet at Kanyawara in terms of food species was 2·08. In this period the highest monthly index was 2·14 in January 1972 (in January 1971 it was 2·15) and the lowest was 1·21 in November 1971 (see Fig. 6). By contrast, the index for *C. badius* at Kanyawara for the 17 months, November 1970 to March 1972, varied from 3·05 to 1·97 (Struhsaker and Oates, 1975).

5. FOOD SELECTION

5.1. Plant Species Selection

That only three out of a total of 43 food-plant species were responsible for 69% of feeding records at Kanyawara suggests strong differential selection of food by guerezas. But this apparent selection might simply be a product of differential availability. To investigate selectivity, one would ideally like to be able to compare the annual primary production of each species with its consumption by guerezas. However, such investigations were outside the scope of this study. Instead, I have compared numbers of feeding records with data on tree density. This reveals that the two most frequently consumed food species (*Celtis durandii* and *Markhamia platycalyx*) were also the two most frequently occurring species in the animals' range. So were guerezas showing strong species-selection; or were they allocating their time randomly across food species?

To examine this question I have calculated selection ratios which compare tree densities with numbers of feeding records. For each species the ratio is:

$$\frac{\text{No. of feeding records on the species}}{\text{No. of individuals of the species per hectare } (0.01\ \text{km}^2)}$$

Ratios for trees in the top 20 food species for the period February 1971 to January 1972 are shown in Table VI. The largest ratios indicate greatest positive selection, on a relative basis (climbing plants cannot be given ratios as their density was not assessed). The ratios do not reveal very marked selection of the medium-sized *C. durandii*, although this species is indicated as more strongly selected (or less avoided) than the small- to medium-sized *M. platycalyx*. The ratios for some relatively uncommon trees (such as *Ficus exasperata*, *Spathodea nilotica* and *Balanites wilsoniana*) are much higher than that for *C. durandii*, while those for some common trees (such as *Strombosia scheffleri* and *Dombeya mukole*) are much lower. Both *F. exasperata* and *B. wilsoniana* are large trees, so the apparently strong preference of guerezas for these species may be partly an artefact of the selection ratio used, which ignores biomass.

The ratios in Table VI use tree density from throughout the range of guereza group 4. But the group concentrated its time in the unfelled sector of its range, and tree densities here were different from those in the felled and hill-top forest. In particular, *C. durandii* (with 3560 trees/km^2) was more abundant in this area than *M. platycalyx* (3020 trees/km^2).

Although these ambiguities mean that a detailed comparison of selection ratios is unjustified, the ratios do at least provide general indications of species preference. For instance, the nine highest ratios are clearly marked off, as a group, from the rest. They are all over 30·0, with the next highest ratio only 14·3. Eight of these nine relate to deciduous trees. By comparison, some very common evergreen trees were strongly avoided. *Diospyros abyssinica* (2300/km^2) and *Bosqueia phoberos* (870/km^2) had ratios of only 0·5. Both these species have tough and leathery mature leaves. Other common trees with similar leaves that were completely ignored by feeding guerezas at Kanyawara were *Chaetacme aristata* (1190/km^2), *Teclea nobilis* (950/km^2) and *Uvariopsis congensis* (840/km^2).

5.2. Plant Part Selection

The feeding data suggest that guerezas selected strongly for young leaves (57·7% of records). Certainly, these were never as abundantly available in the Kanyawara forest as mature leaves, yet in most months they were much more abundantly eaten. Relatively high selection ratios for some deciduous tree species may reflect a greater availability of young leaves on those species compared with evergreens, rather than a preference for young leaves of particular species. An individual deciduous tree will carry more young leaves in several months of each year than will any evergreen tree. At any given time, guerezas might be expected to select individual trees with the greatest number of young leaves.

Guerezas did not seem to be very selective in the precise age of young leaves they ate. Where a variety of *Celtis durandii* leaves was available on the same twig, a monkey would usually pluck those of fresh, light-green appearance, regardless of size. Table VIII compares guereza feeding records for different sizes of *C. durandii* young leaves with their availability, as calculated from phenological scores (see Section 7). This suggests little obvious selection of a particular age class. Although the largest class appears to be more strongly selected than the others relative to its availability, the degree of selection is probably small enough to be insignificant, given the imprecision of leaf size assessment during guereza feeding.

TABLE VIII

Guereza feeding on different sizes of Celtis durandii *young leaves compared with the availability of the leaves*

Leaf size	No. of feeding records*	% of feeding records	Mean phenological scores†
Very small	27	5·3	0·2
Small	149	29·4	1·2
Medium	144	28·5	1·5
Large	186	36·8	1·4

* Data from period 1 August 1971 to 5 January 1972.

† Means of mean monthly scores, each of which is total of individual scores on 0–4 point scale divided by no. of trees in sample; data from six monthly samples between 29 July 1971 and 30 December 1971.

The guereza is not necessarily a preferential selector of leaves over fruits (but see Section 7). The overall biomass of fruits compared with foliage was usually low in the Kanyawara forest, and the low number of fruits in the diet is probably not greatly disproportionate to their availability. The same applies to flowers, which were usually available on a tree for an even shorter period than fruits. However, guerezas certainly do not show a strong preference for fruits and flowers over leaves.

In fruit-feeding, strong selection by guerezas for either ripe or unripe fruits was not apparent, but here my data are inconclusive.

5.3. Selection of "Occasional" Items

At frequent intervals (estimated at once every 2–4 weeks) guereza groups descended from the trees and travelled along the ground to two pools of open water in the swampy valley-bottom. Here they fed on small herbs rooted in the muddy pool margins, sometimes entering the shallow water to feed. Plants eaten included the rooted *Hydrocotyle ranunculoides* and the floating *Lemna minor* ("duckweed"). This behaviour may have been connected with the need to make up for dietary deficiencies of minerals (see Section 12). Mineral requirements might also be the explanation for the consumption of clay for which there was evidence at Kanyawara, although such behaviour could also have resulted from digestive physiological needs.

Food items that were only eaten in small quantities might also have been specially selected for physiological reasons. For instance, *Olea welwitschii* mature leaves were available in large quantities throughout the year and were frequently consumed, but only in small quantities (often only one or two leaves were eaten). This is discussed in Section 12.

6. TEMPORAL PATTERNING OF FOOD CHOICE

It was not obvious that guerezas ate particular foods according to the time of day, or that foods were eaten in a particular sequence. However, it was impossible to examine one individual's sequence of food choice. But I have been able to examine group feeding according to time. This analysis suggests that several plant species and parts had temporal patterns of consumption that differed significantly from the overall pattern.

Records from the 12 five-day samples on Kanyawara group 4 from February 1971 to January 1972 have been isolated from other data and segregated into four three-hour time blocks. This segregation according to food species is displayed in Table IX, together with chi-squared values resulting from a comparison of the distribution of records through time for each species with the distribution for all species combined. The species differing significantly from the overall pattern are *Markhamia platycalyx* (consumed much less than expected in the first quarter of the day) and *Celtis africana*, *Spathodea nilotica* and *Olea welwitschii* (all consumed more than expected in the first quarter). Significant departures for the same species are also found (at a 5% level) if *Celtis durandii* records (50·1% of the total) are excluded from the analysis.

A similar analysis has been performed on plant-part feeding records (Table IX). This indicates significant departures from the overall distribution of records through time for leaf buds (eaten especially more than expected in the third quarter) and floral parts (eaten less than expected in the first and last quarters and more than expected in the middle of the day).

The sample size was less than 100 for all the species and parts (with the exception of *Markhamia platycalyx*) for which there is apparent temporal variation in food choice, and the floral part sample was

TABLE IX

*Temporal distribution of guereza feeding at Kanyawara according to plant species and parts**

	No. feeding records in the time period					
	7.00–10.00 h†	10.00–13.00 h	13.00–16.00 h	16.00–19.00 h‡	χ^2	*P*
A. PLANT SPECIES						
Celtis durandii	167	222	233	435	2·26	>0·5
Markhamia platycalyx	27	74	57	124	16·36	<0·001
Ficus exasperata	33	20	24	49	7·15	<0·1, >0·05
Olea welwitschii	21	8	10	26	11·53	≃0·01
Premna angolensis	7	11	16	31	3·05	>0·3
Spathodea nilotica	26	9	9	21	23·37	<0·001
Celtis africana	20	7	8	29	12·54	<0·01
Ficus brachylepis	17	10	14	22	4·32	≃0·2
Balanites wilsoniana	9	4	13	21	4·02	>0·2
All other species	41	60	77	96	8·30	<0·05, >0·02
B. PLANT PARTS						
Young leaves	210	252	235	522	5·55	>0·1
Fruits	58	61	82	102	7·73	<0·1, >0·05
Mature leaves	40	51	57	110	0·89	>0·8
Leaf buds	17	10	29	29	9·97	<0·02, >0·01
Undetermined age leaves	8	7	12	24	1·77	>0·5
Flowers and floral buds	2	15	14	7	18·70	<0·001
All other parts	33	29	32	60	1·70	>0·5
C. TOTAL	368	425	461	854		

* Group 4, 2108 feeding records from 12 five-day samples, February 1971–January 1972.
† Includes a few records before 7.00h. ‡ Includes a few records after 19.00h.

particularly small. As the data are spread over 60 days, the variations found cannot be given much weight. If there was genuine temporal variation in the consumption of some items the reason is unknown, but physiological factors could have been involved.

7. SEASONAL VARIATION IN DIET

The forest at Kanyawara contained many tree species, which showed great variation in their phenology, growth form, density and dispersion. Guerezas fed not only on trees, but also on climbing plants and aquatic herbs. Consequently, despite a seasonal pattern of rainfall, the pattern of food availability was complex and showed no clear-cut overall seasonality. There was no significant intermonth variation in the proportion of feeding observations in the activity sample in the period February 1971–January 1972 (χ^2; $P \simeq 0{\cdot}30$). However, the composition of the guereza diet did vary and this variation was closely correlated with the seasonal behaviour of *Celtis durandii.*

Although *C. durandii* was the major food species in each month from January 1971 to March 1972, its proportion of all feeding records varied from 22·2 to 75·0% (or to 68·5% if the small March 1972 sample is excluded). The variation in the proportion of different *C. durandii* parts in the diet varied even more markedly: no young leaves were seen to be eaten in August 1971, whereas they formed 70·8% of records in March 1972 and 60·7% in November 1971; mature leaves were eaten in only eight of 15 months, but formed 27·7% of records in August 1971; fruits formed from zero to 16·8% of records.

Unlike some trees at Kanyawara, *C. durandii* showed quite marked seasonality in its leafing pattern, and this seemed to be correlated with rainfall. I have calculated mean monthly phenological scores for each sampled tree species by assigning scores of 0–4 to the "none–many" descriptions of the quantity of structures present. For *C. durandii* the highest mean monthly young leaf score was 3·5 in April 1971 (when all but four out of 15 trees were judged to bear many young leaves) and the lowest score was 0·3 in August 1971 (when only four trees had any young leaves at all). In fact, the species exhibited a biannual cycle of leaf production at Kanyawara during the main study, with most leaf buds noted in April and September 1971 and most young leaves in April–May and October–November 1971 (a similar bimodal pattern was found in his adjacent study area by T. T. Struhsaker). However, individual trees apparently shed all their old leaves only once in the year, before one of the two periods of new leaf production.

When the mean scores for *C. durandii* young leaf availability from February 1971 to January 1972 (collected at the end of each month) are compared with the proportion of young leaves in the guereza diet in the same month, using a Spearman rank correlation coefficient, a significant correlation is found ($r_s = 0{\cdot}74$; $P < 0{\cdot}01$). There was also a correlation between feeding in these months and availability judged at the end of the previous months ($r_s = 0{\cdot}56$; $P < 0{\cdot}05$). Furthermore, there was a negative relationship between diet diversity and feeding on *C. durandii* young leaves ($r_s = 0{\cdot}88$; $P < 0{\cdot}01$); months with high indices of diet diversity (see Section 4.2) were those in which few records of *C. durandii* young leaf feeding were collected, while those with low indices were months in which there was much of such feeding. These relationships are displayed in Fig. 6.

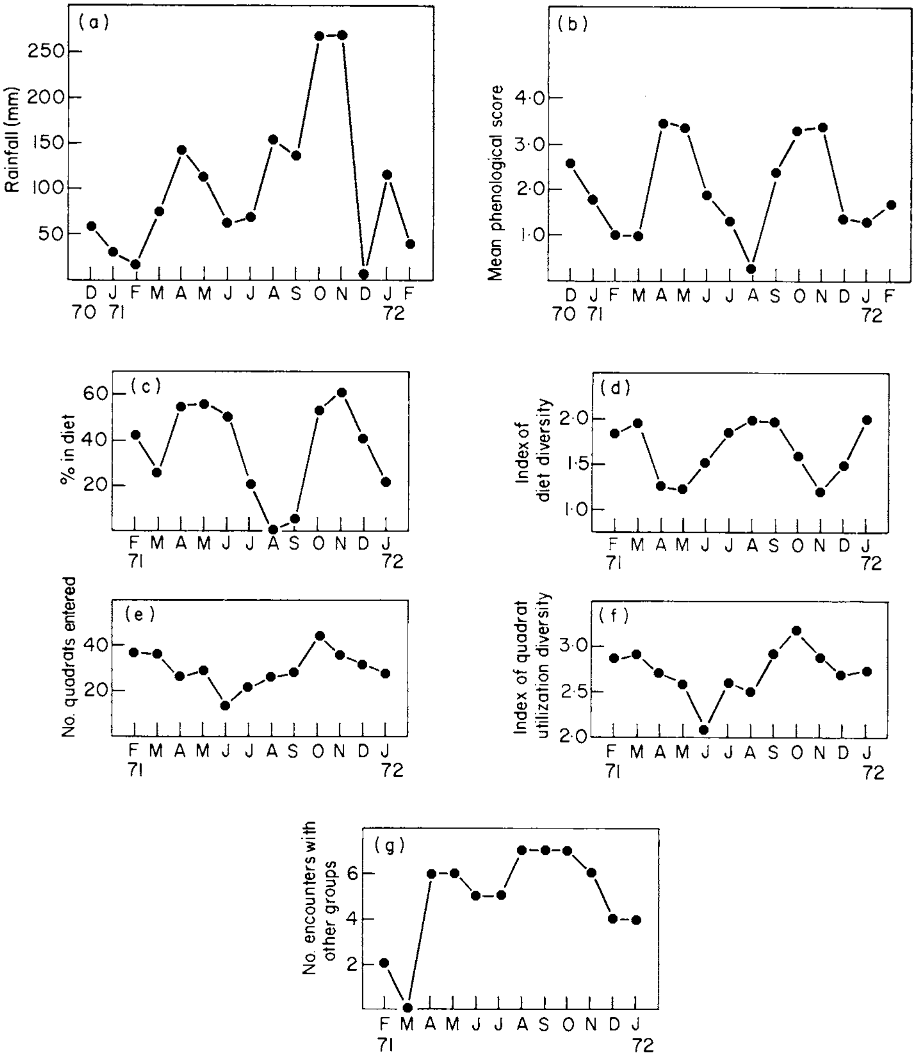

FIG. 6. Monthly fluctuations at Kanyawara in: (a) rainfall, (b) *Celtis durandii* young leaf availability, (c) *C. durandii* young leaf feeding by guerezas, (d) guereza diet diversity, (e) number of grid quadrats entered by group 4, (f) group 4 ranging diversity, (g) number of group 4 intergroup encounters.

New *C. durandii* young leaves were flushed approximately one month after the appearance of wetter conditions following December–February and June–July dry periods (Fig. 6). Mean monthly young leaf scores in different months from January to December 1971 were more closely correlated with rainfall in the previous month ($r_s = 0{\cdot}57$; $P < 0{\cdot}05$) than with rainfall in the same month ($r_s = 0{\cdot}44$; $P > 0{\cdot}05$). The flushing evident in February 1972 may have resulted from an unusually moist January.

The availability of *Markhamia platycalyx* young leaves at the end of each month from January–December 1971 was also related to the frequency with which they were recorded in the guereza diet in the following month ($r_s = 0{\cdot}81$; $P < 0{\cdot}01$). However, a direct correlation cannot be shown between the availability of *Ficus exasperata* fruits at the end of each month and their consumption in the following month ($r_s = -0{\cdot}20$). Rather, most *F. exasperata* fruits were consumed in months when *C. durandii* young leaves were most scarce (Oates, 1974), suggesting preferential selection of the leaves over the fruits.

Despite the complex pattern of variation in the Kanyawara vegetation, there were months when one general food type seemed scarce. For instance, phenological sampling at the end of August 1971 indicated that, in addition to the scarcity of *C. durandii* young leaves, few young leaves were available on four other major guereza food-tree species. In the following month there was a high index of diet diversity (1·98) and mature leaves (not a preferred dietary item) were the top-scoring plant part, regardless of species, in the diet (forming 31·9% of records). In August and September 1971, climbing and scrambling plants were important in the diet and more observations in the activity samples were recorded from below 6 m in the forest than in any other months (the result of guerezas feeding low down on scrambling plants at the forest edge and in areas of secondary growth). This behaviour closely follows the model of Emlen (1968) which predicts that predators will feed more and more indiscriminately as food becomes scarce.

Although different years at Kanyawara show a broadly similar pattern of rainfall, quite marked year-to-year variations occur. Probably for this reason, both the availability and level of consumption of *C. durandii* young leaves were not always similar in the same months in different years. The mean phenological score for this item in the tree sample was 3·3 in November 1971 but only 1·1 in November 1973, while its proportion in the guereza diet was 60·7% in November 1971 but only 28·7% in 1973 (in 1973, rainfall was much higher than usual in April, May and September). In August 1974, however, the situation was very similar to that in August 1971. Very few *C. durandii* young leaves were available (the tree sample gave a mean phenological score of 0·1 compared with 0·3 in 1971) and only one feeding record out of 299 was of this item (compared with no records in 1971). In August 1974, *Markhamia platycalyx* leaf buds were the top-scoring food item (12·4% of records), closely followed by *C. durandii* mature leaves (12·0%). In August 1971, *C. durandii* mature leaves had been the top-scoring item (27·7% of records).

8. RANGE UTILIZATION

8.1. Group Movements

During movements through their range, group members would commonly follow a similar path to the leading animal. Individuals would keep close, with the last animal rarely following the leader at an interval much greater than 15 minutes (there were exceptions, such as when males moved towards another group during an intergroup encounter). Movements in Kanyawara group 4 were often initiated by one adult female, believed to be the oldest animal in the group, but although initiating progressions she rarely remained at their head.

In moving from one resting site to another, guerezas did not forage continuously. Instead, they tended to stop at a limited number of distinct feeding sites *en route*; or they would move to just one site where feeding continued for a long period, after which the group often rested nearby. Sometimes a feeding site was a single large tree, but it often consisted of several trees in a limited area, through which the group moved slowly, individuals spending from a few minutes to an hour in different trees.

8.2. Range Size and Differential Usage

Measurements from the ranging maps made during the 12 monthly five-day observation periods on group 4 at Kanyawara from February 1971 to January 1972, give a mean daily linear travel distance of 535 m, ranging from a minimum of 288 m on 5th November 1971 (a day of very heavy rain) to a maximum of 1004 m on 2nd March 1971.

The total area covered by such daily movements was measured in two ways. Firstly, an arbitrary line was drawn to enclose all the mapped positions in which the group was seen between 1st January 1971 and 7th March 1972 (over which period mean group size was 12 individuals). The area inside this line, excluding large lacunae in which there were no plots, covered 0·151 km^2.

Secondly, a 50-m grid superimposed on the original ranging maps showed that the group used 128 0·0025-km^2 grid quadrats over the same period, a total of 0·320 km^2. This method over-estimates the range size, as many of the 128 quadrats were only marginally occupied.

During the 12 monthly observation periods from February 1971 to January 1972, the group entered 111 quadrats (0·278 km^2), but these 111 were not equally used. Twenty-eight were only entered on single days, while rank-ordering the quadrats according to duration of occupancy shows that 49·3% of the group's time was spent in the top 14. Eleven of these 14 formed a contiguous block (0·0275 km^2) which was occupied for 42% of the time. This block lay towards one edge of the group's range (see Fig. 7), almost entirely within the unfelled sector of compartment 30 (though two of the 11 quadrats just overlapped into the felled sector). In each monthly sample the group spent at least some time in this "core area" (Kaufmann, 1962).

Group 4 appeared to have a regular cycle of range usage, spending several days within the core area (in which relatively short distances were moved each day) and then ranging more widely outside it for several days.

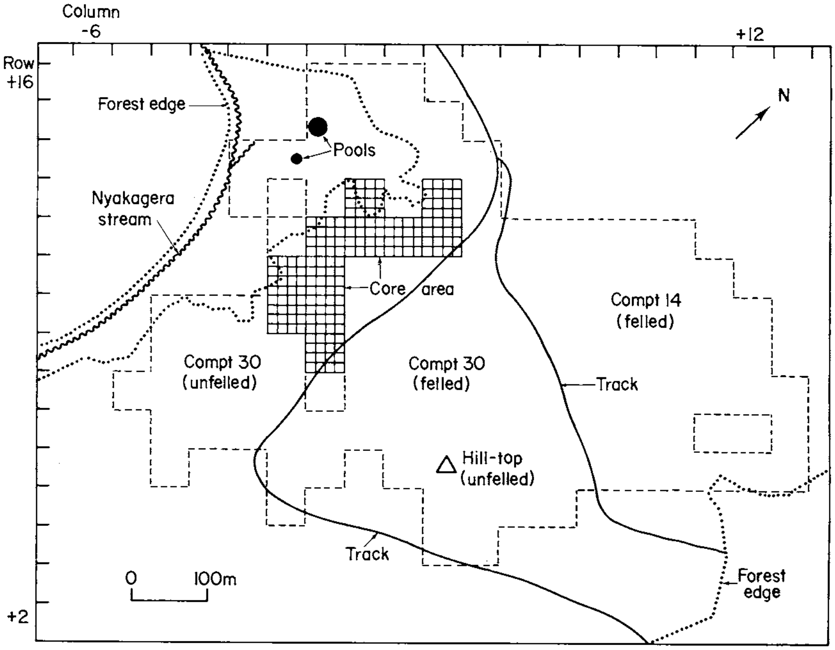

FIG. 7. The range of guereza group 4 in the Kanyawara study area in terms of 0·0025 km^2 grid quadrats (dashed line), with position of core area indicated.

The number of quadrats entered by the group varied significantly between monthly samples (χ^2, $P<0{\cdot}02$). A maximum of 44 quadrats was entered in October and a minimum of 14 in June 1971, and the variation over 12 months was biphasic (Fig. 6). As might be expected, the number of quadrats entered in each sample correlates strongly with monthly indices of quadrat utilization diversity, as calculated from Shannon's formula ($r_s=0{\cdot}72$; $P<0{\cdot}01$). However, no correlation can be shown with rainfall, with *Celtis durandii* young leaf availability or consumption, with diet diversity or with the number of encounters with other groups (see Fig. 6). There is a possibility that the biphasic form of the ranging graph results from the sampling period (*c.* 30 days) being slightly out of phase with a cycle of range usage. But I have no evidence to support this.

Although intermonth variation in ranging was apparently not related directly to variation in feeding behaviour, there were clear vegetational differences between the unfelled sector of group 4's range, in which its core area lay, and the felled and hill-top sector, which was widely ranged-over but not heavily used. Enumeration revealed differences in the abundance of the three most important food-tree species. These differences were additional to those caused by felling operations, as the species had not been cut. But despite the differences, there was remarkable consistency in the frequency with which these major food sources were exploited by group 4 in the two areas (Table X). This suggests that the extent to which these major foods were consumed at Kanyawara was not related directly to their density.

TABLE X

The consumption by guereza group 4 of three major food-tree species in two forest sectors at Kanyawara compared with the density of the trees

	Celtis durandii	*Markhamia platycalyx*	*Ficus exasperata*
No./km^2 in unfelled forest	3560	3020	100
No./km^2 in felled and hill-top forest	3100	5430	60
% of feeding records from unfelled forest*	50·8	14·0	5·7
% of feeding records from felled and hill-top forest†	50·8	12·1	5·2

* Sample of 1152 records from 32 days between February 1971 and January 1972 when group remained entirely within unfelled forest.

† Sample of 602 records from 17 days over same period when group remained entirely within felled and hill-top forest.

This could explain the differential range usage of group 4. To maintain the same quantity of *Celtis durandii* leaves in its diet, the group would have had to move over a wider area in the same time period in the felled and hill-top sector as in the unfelled sector. There is evidence that in its core area the group would have had to move even less widely than in the whole unfelled sector of its range. The eight circular enumeration plots which lay within this core area contained a total of 14 *C. durandii* trees, equivalent to 5570/km^2, while a single square plot with 50-m sides, which overlapped the most intensively-used of group 4's range quadrats contained 20 *C. durandii*, equivalent to 8000/km^2.

However, feeding was not totally similar in all parts of the group's range. I have noted that the group moved to one particular part of its range to consume water plants. In addition, a number of tree species completely absent from the core area (and surrounding unfelled forest) occupied quite a high proportion of feeding in the felled sector. *Balanites wilsoniana* formed 5·2% of feeding observations in the felled sector, *Rauvolfia oxyphylla* 3·7% and *Schrebera arborea* 2·8%.

9. RELATIONSHIPS BETWEEN GROUPS

The ranges of Kanyawara groups had long-term stability (in 1973 and 1974 group 4 occupied the same areas as in 1970–72) and overlapped considerably. In 1970–72, other groups were seen in 95 (74%) of the 128 0·0025 km^2 grid quadrats in which group 4 was observed. The remaining 26% of quadrats were not amongst those most intensively used by group 4 and they may well have been used by other groups at some time.

Although there was range stability, group composition did not remain stable between March 1972 and August 1974 (Oates, in press). In particular, male membership of groups changed. At Kanyawara, an adult male competition was evident for the "possession" of groups, whose stable element is a nucleus of adult females that remain in one area of forest. Male competition is reflected in intergroup intolerance, which contrasts strongly with tolerant intragroup relationships.

During the 12 monthly five-day observation periods from February 1971 to January 1972, group 4 had 65 intergroup encounters: defined as one group being within 50 m of one other group. Forty of these encounters were aggressive, group 4 supplanting, or being supplanted by, another group; 16 were "neutral", with no obvious aggressive interaction; and nine were encounters during feeding in the swamp pools—which all the groups in the study area shared. Large males were primarily responsible for aggressive displays and chases during encounters.

Positional analysis of intergroup encounters showed that group 4 tended to supplant other groups encountered within its core area and to be supplanted from the wider area outside (Oates, 1974). On some occasions the group would make a long and quite rapid movement from a peripheral part of its range to the core area, where it supplanted another group. But there were exceptions to this pattern. For instance, group 4 sometimes supplanted groups well outside its core area. I believe that some sections of the group's range outside its core overlapped the cores of other groups, while some were shared interstices between cores.

Although no correlation was found between the number of quadrats entered by group 4 during monthly observation periods and the number of encounters it had with other groups, selective range usage at Kanyawara was almost certainly influenced by intergroup relationships. Some parts of the unfelled forest sector of group 4's range which it did not use intensively were probably the range cores of other groups (for which I do not have detailed range-usage data).

Although the defence of a particular part of group 4's range at Kanyawara could be regarded as ultimately related to the defence of food, group supplantation over individual food trees was not evident: a group did not seem to chase another from an individual food tree and then feed there itself, but rather it chased another group away from an area of forest. However, in the very different habitat at Chobe (see below), group supplantation for a single food tree was recorded.

10. VARIATION BETWEEN INDIVIDUALS, GROUPS AND POPULATIONS

10.1. Individual and Group Variation at Kanyawara

There was no obvious difference in the diet of different guereza age/sex classes at Kanyawara and all members of a group often ate the same type of food simultaneously. However, although the identity of feeding animals was noted during diet recording, individuals could not always be identified precisely and the sample sizes that have resulted for individual animals are too small to allow detailed comparisons to be made.

Different groups also ate the same foods. Most guereza feeding records collected in 1970–72 came from only one group, but observations made on other groups indicated no marked differences in diet composition. *Celtis durandii* young leaves were the most frequently recorded food item (27·5% of records) in groups other than group 4. The differences that did exist probably resulted not from differences in food selection, but from differences in vegetation between areas. For instance, the tree *Prunus africana* was not seen within the range of group 4. Group 6, whose range contained several *Prunus* trees, contributed most of the 15 feeding records for this species.

In August 1974, the majority (82%) of feeding records was collected from group 6 rather than group 4. All species (except for *Prunus*) eaten by this group were previously known from the diet of group 4. Of the top ten species in the group 6 diet over a five-day period (see Appendix at end of chapter), six were represented in the top ten species from the August 1971 sample.

Although the ranging behaviour of only group 4 at Kanyawara was studied systematically, sightings of other groups indicated that they had range sizes of the same order of magnitude and that they concentrated their activities in limited parts of their ranges.

10.2. Interpopulation Variations

Outside Kanyawara, only the guereza population at Chobe was subjected to careful observation over many days. Although groups seemed to be smaller, on average, in riparian forest and small forest patches, brief observations throughout East Africa suggested little variation in the internal structure and behaviour of groups, other than differences (such as diet composition and height of activity) which derived inevitably from differences in the composition and structure of the vegetation. Guerezas usually included in their diet second-growth or forest-edge species common in their habitat, though the particular species varied from place-to-place: *Polyscias fulva* at Bwindi, *Polyscias kikuyuensis* at Limuru, *Rauvolfia oxyphylla* at Lake Nyamusingire and *Rauvolfia caffra* at Arusha.

At Chobe, guerezas fed lower (because of the nature of the vegetation) than at Kanyawara, and they also fed less frequently; 51·9% of feeding records from activity samples came from below a height of 7·5 m, while 79·7% came from below 15 m (Kanyawara equivalents: 6·9 and 59·5%). Much of this feeding occurred in the bushes (<3 m) of the scrub below the trees. The diurnal pattern of feeding was similar to that at Kanyawara, with an obvious peak in the late afternoon, but feeding occupied only 13·2% of all activity observations, compared with 19·9% at Kanyawara. Inactivity was correspondingly more frequent, occupying 70·1% of records compared with 57·4% at Kanyawara. This may have been the result of the higher environmental temperatures at Chobe.

The dominant guereza food species at Chobe was one of the major Kanyawara food species, but all the other foods were different. *Celtis durandii* was absent in the degenerate riparian forest at Chobe, but *Markhamia platycalyx* was the most abundant tree in the groves frequented by guerezas (though not the most abundant tree in the forest as a whole). It dominated the Chobe feeding records in 1971 in both June and October (Table XI). The lack of variety in the woody vegetation resulted in only seven species being recorded in the guereza diet, with records coming from every tree species identified in the habitat, except for *Spathodea nilotica* (of which only two individuals were seen within group 1's range). Indices of diet diversity, calculated as for Kanyawara, were 1·57 in June and 0·90 in October. The June index is similar to the June Kanyawara index, but the October figure is the lowest recorded.

Seasonal influences are apparent in Table XI, as *M. platycalyx* flowers, floral buds and young leaves were more abundant on the trees in October than in June (when floral parts were completely absent). Young leaf production by *M. platycalyx* seemed more constant low down in the scrub, possibly as a result of large herbivore browsing.

M. platycalyx leaf petioles were eaten by guerezas at Chobe, but never consumed at Kanyawara, where they were commonly eaten by *Colobus badius*. Interspecific competition between monkeys at Kanyawara seemed to be responsible for the small percentage of *M. platycalyx* floral buds, flowers and fruits in the guereza diet there, for their availability was generally very low. In October 1971, however, these parts formed 30·3% of guereza feeding records at Chobe. In 1973, heavy flowering by *M. platycalyx* at Kanyawara swamped browsing pressure, so that fruits were noted in the study area for the first time in November, when complete pods were eaten by guerezas.

The nature of the Chobe habitat resulted in guereza ranging patterns quite different from those at Kanyawara, although group 1 did concentrate its time in a limited area of its total range. Two small groves, both intensively used, were separated by some 1500 m of scrub and scattered trees. Group 1 moved on the ground between the groves, and to two large isolated fig trees. The result was a thin, stretched-out range: approximately 2 km long and in most places under 50 m in width. The area of ground covered by the group (calculated by adding the area inside lines encircling areas of intensive use to that represented by the thin connecting travel routes and isolated trees) has been calculated as close to 0·01 km^2. Group 1 entered 35 100-m grid quadrats

TABLE XI

The percentage distribution of guereza feeding records collected at Chobe in June and October 1971

	June ($n = 148$)	October ($n = 122$)
A. PLANT PARTS		
Young leaves	26·3	38·5
Mature leaves	33·1	4·9
Fruits	15·6	2·5
Flowers and floral buds	0	27·9
Leaf buds	0	13·9
Possible foliaceous bracts	10·1	0·8
Leaf petioles	5·4	2·5
Wood, bark and fruit stem	0·7	5·7
Undetermined age leaves	0	3·3
Undetermined	8·9	0
B. PLANT SPECIES		
Markhamia platycalyx (Bak.) Sprague	37·8	70·4
Margaritaria discoidea (Baill.) Webster	25·0	7·4
Ficus natalensis (Miq.) Hochst.	20·9	0
Acacia sieberana DC.	4·1	16·4
Kigelia aethiopum (Fenzl.) Dandy	2·0	5·7
Teclea nobilis Del.	5·4	0
Ficus brachypoda Hutch.	4·1	0
Thunbergia alata Boj.*	0·7	0
C. FOOD ITEMS		
Markhamia platycalyx young leaves	16·9	32·8
Markhamia platycalyx floral buds	0	23·0
Ficus natalensis mature leaves	20·9	0
Margaritaria discoidea fruits	11·5	0
Acacia sieberana leaf buds	0	11·5
Markhamia platycalyx possible foliaceous bracts	10·1	0·8
Margaritaria discoidea mature leaves	8·1	0·8
Margaritaria discoidea young leaves	4·7	4·1
Markhamia platycalyx flowers	0	4·9
Teclea nobilis young leaves	4·7	0
All other items	23·1	22·1

* Climbing herb.

(0·35 km^2) in the June and October 1971 five-day observation periods, and it was not seen elsewhere on other observation days. The group's mean daily travel distance was 703 m, with a range on individual days from zero (when it stayed in one tree) to 1840 m (when it moved from one end of its range almost to the other).

Only one other guereza group was located along over 6 km of the Nile bank at Chobe. The range of this other group (group 2) overlapped 200 m into one end of group 1's range (10% of its long axis). Neither group was seen in an area used intensively by the other. This was very different from the situation at Kanyawara, where there were many groups, extensive range overlap and intrusion by other groups into a group's "core area". Only one direct intergroup encounter was seen at Chobe, when group 2 supplanted group 1 from a large fig tree on the extremity of group 1's range.

11. PREDATION

In most localities visited, birds of prey, particularly crowned hawk-eagles (*Stephanoaetus coronatus*), were probably the chief predators on guerezas. Capture by a raptor was never seen but the remains of a large guereza were found on a track a few hundred metres from the main Kanyawara study area. With these remains were a number of brown-and-white barred feathers. On five occasions during the main study at Kanyawara, the adult male of group 4 rushed towards a raptor (twice identified as a crowned hawk-eagle) which had flown low and perched near the group; on four of these occasions the male produced roaring vocalizations and always the bird flew away. On several other occasions roaring was heard from guerezas when birds of prey were sighted flying over or through the forest. Allen and Loveridge (1933) have noted a large male *Colobus angolensis* chasing off an eagle, and record a crowned hawk-eagle shot while eating a *C. angolensis*. There were maggots in the latter monkey's limb, so it might not have been killed by the eagle.

I found no evidence of mammal predation on guerezas, but Allen and Loveridge (1933) found *C. angolensis* fur in leopard excrement in the Nkuka forest, Tanzania, while Nishida (1972) has reported finding hairs and a lower jaw, probably belonging to *C. angolensis*, in leopard food remains in western Tanzania. Suzuki (reported in Kingdon, 1971) has observed chimpanzee predation on guerezas in the Budongo forest. At Kanyawara, guerezas acted nervously towards chimpanzees: on one occasion they reversed the direction of a progression after detecting chimpanzees in a fig tree they were about to enter; on another occasion several moved hastily from a fig, in which they had spent the night, as two chimpanzees entered the tree from below.

12. DISCUSSION

12.1. Problems of a Leafy Diet

The guereza is a medium-sized mammal which lives in tropical African wooded habitats and feeds primarily on the above-ground parts of trees. Leaves, the most abundant and constantly available non-woody tree parts, form a high proportion of its diet. Only a few other species seem to occupy a similar niche: other colobus monkeys (*C. badius* and *C. verus*) and the tree hyrax (*Dendrohyrax arboreus*) are superficially similar in size, habitat and diet.

There is no detailed information on the diets of *C. verus* or *Dendrohyrax*, but *C. badius* (the red colobus) has been carefully studied (Clutton-Brock, 1972, 1975a; Struhsaker, 1974, 1975). Using the same study techniques, red colobus diet at Kanyawara has been found to be more diverse than that of the guereza, both in terms of plant species and plant parts (Struhsaker and Oates, 1975). The blades of large young leaves and mature leaves are much less common in the red colobus than in the guereza diet (the highest monthly proportion of mature leaves in the red colobus diet was 7·4%, compared with 33·7% in the guereza). The red colobus diet includes large quantities of leaf buds, leaf petioles, flowers and floral buds in addition to young leaves.

Compared with the red colobus, the guereza diet is monotonous and dominated by large leaf-blades. Several problems must be overcome in the handling of such a leafy diet. Firstly, the diet will have a high cellulose content and therefore be relatively indigestible for a mammal. Even if the cellulose can be digested by micro-organisms, these will be ineffective if the leaves contain large quantities of lignin (Harkin, 1973).

The second major problem faced by tropical tree-leaf feeders is the presence of toxins in their food. These are the plant "secondary" compounds, such as non-protein amino acids, alkaloids and phenolics, whose major function may be to deter animal feeding (see Bate-Smith, 1972; Freeland and Janzen, 1974; Swain, in press). For instance, tannins (which are polymeric phenolics) precipitate food proteins and digestive enzymes, withdrawing their usefulness. Although both the stomach bacteria and its own microsomal system provide a detoxification capacity to a ruminant-type mammal, it will be advantageous for the animal to select a diet with a minimal toxic component.

Thirdly, a diet of plant material may lack essential nutritional components. Sodium, in particular, is deficient in the normal diet of many herbivorous animals and is obtained from soil or special plants (Weir, 1972; Botkin *et al.*, 1973; Arms *et al.*, 1974). Guerezas might be expected to adopt strategies to counteract dietary mineral deficiencies, such as the feeding on aquatic vegetation observed at Kanyawara. This is discussed elsewhere (Oates, in prep.).

12.2. Coping with Indigestibility and Toxicity

Colobine monkeys probably cope with the cellulose in their food by means of their forestomach, which is modified as a fermentation chamber (Kuhn, 1964). However, several studies have found little evidence of cellulose digestion in colobus (Kuhn, 1964; Ohwaki *et al.*, 1974). This may have been because the animals examined had been feeding largely on fruit and had very little plant fibrous material in their stomachs, since Bauchop and Martucci (1968) have reported high numbers of cellulolytic bacteria in the stomachs of *Presbytis cristata* and *entellus*, while Kay *et al.* (1976) have found evidence of considerable cellulose digestion in the forestomach of two captive *C. guereza* maintained on a leafy diet in Kenya.

Although cellulose may be digested by bacterial fermentation, lignin is less easily coped with. It would be interesting to compare the lignin content of a wide variety of trees in a guereza habitat, from both food and non-food species.

The presence of a stomach fermentation chamber probably dictates relatively long periods of non-feeding while a "fill" is fermented. When densely-packed leaves are browsed, a relatively short time will be needed to fill the forestomach. However, these leaves, which form the major part of the guereza diet, can probably be less rapidly digested than many of the dietary items of red colobus. This may explain the much greater inactivity of the guereza compared with the red colobus (57·4% of records compared with 34·8%, using the same recording technique: Struhsaker and Oates, 1975).

The bulky and indigestible nature of the guereza diet presumably give it a low energy profit (after the losses of gathering, chewing and digesting). This may explain such energetic economies as early-morning sun-bathing, a common behaviour pattern, in which the black thinly-haired undersurface is typically oriented towards the sun. Hamilton (1973) has reviewed black coloration and sun-bathing, presenting evidence that heat gain from such behaviour reduces energy expenditure.

As yet, little information is available on the toxic constituents of monkey foodstuffs. But it may be significant that, in the Kibale forest habitat, guerezas feed very little on species of large "dominant" tree, restricting most of their attention to species in the lower forest layers and at the forest edge, and to non-woody climbers. Most of the tree species on which they feed are deciduous and more typical of dry forest and colonizing situations than of mature moist high forest. In the 12 months February 1971–January 1972, 87·2% of guereza feeding observations at Kanyawara came from only nine tree species, of which eight were deciduous and the ninth (*Olea welwitschii*) was typical of forest edge. It may be that such species concentrate more material and energy into rapid growth than the big trees of mature forest, and put fewer resources into the accumulation of secondary compounds and lignin. Certainly the leaves of *Celtis durandii* at Kanyawara suffered extremely heavy insect attack, suggesting a low level of toxicity. Selection of a low-toxin diet could be made on the basis of taste (see Bate-Smith, 1972), while texture and colour could presumably have important influences.

At Kanyawara, the diverse red colobus diet includes, as important constituents, several species of large forest trees—such as *Newtonia buchananii* and *Aningeria altissima*. The red colobus also has a more diverse pattern of ranging than the guereza and groups have a larger range size (Struhsaker and Oates, 1975). The red colobus could be better adapted to mature moist tropical forest than the guereza. To exploit the production of trees in such a forest, exposure to a fairly high level of toxins may be unavoidable. It may be possible to cope with the situation, however, by avoiding old leaves and by diversifying the diet, as small amounts of a range of toxins are better handled by detoxification systems than large quantities of a few (Freeland and Janzen, 1974).

Diversification of an herbivorous diet in a mature forest might be a means of coping with both toxicity and indigestibility. The old leaves of many large forest trees are probably highly indigestible (for instance, with a high lignin content) compared with the leaves of deciduous colonizing species. Leaf buds, flowers and fruits are presumably more easily digested than leaves, but are usually more widely spread (in large trees) through space and time. A diverse diet might be expected to result in a diverse pattern of ranging, and in large range size.

It should be noted, however, that plant secondary compounds may not always be deleterious to a guereza. Captive colobines commonly suffer from "bloat" or tympanites (a foaming of the digesta in the forestomach), as do true ruminants (Hill, 1964; Hollihn, 1969). The ingestion of tannins may inhibit the occurrence of bloat in ruminants

(Jones *et al.*, 1970). Therefore, although a constant high level of tannins in the guereza diet cannot be beneficial, the advantages of their consumption at certain times or in certain concentrations might outweigh the disadvantages. Similarly, tannins could sometimes act as a detoxification device for alkaloids, which they precipitate (Freeland and Janzen, 1974). Such factors might be involved in the relatively frequent consumption of only small quantities of some foods by guerezas.

12.3. Habitat Preference

If the guereza and red colobus are adapted to different types of forest, why do they coexist at Kanyawara? One possible reason is that the forest there consists of a mixture of species typical of both mature and colonizing forest. There was probably a much larger human population in the area up until 70 years ago (Osmaston, 1959), impinging destructively on the forest, though leaving much of it intact (today many large trees present are almost certainly much older than 70 years). Steep slopes keep parts of the old forest in a state of semi-regeneration, as tree falls are common during storms. Swamps also provide a source of perpetual colonizing vegetation. This mixture of vegetation presumably provides conditions to suit each colobus: their dietary overlap is very small, although there is complete spatial overlap between groups of the two species. In biomass terms, however, the red colobus is more successful at Kanyawara, with an estimated 1760 kg/km^2 compared with 570 kg/km^2 for the guereza in its area of maximum abundance (Struhsaker and Oates, 1975). In some unfelled parts of Kibale forest the guereza is even less abundant.

In many areas of colonizing forest, dry woodland, riparian and montane forest and in small forest patches in East Africa, guereza densities are much higher and other arboreal monkeys are sometimes completely absent. A guereza biomass of at least 1800 kg/km^2 (and possibly as high as 3000 kg/km^2) may be estimated from the Limuru, Kenya, data of Schenkel and Schenkel-Hulliger (1967). In these situations the vegetation may have low toxicity but exhibit low species-diversity and pronounced seasonality (see also Clutton-Brock, 1974a). In some months mature leaves may be the only abundant food source in the tree crowns. The guereza will feed on a small variety of plants (only seven species were eaten at Chobe) and will eat mature leaves in abundance when other foods are scarce.

The small group size of the guereza and its aggressive intergroup relationships (based on spatial factors) may be adaptations to these "marginal" forest situations, where trees are often distributed in small clumps: most efficiently exploited by small groups having exclusive use. The presence of a single male may be explained in terms of male competition for females, and may not necessarily be related directly to diet.

A willingness to undertake terrestrial movement, frequently noted at Chobe and seen in many other habitats, is also essential in patchy forest situations. Frequent terrestrial activity has also been described by Dunbar and Dunbar (1974b).

I suggest that the guereza's way of life is primarily adapted to a "marginal" forest situation, but that the species can still exploit mature forest vegetation, where colonizing-type trees are usually present but patchily-distributed. In such forests, epiphytic growth also forms an important element in guereza diet.

12.4. Interpopulation Differences in Ranging Patterns

The guereza population density at Kanyawara was approximately one animal per hectare (100/km^2) (Oates, 1974). There is evidence that at higher densities guerezas occupy much smaller ranges (similar in size to the core area of group 4 at Kanyawara) which are defended and exclusively used. At Limuru, Schenkel and Schenkel-Hulliger (1967) have reported a system of small, exclusive territories. From their sketch-map, a density of up to 500/km^2 may be estimated, with individual territories of from 0·013 km^2 for a group of six monkeys to 0·031 km^2 for a group of 12. Similarly, Dunbar and Dunbar (1974b) found small group range sizes in the Bole valley, Ethiopia, with a maximum density in one part of the gallery forest of 370/km^2. The larger range sizes found at Kanyawara could be the result of the relatively wider dispersion there of colonizing tree species as compared with the Limuru forest (dominated by species such as *Polyscias kikuyuensis*) and the Bole forest (dominated by *Ficus* spp., *Syzygium guineense* and *Albizia grandibracteata*).

The situation at Chobe is difficult to relate to these examples because of the extremely patchy nature of the forest there. If only the tree-clumps fed in are considered, the study group had a very small range (similar to groups at Limuru and Bole). However, if travel areas between clumps are included (and measured in terms of grid quadrats entered) the range is very large. At Chobe, some longitudinal overlap between group ranges existed. The elongated nature of the habitat did not allow effective buffering of each other's movements as occurred between groups in the high density populations of Limuru and Bole.

If the large range sizes at Kanyawara resulted from the wide dispersion of suitable food, why was there such extensive range overlap? If food is shared, is not the advantage of moving over a wider area lost?

Food, though, was not equally shared throughout a group's range. The main study group defended one part of its range (the "core area") where it spent most of its time and acquired most of its food. Here there was a high density of the chief food species (and an abundance of resting trees). However, it seems that the core did not contain sufficient resources for maintenance over long periods and the group moved out of the core frequently, partly to feed on water plants (which many groups shared and which may have provided an essential mineral or minerals) and partly to range widely through an area of felled and hill-top forest (also used by several groups). It may be that the resources in the felled forest were too widely spaced to be worth defending, while the water plants may have been shared because they provided an essential requirement available at only one restricted site (as do water holes in many savannah situations).

I disagree with the suggestion of Dunbar and Dunbar (1974b) that mature rain forest may be assumed to be more productive than riverine forest and to contain an abundance of preferred guereza foods. On the contrary, many colonizing and riverine forests may support a greater abundance and production of suitable guereza foods than mature forest. However, it is possible that the large, overlapping ranges found at Kanyawara reflect a population still below the maximum in relation to available resources. It could be that the population will grow and groups come to occupy small, defended ranges. But there was no evidence for such a trend over the 1970–74 period. It is also possible that the Kanyawara population is limited not by the overall abundance of food, but by the abundance of special requirements, such as the water plants used by all groups.

Whatever the explanation for the differences between guereza populations, it is clear that the species is able to occupy a great variety of wooded habitats. In these it exploits similar resources but shows flexibility in group range size and the division of space between groups. However, it does not adapt by marked changes in group size or composition, or by great individual flexibility. In fact, the guereza presents a remarkably stereotyped way of life over a wide geographical and environmental range.

13. SUMMARY

1, 2. *Colobus guereza* was observed in East Africa for 1627 hours in 1970–74. Observations were concentrated at Kanyawara in the Kibale forest, Uganda, a moist tropical high forest.

3. Over 70% of feeding occurred below a height of 18 m in both felled and unfelled forest. Feeding occupied about 20% of the guereza day and showed a peak in late afternoon.

4. Forty-three plant species were eaten at Kanyawara in 1970–72, but feeding was concentrated on a few species, of which the deciduous middle-storey *Celtis durandii* (50·1% of records) was the most important. Leaves were the chief guereza food, with young leaves forming 57·7% of records.

5, 6. The two major guereza food trees were also the two most abundant trees in the forest. Guerezas apparently selected deciduous trees as food and avoided several common evergreen species. Water plants were frequently eaten. Some foods were consumed disproportionately at certain times of day, perhaps for physiological reasons.

7. Although the pattern of food availability at Kanyawara was complex, *C. durandii* young leaves varied seasonally in abundance with rainfall and this affected the guereza diet. When these leaves were scarce, mature leaves became important in the diet, which diversified.

8. One intensively studied guereza group occupied 0·15 km^2 of forest but concentrated its time in a "core area" of 0·0275 km^2. This core contained a high density of *C. durandii*, but probably failed to satisfy all nutritional requirements.

9. Group ranges at Kanyawara overlapped extensively but inter-group relationships were aggresive. A group chased other groups from its core area.

10. Guerezas inhabiting riparian forest at Chobe on the Nile bank fed at lower heights and for less of the day than those at Kanyawara. All but one of seven tree species in the habitat were eaten but feeding was concentrated on *Markhamia platycalyx* (also important in the Kanyawara diet). Group ranges were elongated and two adjacent groups overlapped slightly and interacted aggressively. Animals frequently travelled on the ground.

11. Crowned hawk-eagles, chimpanzees and leopards have been implicated as guereza predators.

12. It is suggested that the guereza is primarily adapted to exploiting colonizing and dry forests, feeding on leaf blades. Leaves of tree species (particularly deciduous species) in these forests may be more digestible and less toxic than those of mature high forest trees. Suitable guereza food species occur in many habitats, but may be patchily dispersed in mature forest. Tree density will affect guereza population density and tree dispersion will influence ranging patterns, but many aspects of the guereza's life are stereotyped over a wide habitat range.

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APPENDIX

A comparison for sampling methods

It might be argued that the feeding data presented here are difficult to compare directly with those collected in other studies. In particular, Clutton-Brock's *Colobus* study employed different methods to sample both time spent feeding and the importance of different foods in the diet (Clutton-Brock, 1974b, 1975a).

To examine activity patterns I followed Struhsaker (1975), sampling activities sustained for at least five seconds. The intention was to avoid recording momentary acts occurring during a period devoted primarily to a different activity (for instance, shifts of position during a feeding bout, or pauses during a grooming session). Clutton-Brock also used scan-sampling, but recorded activities at the instant of sighting. In practice, these methods probably give similar results for *C. guereza*, as a comparison made on four days between the results obtained by sampling activities sustained for five seconds, and those sustained for only two (equivalent to an instantaneous sample), produced a marked divergence only for records of "moving", which formed 5·5% of 2-sec observations compared with 2·4% of 5-sec observations. Feeding formed 21·6% of 2-sec observations and 22·7% of 5-sec observations (Oates, 1974).

Secondly, I used a frequency method to sample food choice, whereas Clutton-Brock used a time-interval technique. If animals were recorded as feeding in Clutton-Brock's 15-min interval activity scans, the food items were noted. Waser (1974) used a similar method on *Cercocebus albigena* at Kanyawara, but employed 30-min intervals. I believe that the time-interval methods allow a closer estimate of the time spent feeding on different foods than the frequency method. The latter, although it allowed the full range of guereza foods to be quantitatively recorded, would have overestimated the time spent feeding on any items which guerezas consistently fed on for short periods. My method also differed from Struhsaker's (1975) in that he did not score an additional record for feeding in a different individual tree if the same animal had fed on the same part of that species within the previous hour. In comparison, my method could have overestimated the time devoted to a species which guerezas exploited by feeding for short periods in a number of different individual trees. Furthermore, my method is unsuited to sampling climbing-plant and water-plant feeding, as it is often difficult to distinguish between individuals of such species.

However, in practice there was little difference in the picture of guereza diet presented by these different techniques. This was shown by a comparative sample in August 1974. During a five-day observation period on Kanyawara guereza group 6, I scored feeding both by my original method, by Struhsaker's method and by Waser's method. The results of this comparison are shown in Table XII. The sample size derived using the 30-min time-interval method is half that obtained using the other methods. Presumably the use of 15-min intervals would have produced more similar sample sizes.

Spearman rank correlation coefficients comparing the scores obtained for the different food species show strong correlations between the results from my method and from Struhsaker's ($r_s = 1{\cdot}00$, $P \ll 0{\cdot}01$), and between the results from my method and Waser's ($r_s = 0{\cdot}91$, $P \ll 0{\cdot}01$). It is particularly noteworthy that *Celtis durandii* was very similarly scored by all methods, suggesting that it is indeed the species on which most Kanyawara feeding is concentrated.

In terms of plant parts, differences between the results from the three methods are even smaller, perhaps because fewer categories of parts were recognized than species, resulting in greater sample sizes for each category. The biggest difference was in the "undetermined" category, probably because the frequency method gave a longer period for identifying uncertain items than the time-interval method.

TABLE XII

*A comparison of three diet-sampling methods used contemporaneously on Kanyawara guereza group 6 in August 1974**

	Frequency methods (Oates) $n=214$	Frequency methods (Struhsaker) $n=207$	Time-interval method (Waser) $n=101$
A. PLANT SPECIES†			
Markhamia platycalyx	23·4	22·7	17·8
Celtis durandii	21·0	21·3	22·8
Premna angolensis	13·6	14·0	16·8
Millettia dura Dunn	7·9	7·3	5·0
Celtis africana	6·5	6·8	10·9
Ficus exasperata	5·6	5·8	6·9
Oncinotis sp.	4·7	4·8	5·0
Prunus africana	4·2	4·4	1·0
Cardiospermum grandiflorum	3·3	2·9	2·0
Olea welwitschii	3·3	3·4	4·0
Balanites wilsoniana	2·8	2·9	2·0
Epiphyte (undetermined)	1·4	1·5	3·0
Apodytes dimidiata E. Mey. ex Arn.	0·9	1·0	2·0
Dombeya mukole	0·5	0·5	0
Strombosia scheffleri	0·5	0·5	0
Tree (undetermined)	0·5	0·5	1·0
B. PLANT PART			
Mature leaves	31·3	31·9	29·7
Young leaves	26·6	25·1	24·8
Unripe fruits	16·4	16·4	17·8
Leaf buds	15·9	16·4	15·8
Probable leaf buds	2·8	2·9	4·0
Ripe fruits	1·9	1·9	0
Floral buds	0·9	1·0	0
Stem	0·9	1·0	0
Undetermined age fruits	0·9	1·0	1·0
Dead wood	0·5	0·5	0
Undetermined parts	1·9	1·9	6·9

* % of all feeding records.

† Authorities not shown here are given in Table VI.

11

A Comparative Study of the Feeding Strategies of Two Sympatric Species of Leaf Monkeys: *Presbytis senex* and *Presbytis entellus*

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1. INTRODUCTION

Since the publication of our ecological work concerning the food choices and food availability for primates in Sri Lanka (Hladik and Hladik, 1972), we have obtained new results concerning the composition of the foods used by these primates, which allow a different type of interpretation of the relationship between feeding behaviour, and social and individual behaviour. The details about methods and interpretation of the analysis of the food samples will be published in a separate paper (Hladik *et al.*, in press), but we must refer to these recent results as a basis of objective comparison between the food choices of two sympatric species of *Presbytis*: the purple-faced langur, *P. senex* (Fig. 1) and the gray langur, *P. entellus* (Fig. 2).

The ecological data concerning these two species have been complemented with information from other primatologists. Ripley (1967, 1970) developed the theoretical aspects of territorial behaviour and social foraging strategy of the gray langur in the field station of Polonnaruwa (Sri Lanka): we utilized her data on ranging patterns to estimate the food available for the different groups of langurs. Rudran (1970, 1973) and G. Manley studied the ecology and reproductive behaviour of the purple-faced langur, in the same field station, in the semi-deciduous forest of Polonnaruwa; we have used their information to help calculate the amount of food available for each group of purple-faced langur (Hladik and Hladik, 1972). Most of this research was part of the Smithsonian Biological Program in Ceylon, Primate Survey, initiated by Drs J. F. Eisenberg and S. Ripley.[a]

2. METHODS OF MEASURING FOOD CHOICES

2.1. Direct Observation v. Stomach Content

It might appear surprising that the most simple method of quantification of feeding behaviour, direct visual recording, has not been utilized by many investigators, except the author (Hladik and Hladik, 1969, 1972; Hladik and Charles-Dominique, 1971, 1974; Hladik, 1973, 1975)

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[a] Smithsonian Institution Foreign Currency Program, grant no. SFG-9-7004 and NIH grant no. MH 15673.

FIG. 1. A group of *Presbytis senex* at Polonnaruwa.

FIG. 2. *Presbytis entellus* feeding on the young leaves of a Palu tree, *Manilkara hexandra*, at Polonnaruwa.

and fairly recently Iwamoto (1975). The observation of one monkey during the whole day, and the continuous recording of the number of fruits and leaves eaten, are practicable only when the conditions of visibility are exceptional and when the monkeys tolerate the presence of an observer very close to the group. For this reason, the field stations chosen for such studies were carefully selected.

Records of the daily feeding activity of one monkey are necessarily inaccurate to some degree: even in the best field conditions, the animal chosen may be partly hidden in a tree for short periods. In such cases, we extrapolated from the feeding rates observed in the preceding or following minutes. In a few other cases, when the identification of one individual monkey among a group was very difficult, we had to shift to another individual in the same group (our observations only concerned the adults). These occasional shifts were not important in this study, since the feeding bouts were closely synchronized within each group.

When the feeding rates were too fast to allow note-taking, we used a small tape recorder to describe the feeding bouts observed. The counts of leaves and fruits eaten were made afterwards. At any change of activity, a reference to the time was noted (± 0·5 min). Thus it is possible to refer to our notes to calculate the time spent feeding (see Section 2.2). In order to keep continuous day-records, the author was partly assisted by Annette Hladik and two students of the University of Sri Lanka: F. P. Amerasinghe and B. W. B. Van Cuylenberg.

The food samples were collected the day after (or a few days after) the period of feeding observation. One-hundred fruits or leaves were immediately weighed to obtain the average fresh weight estimates of the different samples eaten. The most difficult and probably the least accurate estimates concern the small leaf shoots and flushes and the small flower bunches that the leaf monkeys pick directly by mouth. After the period of field observation and collection of the food specimens, we reproduced 100 "picks" or "mouthfuls" and weighed the quantity obtained. From these data, the estimates of the fresh weight eaten may have a bias of 20 to 30% concerning the leaf shoots but the accuracy is better than ± 5% for all the materials recorded as units, such as fruits and large leaves which form the main part of the total amount ingested.

Estimates of diet based on observation were checked against weighed contents of the first part of the stomach of some leaf monkeys which were shot [permit no. WL/P 91 (1) of the Department of Wild Life of Sri Lanka]. The relative proportions of leaves and fruits eaten were in good agreement with our direct recording, though we were unable to identify the different food species.

Some more reliable tests were made by the author on howler monkeys and capuchins of Barro Colorado Island (BCI) and in mainland Panama (Hladik and Hladik, 1969). One of the capuchins, accidentally introduced several months before, was shot from the group under direct observation. In its stomach content, the different food items could be clearly identified and the relative proportions of their fresh weight corresponded (± 10%) to our quantitative estimates from direct observation.

The differences between the diets of different primate species are generally large enough to rely on the method of direct observation, in spite of its lack of accuracy. It seems that there is no alternative method of measuring feeding behaviour which allows interspecific comparison.

2.2. Time Spent Feeding

The most accurate data published on feeding behaviour concern the time spent feeding, measured by different methods (Clutton-Brock

1975a; Struhsaker, 1975). Unfortunately, the time spent feeding cannot be accepted as an estimate of the food intake, since feeding rate may differ considerably between food items. Tables I, II and III illustrate these variations in the feeding rates of *P. senex* and *P. entellus* on different food items of the Polonnaruwa forest. Our field notes from different days of continuous observation have been used to compare the percentages of feeding time and the percentages of food intake, from the method described in the preceding section.

In the example concerning *P. senex* (Table I), half of the feeding time was spent on the mature leaves of two species of trees. The proportion of leaves actually ingested is slightly higher in terms of fresh weight and represents 75·9% of the dry weight ingested. Conversely, the proportion of feeding time spent on the young leaves and shoots is higher than the proportion of food ingested.

The differences between the time spent feeding on particular foods by *P. senex* and food intake (fresh weight) are generally small, particularly if we compare seasonal variation in the two measures (Figs 3 and 5). These two graphs show a close correlation between the two measures, except for the details of small peaks probably due to the small size of the sample and the relative inaccuracy of the second method. The highest proportion of time spent feeding on young leaves and shoots (Fig. 3) and the largest amount of intake of mature leaves at the

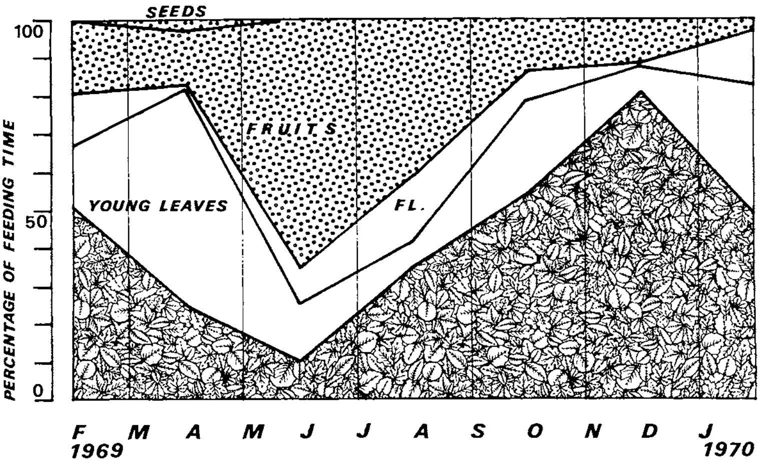

FIG. 3. Percentage of feeding time of *Presbytis senex*, on different food categories and throughout the year, after data of Rudran and Muckenhirn, in press. Food categories are (from bottom to top): mature leaves; young leaves and shoots; flowers; immatures and mature fruits; seeds.

TABLE I

Time spent feeding and food intake in Presbytis senex *at Polonnaruwa* (8th April 1969; from 6.32 to 18.30h)

Sample eaten	Time spent feeding (min)	(%)		Amount ingested, fresh weight (g)	(%)		Amount ingested, dry weight (g)	(%)	
Mature leaves of *Adina cordifolia*	57	30·0	51·1% of the feeding time spent on leaves	165	30·0	57·3% of the fresh weight ingested from leaves	56·0	29·8	75·9% of the dry weight ingested from leaves
Mature leaves of *Schleichera oleosa*	40	21·1		150	27·3		86·7	46·1	
Young leaves and shoots of *Schleichera oleosa*	52	27·4	46·3% on young leaves and shoots	115	20·9	39·1% from young leaves and shoots	22·9	12·2	20·8% from young leaves and shoots
Young leaves of *Garcinia spicata*	27	14·2		70	12·7		7·1	3·8	
Leaf flushes (and some flowers) of *Walsura piscidia*	9	4·7		30	5·5		9·0	4·8	
Green fruits of *Adina cordifolia*	5	2·6		20	3·6		6·3	3·3	

TABLE II

Time spent feeding and food intake in Presbytis entellus *at Polonnaruwa* (15th June 1969; from 5.30 to 18.30h)

Sample eaten	Time spent feeding (min)	Time spent feeding (%)		Amount ingested, fresh weight (g)	Amount ingested, fresh weight (%)		Amount ingested, dry weight (g)	Amount ingested, dry weight (%)	
Fruits of *Ficus benghalensis*	36	28·1		1200	77·3		250·9	71·2	
Fruits of *Drypetes sepiaria* (stones not included in weight)	19	14·8	28·1% of the feeding time spent on *Ficus benghalensis* 46·8% on other fruits	126	8·1	77·3% of the fresh weight ingested from *Ficus benghalensis* 16·6% from other fruits	31·5	8·9	71·2% of the dry weight ingested from *Ficus benghalensis* 19·8% from other fruits
Fruits of *Schleichera oleosa*	20	15·6		68	4·4		22·1	6·3	
Fruits of *Walsura piscidia* (with seeds eaten)	11	8·6		24	1·5		6·4	1·8	
Fruits of *Alseodaphne semecarpifolia*	10	7·8		40	2·6		9·8	2·8	
Young leaves of *Streblus asper*	5	3·9	13·3% on young leaves and flowers	4	0·3	1·3% from young leaves and flowers	0·7	0·2	1·2% from young leaves and flowers
Young leaves of *Tamarindus indica*	10	7·8		13	0·8		2·9	0·8	
Flowers of *Tamarindus indica*	2	1·6		3	0·2		0·8	0·2	
Leaves of *Alangium salvifolium*	6	4·7	11·7% on leaves	60	3·9	4·8% from leaves	23·1	6·6	7·8% from leaves
Leaves of *Mimosa pudica*	9	7·0		14	0·9		4·3	1·2	

TABLE III

Time spent feeding and food intake in Presbytis entellus *at Polonnaruwa* (11th August 1969; from 5.40 to 18.00h)

Sample eaten	Time spent feeding (min)	Time spent feeding (%)		Amount ingested, fresh weight (g)	Amount ingested, fresh weight (%)		Amount ingested, dry weight (g)	Amount ingested, dry weight (%)	
Immature fruits of *Walsura piscidia* (with seeds)	53	19·4	30·0% of the feeding time spent on fruits	425	29·1	36·3% of the fresh weight ingested from fruits	46·8	16·1	25·7% of the dry weight ingested from fruits
Green fruits of *Elaeodendron glaucum*	9	3·3		35	2·4		10·3	3·6	
Green fruits of *Syzygium cumini*	20	7·3		70	4·8		17·4	6·0	
Flowers of *Cassia fistula*	26	9·5	27·4% on flowers	170	11·6	19·1% from flowers	26·5	9·1	16·9% from flowers
Flowers of *Cassia roxburghii*	5	1·8		10	0·7		3·1	1·1	
Flowers of *Tamarindus indica*	33	12·1		40	2·7		10·3	3·6	
Flowers of *Glenniea unijuga*	6	2·2		10	0·7		4·1	1·4	
Flowers (and a few leaves) of *Tridax procumbens*	5	1·8		50	3·4		5·0	1·7	
Young leaves of *Ficus religiosa*	29	10·6	34·4% on young leaves and shoots	310	21·2	37·7% from young leaves and shoots	81·9	28·2	47·6% from young leaves and shoots
Young leaves of *Alangium salvifolium*	12	4·4		120	8·2		31·4	10·8	
Shoots of *Bridelia retusa*	9	3·3		25	1·7		4·6	1·6	
Young leaves of *Streblus asper*	39	14·3		65	4·5		11·0	3·8	
Young leaves of *Walsura piscidia*	5	1·8		30	2·1		9·2	3·2	
Leaves of *Cassia roxburghii*	5	1·8	8·0% on leaves	40	2·7	6·8% from leaves	11·4	3·9	9·8% from leaves
Other leaves not identified	17	6·2		±60	4·1		±17·1	5·9	

beginning of 1969 (Fig. 5) are easy to understand (see Table I) since large leaves require less time to be gathered and eaten than the small shoots. *Per contra*, the fruits generally eaten by *P. senex* are green and unripe small-sized objects (about 2 g, like the large leaves), thus ingested approximately at the same rate as the leaves.

In the examples concerning *P. entellus* (Tables II and III) there is an obvious lack of correlation between the time spent feeding on different categories of foodstuffs and the food intake, especially for leaves and fruits. In the data given as examples, the measures are accurate (±5%) for the food intake of large quantities and for the longest feeding times (each total time includes two or three feeding bouts, so the resulting accuracy is ±3% for more than 30 min). The gray langur spent 28·1% feeding time eating the large fruits of *Ficus benghalensis* that composed 77·3% of the total fresh weight ingested (Table II). All the other fruits eaten the same day account for 16·6% of the fresh weight ingested and 46·8% of the feeding time. The proportion of time spent feeding on flowers and leaf buds is ten times higher than the food intake.

The last example (Table III) shows that these relative proportions are not as different when the gray langur feeds on green unripe fruits which are more similar in size and texture to leaves. When feeding on young leaves of large size, the amount eaten is high per unit time (for *Ficus religiosa* young leaves, 21·2% of the fresh weight corresponding to 10·6% of feeding time). Conversely, for small leaves such as *Streblus asper*, the amount eaten is low per unit time.

For insect feeders like macaques and capuchins, time spent feeding is almost totally meaningless: a small amount of prey necessitates a very long foraging time and the definition of the feeding time is necessarily arbitrary (see discussion about chimpanzees, Hladik, this volume).

Detailed comparison of the diet or food choices of different species of primates cannot be achieved by measurement of time spent feeding on different food items. Nevertheless, measures of feeding time may be sufficiently accurate to compare different groups of population of the same species which are feeding on fairly similar items.

2.3. Size and Distribution of Observation Samples

Days of uninterrupted observation were spent alternatively on *P. senex*, *P. entellus* and *Macaca sinica*, at the Polonnaruwa field station. Each month, one week or more was spent in this study area, from March 1969 to February 1970.

The results concerning feeding behaviour of the Polonnaruwa primates have been extracted from 5790 minutes of observation of *P. senex* and 7125 minutes concerning *P. entellus*. The distribution of these observations throughout the year is shown on Fig. 5: the days during which the observations have been carried on are marked with dots along the time axis.

The diets of both species of leaf monkeys were generally fairly constant from day-to-day since a limited number of food species were available at any one time. For this reason, the average diet for one season could be obtained from a small sample of data (about 2000 minutes of observation). The agreement of the general shape of the graph of the seasonal variations with the figure obtained from another sampling technique (Fig. 3) is an indirect evidence of the sufficient size of the observation sample.

2.4. Collection and Processing of the Food Samples

A large part of the time involved in this comparative study of the diets was devoted to collecting and preparing food samples for analysis. The resulting restriction of the time spent on direct observation cannot be avoided in a study aiming to attain complete information on the diets.

Collection of the food samples at Polonnaruwa was possible without climbing the trees, with the help of a tree-pruner mounted on a series of bamboo poles. Samples were kept in large polythene bags, to avoid desiccation before weighing the series of fruits or leaves as described in Section 2.1. Alcoholic and dry fixations were made from the different samples and stored for further analysis (see Appendix II).

One of the most important problems was to deal with shoots and young leaves in which size and composition vary rapidly during the flushing periods. To allow an accurate calculation of the food intake, the best method would have been to collect and weigh the samples corresponding to each day of observation, which would have required most time that was available. As a compromise, the leaf flush specimens were collected only when the differences were obvious (colour and size) and we utilized these average data for the entire period of observation.

We tested a few food specimens for the local variations in size and composition of the mature leaves and for differences between male and female specimens in dioeceous trees. Variations in composition among different trees of a given species were small and would not have affected our estimates of food intake.

3. COMPARISON OF SELECTIVITY AND DIVERSITY IN THE LANGUR SPECIES

3.1. The Study Area

The field station of Polonnaruwa was chosen for its exceptional convenience for direct observation of the primates. The undergrowth of this forest has been cleared by the archaeologists to bring to light the ruins of a city of the twelfth century. In this "sacred area", where most of the observations on primates were carried out, the canopy is intact. The conditions of visibility are extremely good and it was possible to follow the different species of primates because they have been habituated to the presence of buddhist pilgrims for centuries.

The vegetation is typical of the dry zone of Sri Lanka (Mueller-Dombois, 1969): a semi-deciduous tropical forest with trees not exceeding 20–25 m in height. The annual rainfall is 1700 mm, but the dry season of June/July/August is generally very marked.

The frequency of the main tree species of the Polonnaruwa Field Station is shown in Table IV, from two plots of 10 ha (plot 2) and 5 ha (plot 3) which have been compared to the undisturbed forest nearby (Hladik and Hladik, 1972).

A large area covering 54·5 ha (2 km in length) was surveyed and mapped, using a large-scale aerial photograph. The canopy of each tree was measured after ground identification, to allow calculation of the total production in leaves and fruits after sampling the average production of each species from a square metre of canopy. Distributions of the two *Presbytis* species were recorded in the same area (Figs 7 and 8), thus making it possible to predict the availability of their food. Except for primates, mammalian fauna is fairly scarce at Polonnaruwa and there are no longer large predators.

3.2. Food Selection by *P. senex*

At Polonnaruwa, the social units of *P. senex* are generally "one-male groups" (Rudran, 1970, 1973) including three to five females and some juveniles. These groups are barely mobile in small territories of about 2–3 ha in which the food is obtained from the most common tree species.

The food ingested during one year includes an average (fresh weight) of 60% leaves, 12% flowers and 28% fruits. Among the leaves, about two-thirds (i.e. 40% of the total food ingested) were "mature leaves" but the distinction between young and "mature"

TABLE IV

*Frequency of tree species at Polonnaruwa**

Tree species	Trees per hectare plot 2	plot 3
Alangium salvifolium (Alangiaceae)	0	2·0
Elaeodendron glaucum (Celastraceae)	1·7	1·0
Diospyros montana (Ebenaceae)	0·4	1·0
Bridelia retusa (Euphorbiaceae)	0·4	0
Drypetes sepiaria (Euphorbiaceae)	10·6	1·4
Garcinia spicata (Guttiferae)	1·9	0·2
Alseodaphne semicarpifolia (Lauraceae)	0·9	0·2
Cassia fistula (Leguminosae)	3·9	0·4
Cassia roxburghii (Leguminosae)	1·4	0·2
Strychnos potatorum (Loganiaceae)	2·8	0
Aglaia roxburghiana (Meliaceae)	0·2	1·4
Chloroxylon swietenia (Meliaceae)	0·2	0
Walsura piscidia (Meliaceae)	3·6	0
Ficus amplissima (Moraceae)	0·7	0·2
Ficus benghalensis (Moraceae)	0·1	0
Ficus retusa (Moraceae)	0·1	0·6
Syzygium cumini (Myrtaceae)	0·2	0·2
Adina cordifolia (Rubiaceae)	10·3	10·8
Ixora arborea (Rubiaceae)	1·1	0·6
Glenniea unijuga (Sapindaceae)	2·2	0·2
Lepisanthes tetraphylla (Sapindaceae)	0·9	0·2
Sapindus trifoliatus (Sapindaceae)	1·4	0·4
Schleichera oleosa (Sapindaceae)	2·0	1·0
Manilkara hexandra (Sapotaceae)	0·7	0·2
Sterculia foetida (Sterculiaceae)	0·1	0
Grewia polygama (Tiliaceae)	1·8	2·8
Holoptelea integrifolia (Ulmaceae)	0·4	8·4
Premna tomentosa (Verbenaceae)	0·3	0
Vitex pinnata (Verbenaceae)	5·6	3·2

Variations between plots 2 and 3 show uneven distribution.

* The naming authorities of the plant species are those mentioned in Hladik and Hladik (1972).

leaves is not always obvious. Any leaf of maximum size was included as "mature", except when its texture was very soft. Since a similar criterion was used to qualify the food of the other langur species, a comparison is nevertheless meaningful.

Most of the food ingested by *P. senex* (more than 90%) was taken from 12 species of trees listed in Table V (in fact, *Ficus* includes seven species but all of them are not present in each group's territory). The first species in the list accounts for the main part of the food: *Adina*

TABLE V

Plant species eaten by Presbytis senex *at Polonnaruwa*

Species eaten	Percentage of total food intake accounted for
Adina cordifolia (Rubiaceae)	40
Schleichera oleosa (Sapindaceae)	
Drypetes sepiaria (Euphorbiaceae)	70
Alangium salvifolium (Alangiaceae)	
Elaeodendron glaucum (Celastraceae)	
Grewia polygama (Tiliaceae)	
Syzygium cumini (Myrtaceae)	
Holoptelea integrifolia (Ulmaceae)	
Garcinia spicata (Guttiferae)	
Walsura piscidia (Meliaceae)	
Ficus spp. (Moraceae)	
Sapindus trifoliatus (Sapindaceae)	>90

cordifolia, from which leaves, flowers and fruits are eaten, accounted for 41% of the animals' diet and, together with *Schleichera oleosa*, for 58% of the total. The top three food species accounted for around 70%.

This low dietetic diversity is similar to that observed by Oates (1974 and this volume) for *Colobus guereza*. Three food plants accounted for 69% of Oates' feeding observations. The main food species, *Celtis durandii*, which accounted for 46·8% of observations, can be compared to the *Adina* trees which gave the bulk of the food of *P. senex*. Shoots and young leaves account for 58% of feeding time in *Colobus guereza* though the proportion of intake is probably smaller. The strategy of this type of leaf monkey is to obtain the main part of its food from a very small number of common tree species, even if a large amount of mature leaves has to be ingested.

The proportions of shoots and young leaves could be more important in the diet of *Presbytis senex monticola*, the subspecies which inhabits the montane rain forest of Sri Lanka. After a small sample of observation (25 hours of contact; see Hladik and Hladik, 1972), we obtained an estimate of 75% young leaves, 16% coriaceous leaves and 10% flowers and fruits.

3.3. Food Selection by *P. entellus*

The gray langurs at Polonnaruwa are grouped in multimale units (Ripley, 1967, 1970) that comprise 20 to 30 animals. They occupy territories of 10 to 15 ha. They are less arboreal than *P. senex* and move around frequently, collecting a wider variety of foodstuffs from tree species which are more widely dispersed.

The average yearly diet of gray langur includes 48% leaves, 7% flowers and 45% fruits. Less than half of the leaves (21% of the food intake) are "mature leaves". The diet is more diverse than that of the purple-faced langur. The types of fruits eaten by *P. entellus* are generally mature and fleshy while those eaten by *P. senex* tend to be fibrous and desiccated.

Many food tree species are eaten by both langurs at Polonnaruwa though they do not account for the same proportion in the diet of the two species. Larger numbers of foods are utilized by *P. entellus*: 23 tree species make up 90% of its total food intake (Table VI). Ten species

TABLE VI

Plant species eaten by Presbytis entellus *at Polonnaruwa*

Species eaten	Percentage of total food intake accounted for
Walsura piscidia (Meliaceae)	
Drypetes sepiaria (Euphorbiaceae)	
Schleichera oleosa (Sapindaceae)	30
Adina cordifolia (Rubiaceae)	
Ficus benghalensis (Moraceae)	50
Strychnos potatorum (Loganiaceae)	
Mimosa pudica (Leguminosae)	
Cassia fistula (Leguminosae)	
Cassia roxburghii (Leguminosae)	
Streblus asper (Moraceae)	70
Elaeodendron glaucum (Celastraceae)	
Sapindus trifoliatus (Sapindaceae)	
Holoptelea integrifolia (Ulmaceae)	
Ficus religiosa (Moraceae)	
Ficus amplissima (Moraceae)	
Ficus retusa (Moraceae)	
Grewia polygama (Tiliaceae)	
Sterculia foetida (Sterculiaceae)	
Tamarindus indica (Leguminosae)	
Vitex pinnata (Verbenaceae)	
Lepisanthes tetraphylla (Sapindaceae)	
Glenniea unijuga (Sapindaceae)	
Bridelia retusa (Euphorbiaceae)	>90

account for 70% (versus three species only accounting for the same proportion in the diet of *P. senex*) and there is no predominant food species. The young leaves of *Adina cordifolia* are occasionally eaten but they form only a small part of the total food intake.

A comparison of the "dietograms" of the two species (Fig. 4) shows a difference in the relative proportions of leaves and fruits as well as differences in particular types of food. Both species eat small amounts of earth, like many other folivorous primates (Oates, 1974; Pollock, 1975b; Hladik, 1973) without any need for mineral intake (see Section 6.3, and Hladik and Gueguen, 1974). *P. entellus* may eat large amounts of fruits (up to 80–90%) while *P. senex* never eats more than 50% and generally selects coriaceous fruits. *P. entellus* never utilizes more than 50% mature leaves, while *P. senex* can eat up to 80% mature leaves over periods of several days. Both langur species do not select insects intentionally though *P. entellus* may ingest rather more animal matter than *P. senex* when feeding on *Ficus* fruits.

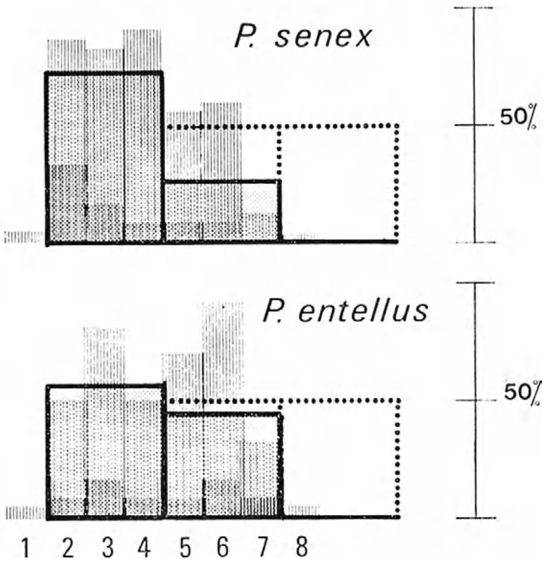

FIG. 4. Comparison of the "dietograms" of *Presbytis senex* and *P. entellus*. Variation of daily food intake is shown in columns as follows: (1) earth, (2) mature leaves and bark, (3) young leaves, (4) flowers, (5) immature fruits, (6) mature fruits, (7) seeds, (8) insects. The grey rectangles show the average proportion for the whole year.

The red colobus, *Colobus badius*, observed in the Gombe National Park by Clutton-Brock (1974a, 1975a) may be ecologically similar to the gray langur: there is no dominant species in the diet and nine species accounted for 70% of Clutton-Brock's feeding records. A very similar dietary diversity was found by Struhsaker (1975). In both studies, a large amount of shoots and young leaves was eaten by the red colobus. Furthermore, the groups of red colobus are multimale social units utilizing medium-sized territories, just like the groups of gray langurs. The species may differ in the selection of higher feeding levels by the red colobus (Clutton-Brock, 1973) and eventually more humid habitats, though *Colobus badius temmincki* can survive in very dry conditions (Gatinot, 1975).

4. SEASONAL VARIATIONS IN FOOD CHOICES

The daily records of food intake of *P. senex* and *P. entellus* did not show any marked differences in food choices between consecutive days. The diet of *P. entellus*, with around ten to 12 food species being eaten each day, varied slightly more from day-to-day than that of *P. senex*. The sample is not sufficient to study these short-term variations but we can assume that the diet of each species is very stable over successive periods of two to three days.

Availability of particular food species changes throughout the year (Hladik and Hladik, 1972) as does progressively the diet of both *Presbytis* species (Fig. 5). On these graphs, data concerning the food intake of both species have been grouped together for each period of two months and one period of three months, to make samples of about 2000 minutes corresponding to each season.

During the winter monsoon (February–March) *P. senex* feeds on a very high proportion of leaves (95%) including a high amount of young leaves and shoots. *P. entellus* at this time also eats many shoots, especially those of *Walsura piscidia* and *Drypetes sepiaria*, and a smaller amount of mature leaves. In the dry season that follows (May–June), the amount of leaves eaten by both langurs decreases because fruits are available, mainly those of *Drypetes sepiaria* and different *Ficus*; but *P. senex* utilizes less fruits than *P. entellus*, and mainly unripe fruits such as *Elaeodendron glaucum*. During the major dry season (July–September) a large amount of flowers, mainly those of *Adina cordifolia*, is eaten by *P. senex*, while *P. entellus* still utilizes many fruits such as *Schleichera oleosa* and *Walsura piscidia*. Many shoots and young leaves are available during the next monsoon (October–November), on which *P. entellus* takes the major part of its food, while *P. senex* eats a lesser amount mixed with *Adina* mature leaves. In December to January, the rain being uninterrupted, leaves increase in proportion in the diet of *P. entellus* as

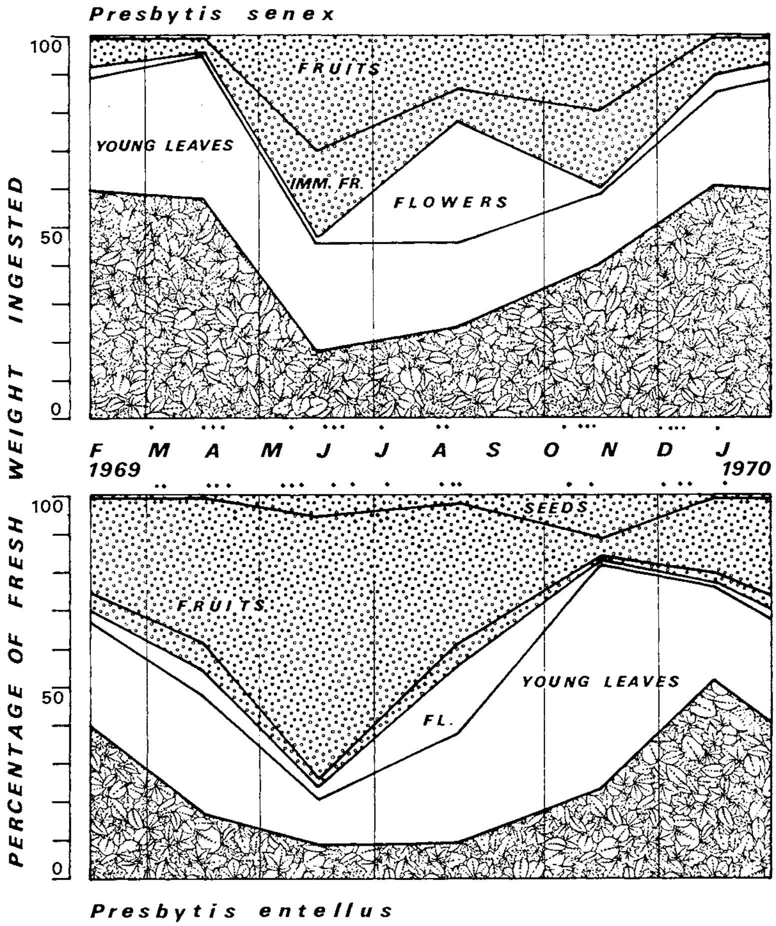

FIG. 5. Percentage of the fresh weight ingested of different food categories, throughout the year, by the two langur species of Polonnaruwa. Food categories are (from bottom to top): mature leaves; young leaves and shoots; flowers; immature fruits; mature fruits; seeds (small amounts of bark and stems have been included in the "mature leaves" category).

shoots become less available; but leaves are also utilized in larger amount at this time by *P. senex*.

In spite of the important variations of the availability in shoots, young leaves, fruits, etc. each of the *Presbytis* species maintains its own tendency, shown by a typical choice. Marked seasonal variations follow the seasonal cycle in both diets; but the dietetic differences remain approximately constant: at any time of year, *P. senex* eats more leaves and *P. entellus* more shoots and fruits.

5. THE SUPPLYING AREA AND ITS RELATION TO FEEDING BEHAVIOUR

5.1. Ranging Behaviour: Definition of the Supplying Area

The inventory of the food resources available for each group of langurs of Polonnaruwa necessitates a clear definition of what is actually available for the different groups in the overlapping parts of their home ranges (Fig. 6). For example, group A has the exclusive utilization of all the resources in the core area and in the rest of area 1. In area 2 where A and B's ranges overlap, an equivalent amount of the food is available for each group. The supplying area of group A thus includes half of area 2 and one-third of area 3 where the ranges of group A, B and C overlap. The limits of the "supplying area" (dashed lines on Fig. 6) are fictitious but are useful in calculating the quantity of food available for each group in an homogeneous environment.

5.2. Distribution of Food Resources for *P. senex*

The supplying area of each group of purple-faced langur observed at Polonnaruwa was measured according to data collected by G. Manley

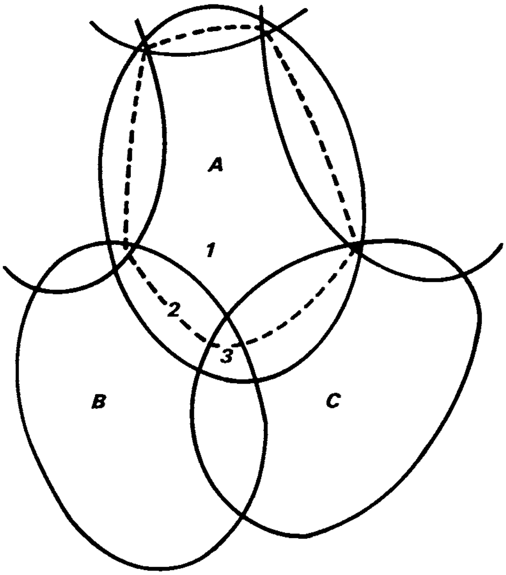

FIG. 6. Diagram showing the home ranges of groups A, B and C (solid line) and the supplying area of group A (dashed line).

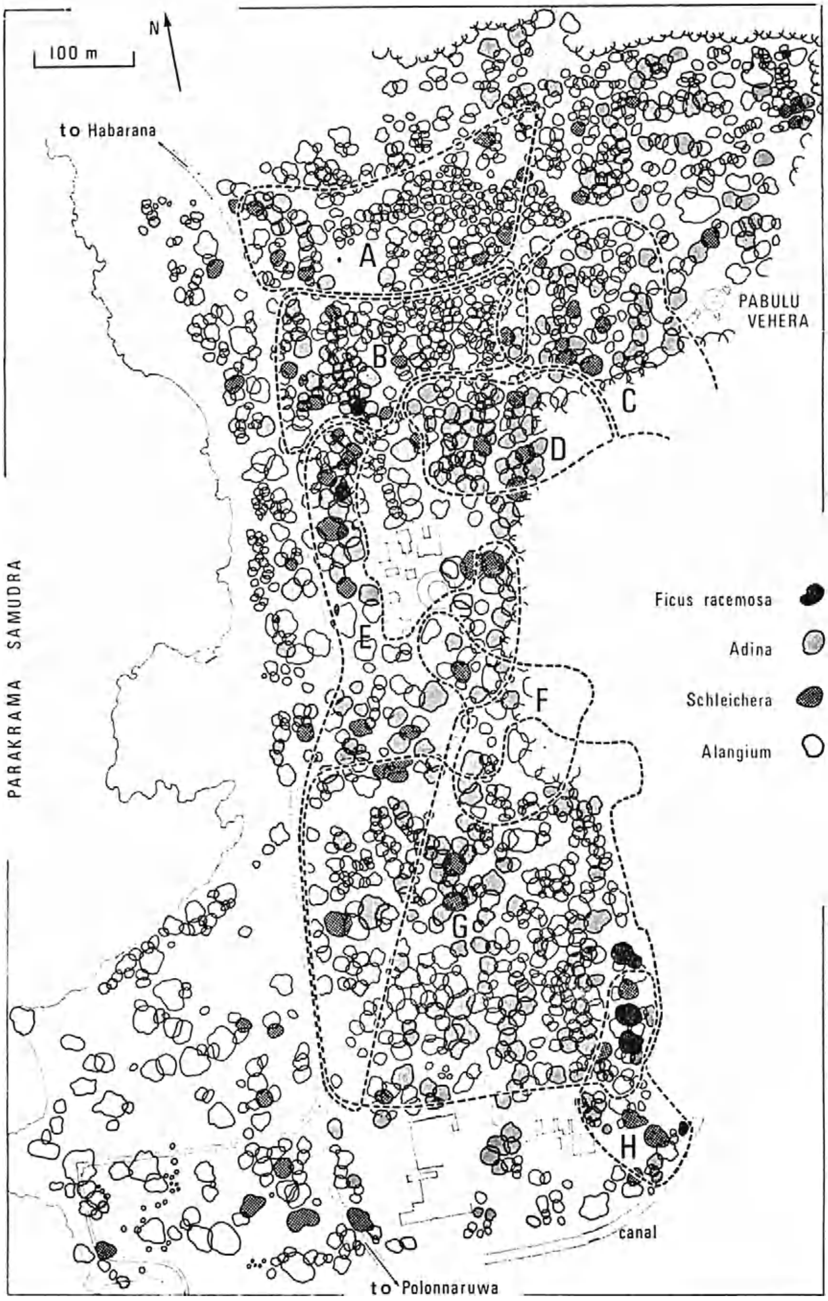

FIG. 7. Distribution of the main food-producing trees in the home ranges of the groups of *Presbytis senex*, at Polonnaruwa.

(pers. comm.) and Rudran (1970 and pers. comm.) (see Fig. 7). In each of the supplying areas, the total production of food (i.e. of food species actually selected by *P. senex*) was calculated (see Hladik and Hladik, 1972) and the main results are presented in Table VII. Taking into account the number of monkeys in each of the groups, we obtained the average production of food per monkey and per year in the different groups. A purple-faced langur ingests about 400 kg (fresh weight) per year (1006 g of food were found in the first part of the stomach of a specimen of 7600 g shot in the evening, but very important variations between days were observed). Thus the potential food supply is more than ten times what is actually eaten, and the variations between different groups are small.

TABLE VII

Total food in kg (fresh weight) available per year for one monkey in the different groups of Presbytis senex *at Polonnaruwa*

Groups	*Adina cordifolia* leaves	*Adina cordifolia* flowers	*Schleichera oleosa* shoots	*Schleichera oleosa* fruits	Other trees leaves
A	1300	60	240	65	1100
B	3500	160	380	105	2200
C	2100	100	420	115	2200
D	4700	215	350	100	2000
E	3500	160	510	160	2000
F	1000	50	200	55	2800
G	6500	300	300	85	5800
H	600	30	130	35	1000

After Hladik and Hladik, 1972.

Eating one-tenth of the food production might be the maximum permissible for a folivore utilizing an important amount of young leaves without endangering the food plant population (C. M. Hladik, 1977). In the supplying area of group H, which is reduced by the pressure of the dominant neighbouring group (Fig. 7), the food available per individual is effectively less than 2000 kg per year. In this particular area, some *Alangium salvifolium* trees were dying because their young leaves were too frequently plucked by the purple-faced langurs. This case can probably be considered as a density limit, since group H will necessarily disappear when too many trees are destroyed.

In each of the supplying areas of groups A to G, there are more than 500 m^2 of total canopy of *Adina cordifolia*, the main food source. The relative abundance and even distribution of the trees utilized by *Presbytis senex* appears clearly on Fig. 7 and Table IV. It allows each group to obtain an equivalent share in a small supplying area. The distribution of the food resources cannot be estimated by a single recording of the number of trees in different plots. Dittus (1974) discussed the different mathematical interpretations of distribution in plots and concludes that a visual estimate is a necessary starting point. The average distance between two trees of a given species, and its variability, might be a useful measure of species distribution; but to measure production it is also necessary to take differences of canopy size into account.

5.3. Distribution of Food Resources for *P. entellus*

Using data supplied by Ripley (1970 and pers. comm.) and N. Muckenhirn (pers. comm.), we measured the supplying areas of the different groups of gray langurs. Our measures of production and calculation of the average quantity of food available for each group allowed us to make comparisons between groups (Hladik and Hladik, 1972—see Table VIII).

The different tree species utilized by the gray langur (Fig. 8) are less evenly distributed than those used by the purple-faced langur. The average distance between the trees of a given food species of the gray langur is greater and varies widely: for example, the mean distance between *Ficus* trees is more than 100 m. Large home ranges allow access to these species with scattered distribution. In many cases, the supplying area of the different troops contains similar amounts of important food species: for example, an average of one female *Drypetes sepiaria* (producing fruits) and one-and-a-half male *Drypetes sepiaria* (producing only leaf shoots) is available for each monkey of different troops. Other types of food-producing trees differ in abundance between groups (Table VIII) but other tree species compensate for what is missing. An average of 500 kg of fruits per individual per year is available from the

TABLE VIII

Annual mean production available for one individual in the different groups of* Presbytis entellus, *for some of the commonest food species at Polonnaruwa*

	Walsura piscidia shoots	*Drypetes sepiaria* shoots	*Drypetes sepiaria* fruits	*Ficus* spp. fruits	*Schleichera oleosa* fruits
North group	40	180	23·5	62·5	30
Central group	20	135	20	262	115
South group	(few)	>50	>10	197	40

* In kg fresh weight.

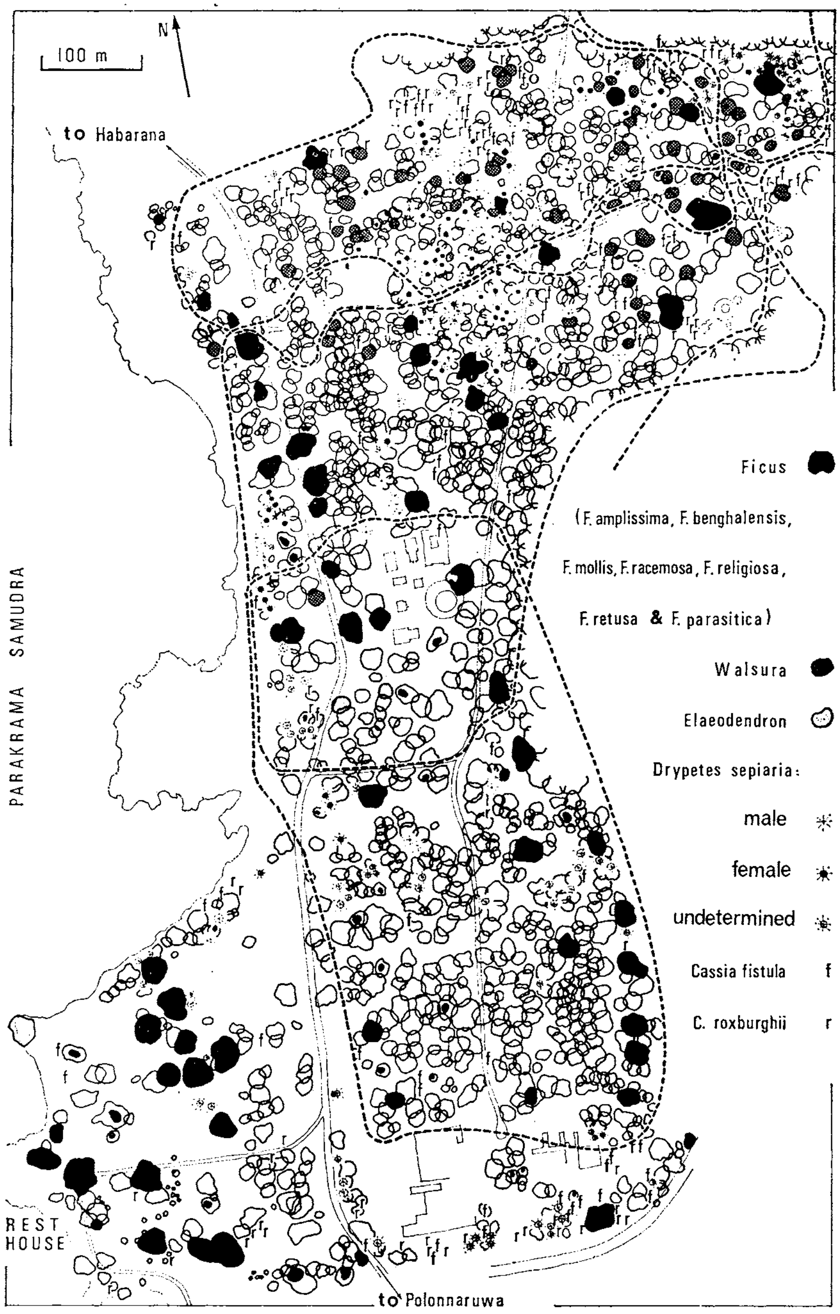

FIG. 8. Distribution of some important food trees in the home ranges of the groups of *Presbytis entellus*, at Polonnaruwa.

ten first species of the list (Table VI) and about half of these fruits are actually eaten.

Both langur species show approximately similar population densities (about two animals per hectare), with biomasses of 10 to 15 kg per ha in maximum density locations. The success of each of the langur species is due to a different strategy of adaptation in the same environment, the large groups of gray langurs dealing with a larger set of scattered food species.

6. COMPOSITION OF THE FOOD SUPPLY

6.1. Composition of the Food Samples

The food samples collected at Polonnaruwa were analysed to allow comparisons of the diets of the primates of Sri Lanka and other primate species (Hladik *et al.*, 1971a; Charles-Dominique and Hladik, 1971; Hladik, 1973, 1975). The results have been compiled out of a set of 1800 analyses (Hladik *et al.*, in press) including several samples of each species of Polonnaruwa collected in different seasons and different places.

For many frugivorous species of primates the leaves, especially young leaves and shoots, are necessary to increase the protein content of the diet (C. M. Hladik, 1977) and plant species with the highest protein contents (such as Leguminosae) are usually selected. By contrast, protein content is less likely to determine food choices in *Presbytis* species whose staple food (leaves) is protein rich. In fact, some samples have a very low protein content though they are selected preferentially by *P. senex*. Food samples selected by *P. entellus* are generally richer in primary compounds, especially in soluble glucids.

6.2. Comparison of the Intake of Protein, Lipids and Glucids

The average composition of the foods ingested was calculated for different periods of the year, using the composition of the different food samples and their proportion in the diet during different seasons (see Section 4).

There is marked seasonal variation in dietary composition (Fig. 9) and the two *Presbytis* species show different characteristics. The dietary pattern of *P. senex* shows less seasonal variation than that of *P. entellus*. The protein intake of *P. senex* is low and approximately constant at 11·5% of the dry weight. *P. entellus*, in contrast, shows the highest average of protein intake for the whole year, but has a rate as low as 10%, reaching 16% during the rainy season when leaf buds and leaf

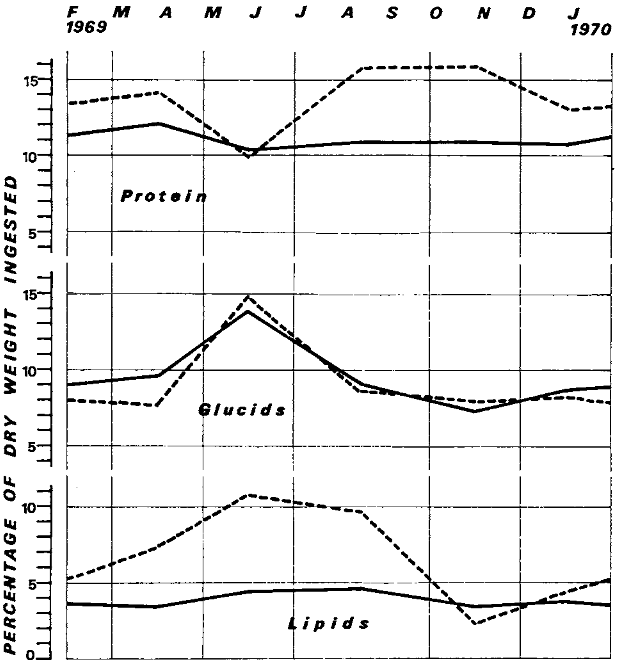

FIG. 9. Seasonal variation in the content of the diet of *Presbytis senex* (solid line) and *Presbytis entellus* (dashed line).

flushing are eaten in large quantity. The same applies to the rates of lipid intake: these vary little and lie around 4% for *P. senex*, while in *P. entellus* they vary from 3 to 11% of the dry weight of the total diet and are generally considerably higher. The amounts of soluble glucids (the results of the analysis, after a short hydrolysis, show approximately the amount of glucids actually assimilable; see Hladik *et al.*, in press) are more similar for the two species and follow seasonal variation in the flowers and fruits available.

As a result, *P. entellus* obtains much more energy from its environment but has to spend more energy than *P. senex* in finding scattered food resources over a wider range. The less mobile system of *P. senex* minimizes energy expenditure but allows a relatively low nutritional gain with little variation throughout the year.

6.3. Mineral Intake and Geophagy of the Leaf Monkeys

Seasonal variation in the intake of some minerals was also found (Fig. 10) but, at any time, rates of intake are generally higher than the minimum requirements for both langur species.

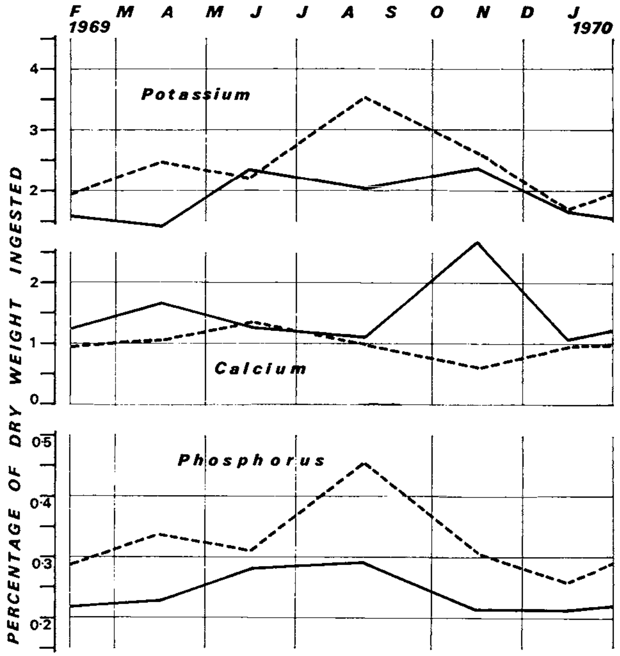

FIG. 10. Seasonal variation of mineral content in the diet of *Presbytis senex* (solid line) and *Presbytis entellus* (dashed line).

Many leaf-eating primates eat small amounts of earth (Ripley, 1970; Hladik and Hladik, 1972; Hladik, 1973; Oates, 1974; Pollock, 1975b). This behaviour (geophagy) has no apparent connection with the mineral nutrition, as might have been expected (Hladik and Gueguen, 1974). If we compare the results of the analysis of a piece of termite mound collected by S. Ripley at Polonnaruwa to the composition of different food samples eaten at the same time by the gray langur (Table IX), the amounts of minerals in the earth sample are very small, with the exception of iron which is not necessary at such a high rate (the iron of leaves and fruits covers all physiological requirements). Sodium and zinc, the only elements that might be low in the diet, are present in the earth sample but in smaller quantities than in many common foods. Several samples of earth eaten by African primates have also been found to contain low mineral levels when compared with leaves.

One possibility is that the small quantities of clay which are eaten by folivorous primates may act as an adsorbant of the tannins and compensate for their inhibitory effect on protein absorption as demonstrated by Feeny (1969). Alternatively, they may have a similar

TABLE IX

Comparison of minerals in earth and in some foods eaten by* Presbytis entellus *at Polonnaruwa*

	P	Ca	Mg	K	Na	Fe	Zn	Mn	Cu
Earth from a termite mound (sample I from S. Ripley)	257	565	1290	773	148	25 000	59	970	22
Walsura piscidia									
young leaves	2580	2290	1540	32 060	87	73·5	47	79·5	8·9
mature leaves	1250	10 250	2400	18 000	87·5	105	185	200	4·5
Drypetes sepiaria									
young leaves	1600	9900	3700	22 100	930	143	35	183	6·5
mature leaves	2000	10 000	4200	27 000	840	155	24	178	3
Schleichera oleosa									
mature leaves	1900	23 000	1850	7500	285	—	28·5	32·5	10
Ficus amplissima									
fruits	1810	9630	3400	21 970	240	78	21	10	8·2

* By dry weight p.p.m.

physiochemical effect on the other secondary compounds which are frequently found in small quantities in leaves.

6.4. Intake of Secondary Compounds by the Langurs

Secondary compounds or allelochemics (Whittaker and Feeny, 1971), such as alkaloids, tannins, saponins, glucosides etc. are generally considered as toxic or repellent for insects and vertebrate plant-eaters. They may represent antipredator devices produced by the plants. Strong evidence of the advantage to the plant of such toxic compounds in seeds has been presented by Janzen (1970). The occurrence of the allelochemics in large quantity in leaves is not so common (A. Hladik, 1977). A variety of secondary compounds is present in the leaves of many species but their concentration is generally low.

Tests for alkaloids were made on a series of dried herbarium samples of the plants eaten by the langurs at Polonnaruwa (Hladik *et al.*, in press). Only three species (out of a set of 41 species) have strongly positive reaction with Mayer's and Dragendorff's reagents and these positive results may eventually be due to a partial decomposition of the protein during hydrolysis. Further investigation was carried out on *Strychnos potatorum* (Fig. 11) whose unripe fruits are eaten by the gray

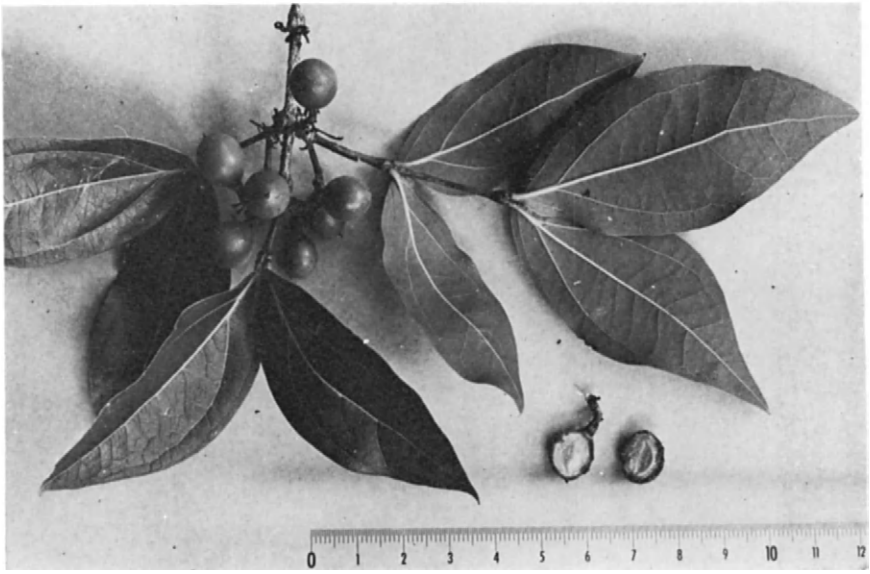

FIG. 11. *Strychnos potatorum* fruits (eaten by *Presbyis entellus*) and leaves (the only part selected by the macaques). Rule in cm.

langur in large quantities and whose leaves are frequently eaten by *Macaca sinica*. We found a large amount of alkaloid (neither strychnin nor brucin) in the fruit but no alkaloid in the leaves (the positive reactions of the screening tests were due to the protein for which the macaques eats the leaves).

It is not surprising that some toxic compounds can be eaten by the langurs since, in contrast to frugivorous species such as macaques, the bacterial flora of their stomach will decompose such products before intestinal absorption (Kuhn, 1964; Moir, 1968). As a protective device against primate leaf-predator, the secondary substances of plants would not be very efficient.

Another type of chemical protection may be more efficient: the small amounts of nutrients in *Adina cordifolia* and some other common tree species (Hladik *et al.*, 1976) would encourage leaf eaters to select the foliage of species with higher nutrient levels. To feed on these low-level nutrients necessitates the highest physiological and ecological specialization of an animal adapted to a low level of energy input and output (such as *P. senex*).

7. DISCUSSION: PHYSIOLOGY AND FEEDING BEHAVIOUR

Physiological and behavioural adaptations of mammals have evolved to meet the requirements of different ecological niches. The result is a tendency to maintain a particular kind of diet but to vary this in accordance with seasonal cycles of food availability (see Section 4).

The behavioural regulation of the *milieu interne* is the prime cause of feeding behaviour (Garcia *et al.*, 1974) but it involves two distinct processes: firstly, a long-term effect via conditioning operating through the beniefical effects of food ingestion and absorption and, secondly, through taste stimulation. Each of these two processes may have a different importance for different species, as shown for the primates of Central America (Hladik *et al.*, 1971a): the long-term effect plays the major role for species which are partly folivorous such as *Alouatta palliata*, while immediate taste stimulation is more developed in frugivorous species such as *Ateles geoffroyi* and *Cebus capucinus* that must be strongly motivated to gather dispersed foods of high nutrient content.

Among the two *Presbytis* species of Polonnaruwa, the long-term effect of the same type of food may be very similar, since the digestive systems of both species are quite similar (with only small variations of the cell populations along the mucosa of the small gut; Amerasinghe *et al.*, 1971). Thus the differences in food choice may be explained by a difference of intensity of the immediate taste response.

Similar differences in the feeding strategies of *Colobus guereza* (see Section 3.2) and *Colobus badius* (see Section 3.3) suggest that the evolution of social structure as described by Oates (1974 and present volume), Struhsaker (1975) and Clutton-Brock (1973, 1974a, 1975a) is associated with the evolution of the intensity of the response to taste stimulation. The difference in feeding behaviour between siamang and gibbon (Chivers, 1973 and this volume) and between gorilla (Casimir, 1975) and chimpanzee (Hladik, 1973 and this volume) also needs to be examined, in terms of sensory physiology, according to the composition of the food selected in natural conditions.

8. SUMMARY

1. Direct observation of the feeding behaviour of two sympatric species of leaf monkeys (*Presbytis senex* and *P. entellus*) was carried out in the semi-deciduous forest of Polonnaruwa, Sri Lanka.

2. The food ingested by these two species was estimated from the weights of samples collected in the field. There are important differences between the proportions of the different categories of food ingested and the proportions of time spent feeding on the same types of food.

3. All tree species were surveyed and mapped in an area of 54·5 ha covering the home ranges of different groups of langurs which were observed. The food produced by each of these trees during one year was also calculated.

Presbytis senex obtained 70% of its food from three tree species only. The food ingested included (by wet weight) 60% leaves, 12% flowers, 28% fruits.

Presbytis entellus obtained 70% of its food from ten tree species. The food ingested included (by wet weight) 48% leaves, 7% flowers, 45% fruits.

4. Seasonal variations in the food choices were marked in both langur species but similar differences between them were present throughout the year.

5. Comparison of the supplying areas of the different groups showed that food resources were distributed similarly between them, with a different model of habitat utilization concerning each species.

6. The composition of the foods ingested varied between the two species. The food of *P. senex* was lower in nutrient contents than that of *P. entellus* but varied less throughout the year.

Geophagy frequently observed among langurs and other folivorous primates does not appear to be associated with the selection of deficient minerals.

Secondary compounds play a small role in the feeding ecology of langur species. Food choice is mainly determined by the distribution of primary compounds with taste stimuli playing a different role in relation to different feeding strategies.

ACKNOWLEDGEMENTS

This paper is a continuation of the Primate Survey (Smithsonian Biological Program in Ceylon) initiated by Drs J. F. Eisenberg and S. Ripley. The biochemical analysis involved several scientists of the "Institut National de la Recherche Agronomique" (France), especially L. Gueguen, M. Mercier, G. Viroben and P. Valdebouze. I would like to thank again the University of Sri Lanka, especially Pr Crusz and two students, B. W. B. Van Cuylenberg and F. P. Amerasinghe, for their participation in the initial project, and the Warden of the Wild Life Department of Sri Lanka, Mr W. L. E. De Alwis. The English version of this text was improved by H. Cooper, and Dr T. H. Clutton-Brock made the final revision.

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The Feeding Behaviour of Siamang *(Symphalangus syndactylus)*

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1. INTRODUCTION

The aim in this chapter is to describe the current state of knowledge about the feeding behaviour of siamang after six years of intermittent study in Peninsular Malaysia, mostly in the Krau Game Reserve in central Pahang. This involves synthesizing and discussing data from various studies—mainly from a two-year study from May 1968 to May 1970 inclusive (Chivers, 1974, 1975), but also from two- or four-month studies in the summers of 1971, 1972 and 1974 (Chivers *et al.*, 1975), and a six-month study in 1973 (MacKinnon, 1977), and three months of an 18-month study in 1974 by J. J. Raemaekers (pers. comm.).

2. METHODS

2.1. Study Areas

The project started with a seven-month countrywide survey to determine the distribution and numbers of hylobatid species, and to choose

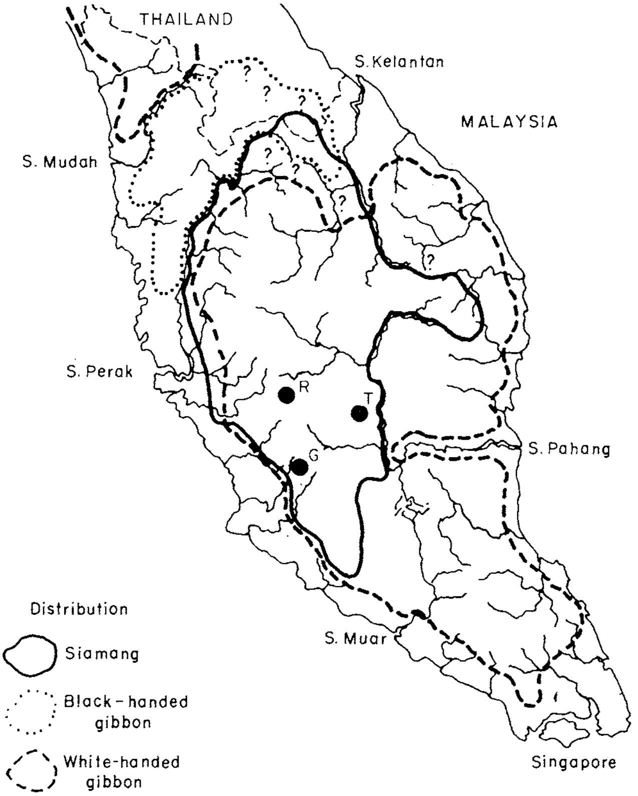

FIG. 1. Map of Peninsular Malaysia showing the distribution of hylobatids and the locations of the study areas. Abbreviations of study areas: G, Ulu Gombak; R, Ulu Sempam; T, Kuala Lompat.

the most suitable and representative study areas for detailed observation of siamang family groups. After this, at least ten days in each of 17 months from January 1969 were spent in two areas—one highland, one lowland—with three days in a third (highland) locality (Fig. 1).

The siamang is mainly an animal of hill forest (Fig. 2), being found usually over 300 m above sea-level (a.s.l.). This habitat with its rugged terrain, however, poses considerable problems for the field worker, and the greatest success was achieved in the lowland study area at about 50 m a.s.l., in the vicinity of the Kuala Lompat Post of the Krau Game Reserve. Nevertheless, observations were made throughout the study in the hill forest of Ulu Sempam between 500 and 750 m a.s.l. In Ulu Gombak, a particularly rugged area, roadside observations were made on three to four days each month from 1968 to 1970, mainly on calling.

The Kuala Lompat study area is at the foot of the central massif of Gunong Benom at the confluence of the rivers Krau and Lompat, eight miles west of the river Pahang. The forest is typical of lowland dipterocarp forest in the Malay Peninsula, being much richer in tree species than hill forest. Species of *Dipterocarpus*, *Shorea*, *Parkia*, *Intsia*, *Dyera*, *Sindora*, *Alstonia*, *Parinari*, *Ficus*, and the magnificent giants *Koompassia excelsa* and *K. malaccensis* (often exceeding 60 m in height) dominate the forest. Conspicuous in lower levels of the canopy are species of *Sloetia*, *Randia*, *Xylopia*, *Eugenia*, *Knema*, *Ficus* and *Nephelium*. The forest margins show some sign of disturbance, being more open with smaller trees. Men from the nearby village are often seen in the forest on their way to fish, harvest fruit or collect rattans, but there is no hunting of animals.

The Ulu Sempam study area is on the northern slopes of Bukit Fraser (1400 m a.s.l.); it has the largest hylobatid population and the least rugged terrain of all the highland areas surveyed. Parts of the forest are logged selectively at intervals of about five years, which apparently produces an habitat enriched for primates and other arboreal animals. Removal of parts of the main canopy encourages the growth of smaller trees, such as species of *Aglaia*, *Cynometra*, *Dialium*, *Durio*, *Glochidion*, *Macaranga*, *Antidesma*, *Mallotus*, *Ficus*, *Xylopia*, *Diospyros*, *Litsea* and *Adinandra*, which provide much of the food of the siamang and other primates. Tree species important for timber provide little or no food, only substrates for moving, resting, sleeping and calling. There are numerous species of *Shorea*, *Dipterocarpus*, *Anisoptera* and of Anacardiaceae such as *Bouea*, *Melanorrhoea* and *Melanchyla*, in addition to large numbers of the palm *Oncosperma horrida* and of the giant rattan, *Calamus urens*, with dense bamboo in disturbed lower-lying areas. There are many small trees of the genus *Saraca* in the rocky gullies which drain the ridges.

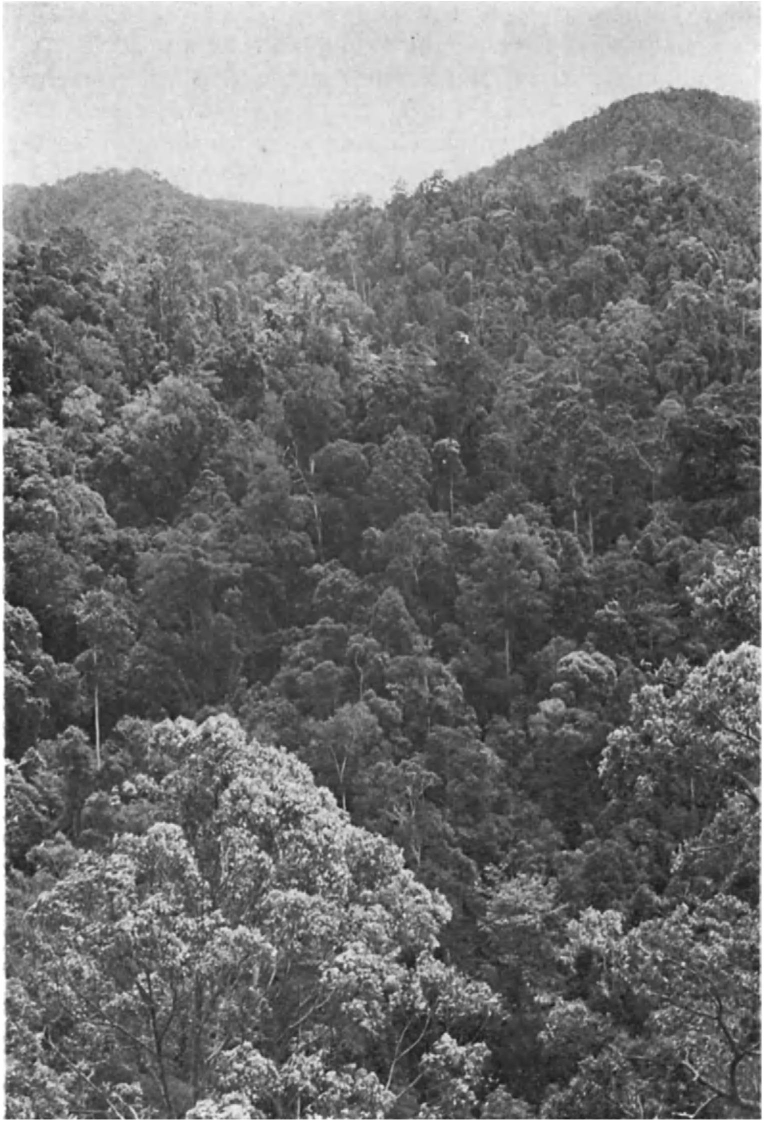

FIG. 2. The tropical rain forest.

A large ape, such as the siamang, living in the canopy of the tropical rain forest and adapted to exploit the terminal branches would appear to suffer little from predation. Risks to the more vulnerable members of the family group, infants, are minimized through the unusual amount of parental care given to them. Nevertheless, snakes, cats and raptorial birds are potential predators as indicated by the alarm reactions of a siamang group. Having a long reproductive cycle (2–3 year interval between births), single births and a long maturation period (8–10 years), the frequent loss of young would have a serious effect on a population of siamang. They sleep safely in the terminal branches of emergent trees; it may be significant that they rarely sleep in the same tree on consecutive nights. During the day they may cringe, and the young dart to an adult, when a raptorial bird flies overhead. Sometimes the adults will start grunting at the proximity of a potential predator and this may develop into a long chorus of barks, booms and bark-chatters (Chivers, 1974: 242).

2.2. Size and Distribution of Observation Samples

In each area efforts were made to obtain detailed dawn-to-dusk observations on ten consecutive days in each month. The behaviour of one individual in the group was sampled at 1-min intervals throughout the day, and that of other group members at 5-min intervals. Social interactions were recorded whenever they occurred. This sampling regime was achieved at Kuala Lompat for one group of five siamang (TS1) from April 1969 to May 1970 inclusive, but never properly for the group of four siamang (RS2) in Ulu Sempam. After August 1969 several half-days of data were obtained, and in February, March and April 1970, 22 complete days were recorded.

Since this first study the emphasis has shifted to 10-min sampling of the behaviour of all group members over five consecutive days. This appears sufficient to describe accurately the behaviour of a group of siamang in any month (Chivers *et al.*, 1975). The start and finish of feeding bouts are recorded according to the first animal to change activity. Where it was possible to view all group members feeding for most of a bout, the posture and hand use of each was recorded at 1-min intervals and the rate of ingestion was measured for five alternate half-min periods for each animal in turn.

Feeding includes the inspection of potential food, the rejection or picking of same, bringing into the mouth, and mastication followed by swallowing. A feeding bout is the period spanning a series of consecutive 5-min samples of feeding (if not measured in terms of start and finish times). It includes pauses in feeding for resting or for moving through the tree. The frequency and duration of feeding in particular food trees is investigated in terms of feeding visits.

The duration of a feeding visit is the time elapsing between the entry of the first animal into the food tree and the departure of the first animal from the same tree. One feeding bout often involves several feeding visits, if it takes less than five minutes for the group to move between food trees. The siamang may visit the same food tree in consecutive bouts, in which event each visit is scored separately. Intake and consumption are used as synonyms for time spent feeding: little effort has been made so far to measure the volume of food ingested, except for figs (Chivers, 1974: 118).

2.3. Food Choice and Availability

Food trees were numbered and tagged for identification where possible. The great diversity of the flora in the Malay peninsula makes identification a difficult and tedious process. The structure of the forest was investigated by classifying trees growing within 10 m on either side of the N–S transects set 150 m apart and the one E–W transect running from the swamp in the west to the Krau river in the east as high, medium or low.

There were 290 trees per hectare in the sample of transects at Kuala Lompat which represented 12% of the home range of the siamang group TS1. Of these only 5% were visited for food during the 14-month study; 8·5% were high (over 36 m in height), 29% were in the middle level (providing the bulk of the canopy) and 63% were in the understorey (between 9 and 24 m in height). Nearer the rivers there were fewer trees overall, with more small trees and fewer in the middle and high levels. Tree species were identified where possible, but there was no regular recording of the phytophases of a sample of trees. This deficiency is now being remedied by Aldrich-Blake and Raemaekers, who are studying the floristic cycles of the trees in several quarter-hectare plots at Kuala Lompat, so as to estimate the availability of potential foods at monthly intervals.

Food items are divided into four mutually exclusive categories: (i) fruit, (ii) leaves—mature, young, shoots, stems, (iii) flowers and buds, and (iv) insects—termites, caterpillars. For each day the location, starting time, duration and food type were recorded for each visit to food sources. Such records yield the daily number of visits and minutes spent feeding on each food category. From these can be calculated sample means for each observation period and the time spent eating each food category as proportions of the daily total and of the alert period (period of daily activity from leaving one night tree until entering the next).

No serious error has been introduced with such a precise definition of a feeding visit because (a) once feeding has started it is a continuous process with individuals consistently spending about 95% of the time actually feeding, and (b) the activities of group members are highly synchronized, so that individuals do not often forage away from the group (Chivers, 1974: 64, 137, 173, 1975).

Until biochemical evidence is available one must be as wary of basing too much interpretation of feeding behaviour on categories of food based on parts of trees as on a classification into tree species (Hladik and Hladik, 1969; Klein and Klein, 1975). It is what parts of plants contain and not what they look like that is important in our efforts to understand the effects of feeding on social behaviour.

Dawn-to-dusk observations of all members of the family group appears to overcome most of the difficulties in obtaining an objective measure of the behaviour of forest primates, by avoiding bias in observations of different age/sex classes and in different types of vegetation (Aldrich-Blake, 1970a). Such continuous observation provides data on aspects of behaviour peripheral to the main aims—information which might subsequently prove to be important in interpreting the main data. In species with small groups sample size of individuals will be small, but this disadvantage is more than offset by the greater reliability of the data. It is very worthwhile making extra efforts in the field to sample the behaviour of particular individuals at regular intervals for long periods, thereby avoiding the need to indulge later in complex statistical operations in efforts (of unknown success) to correct for bias during irregular observations. The collection of unbiased quantitative observations is particularly useful if phenological and nutritional data can also be obtained to help explain what it is that attracts a group to particular parts of its home range at certain times.

3. FEEDING BEHAVIOUR

3.1. Feeding Techniques

Feeding is a continuous social process among siamang; once one has started picking and ingesting food, the other group members soon join in and they are unlikely to stop for some time (every 2 hours for 72 minutes on average, Chivers, 1974: 144).


(a)


(b)

FIG. 3. Feeding postures of siamang (a) and (b) adult female hanging eating figs, *Ficus virens*, (c) adult female hanging eating new leaves of *Sloetia elongata* and (d) adult female sitting eating fruit of *Aglaia* sp.

Exceptions to this are the 3·5% of time spent in each food tree pausing to survey the canopy for the location of food, the 4% spent moving towards that food (Chivers, 1975) and the time taken to move between food trees (each feeding visit lasts 26 min on average, Chivers, 1974: 78; so this happens twice in a bout on average and lasts less than 5 min each time). Less often the group spreads out and feeds here and there as it travels between primary food sources in the manner characteristic of white-handed gibbons (Ellefson, 1974).

Feeding technique varies according to the size and structure of the tree, and the distribution of food. Siamang are more active earlier in the day harvesting fruit, which is more widely distributed through relatively large trees. Suspensory behaviour predominates here with individuals hanging by one arm, assisted by one or both legs, and picking food with the free hand (Fig. 3). Food is rarely picked directly with lips and teeth; instead the animal palpates each fruit and leaves those which are unripe or bad. Larger fruit are held in the corner of the mouth and are opened by manual rotation between the large canines.

In trees with new leaves, particularly those on dense vines, feeding is less active and the siamang sit for long periods picking food within their long reach. In such bouts siamang sit twice as much as they hang, whereas in fruiting trees they hang twice as much as they sit, with scores varying from 1·5–4·5 times according to the tree.

Individuals usually show a preference for using one hand rather than the other for picking food. At Kuala Lompat the TS1 male, female and juvenile were left-handed and the subadult male was right-handed. On average they changed hand every 2–3 min, but used the preferred hand for 1 min longer than the other each time.

Movements within a food tree were classified as "major" or "minor" according to whether the animal moved between or within the primary branches of the tree. At Ulu Sempam on one occasion each individual moved between parts of the tree once, and between secondary or tertiary branches 3–4 times in one hour. At Kuala Lompat during three feeding bouts in a fig tree, individuals moved 5·5 m every 3·5 min on average, 31% of the 78 moves were "major". The rate of feeding usually varied during a feeding visit. At first it was rapid, then there was a steady decline, and finally there was sometimes a marked increase (Chivers, 1974).

Water was consumed at specific times in a characteristic way. In the early morning after a night of rain the siamang would sit by a vertical branch and wipe the hand upwards against the flow of water rivulets; the water would then be licked and sucked from the back of the hand. This is identical to the way in which termites are consumed from their marching columns. A similar action is used to wipe water off leaves.

The most distinctive mode of drinking, seen only in the drier area of Kuala Lompat, occurred during visits to trees containing holes, usually at the junction of branches or at sites of branch loss and rotting, which were filled with water. These occurred every other day on average and lasted for 5–20 min. Each animal would take a turn to sit by the hole, dip his or her hand into the depths, and then raise it rapidly to the mouth (elbow uplifted) to suck and catch the water running off the back of the hand. Similar behaviour has been described for the white-handed gibbon (Ellefson, 1974).

3.2. Feeding Heights and Sites

Most of the arboreal pathways and food of siamang are found in the main canopy level, between 24 and 36 m above the ground. The emergent trees of the high level provide sites for sleeping and calling and some food. It is difficult to travel far in the low level but a certain amount of food (and water) can be found there. Siamang were never

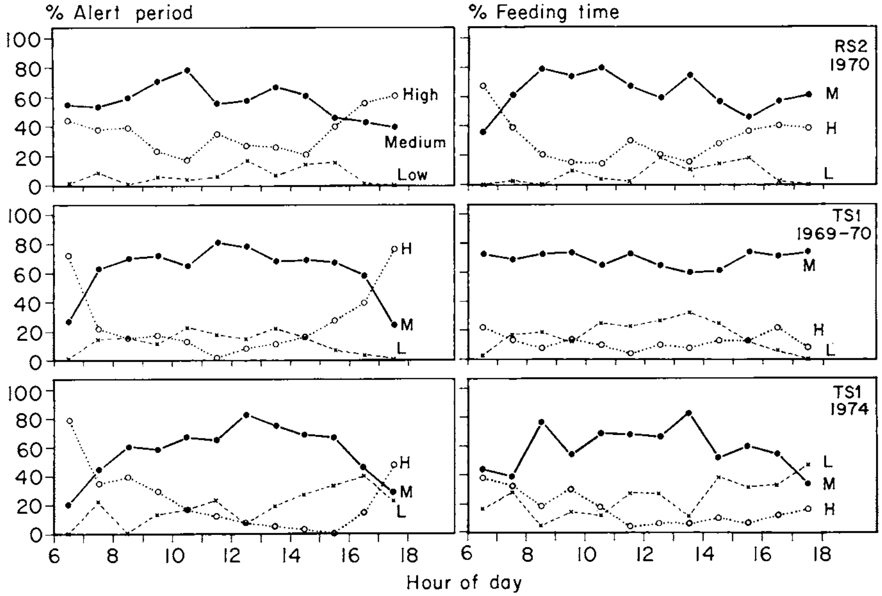

FIG. 4. Hourly pattern of use of different levels of the forest canopy (a) throughout the alert period, (b) during feeding bouts, for RS2 in Ulu Sempam in 1970 and for TS1 at Kuala Lompat in 1969–70 and 1974 (H: high, M: medium, L: low).

seen less than 10 m from the ground (except for two occasions when immature animals fell to the ground, without suffering injury). In some trees food is within reach of large (stable) branches, in others food is mostly near more flexible substrates. Hylobatids are best adapted among primates for exploiting such food sources.

In 1969 and 1970 the siamang at Kuala Lompat spent 25% of the day high, 63% medium and 10% low, whereas those at Ulu Sempam (with a shorter alert period) were high 36%, medium 57% and low 7% of the day. Siamang descend from their sleeping positions in the emergents to spend most of the day in the main canopy, descending to the low level before or after noon (Fig. 4). The study shows the importance of the high level for activities other than feeding, of the main canopy for providing the bulk of their nourishment, and of the low level for providing important nourishment and little else. TS1, for example, feeds for 25% of the 25% of the day that it has been observed in the high level during the last six years, for 54% of the 61% of the day that it has been in the medium level, and for 74% of the 14% of the time it spends in the low level (Table I).

TABLE I

Use of different levels of the forest by siamang

		% alert period			% feeding time			% alert period feeding		
Group	year	H	M	L	H	M	L	H	M	L
TS1	1969	23	63	14	6	68	25	12	49	84
	1970	28	62	10	17	69	14	31	58	69
	1972	29	54	17	19	57	24	31	50	65
	1974	25	57	19	13	62	25	28	56	69
	mean	26	61	14	13	67	21	24	54	74
RS2	1970	36	58	7	28	65	8	35	51	53

H: high; M: medium; L: low.

3.3. Daily Activity Pattern and Proportion of Time Spent Feeding

It is appropriate to refer to the time during which siamang are active each day as the "alert period", as they differ from most other primates in the continual perceptual readiness or alertness sustained by each individual during this time, even when resting (Chivers, 1974: 165). The alert period can be defined from the first to last movement discernible within the group or, more usefully in studies of ranging and feeding, from the time between leaving and entering successive night sleeping trees. Siamang usually rest for about 25 min after the first movement (involving elimination) before leaving the night tree in the morning, but they reach their night sleeping positions within a few minutes of entering the night tree in the evening.

The alert period lasts for about 637 min (10·6 hr) on average; the sample means (Table II) have ranged from 604 to 666 minutes (10–11 hr) which represent 84 to 92% of the 12 hours of daylight. The daily activity pattern of siamang differs from that of most other primates by the lack of a long rest period in the middle of the day, and by the termination of activity as much as two hours before dusk. Peaks of feeding occur not at dawn and dusk (as characteristic of many tropical mammals) but during most of the morning (Fig. 5); the peak of drinking water is around noon. Activity, in terms of feeding and travel, declines steadily thereafter as the day passes. Other gibbons show a similar pattern of activity (Ellefson, 1974; MacKinnon, 1977). Since there is considerable dietary overlap between the primates in this tropical forest habitat, this temporal separation of activity patterns might facilitate their peaceful coexistence (Chivers, 1973).

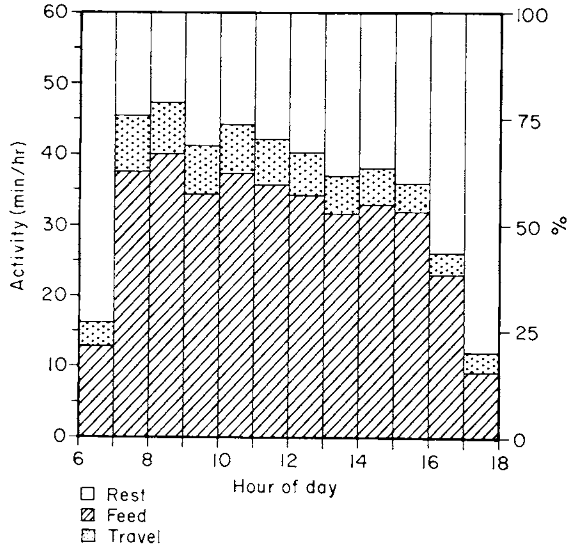

FIG. 5. Hourly patterns of resting, feeding and travel during the day for TS1 at Kuala Lompat. Test period: 148 days in 14 months 1969–70.

Siamang feed for about half the alert period; sample scores have ranged from 40 to 59% (Table II). The concentration of feeding between 7.00 and 11.00h is more marked in dry periods (Chivers, 1974).

TABLE

Means and proportions of various parameters of feeding and ranging behaviour of three siamang family

Group	Year	Months	No. of days	Alert period (min)	Forest level (% time)			Feeding time/day							
					H	M	L	fruit (min)	%*t*	leaves (min)	%*t*	flowers, buds (min)	%*t*	insects (min)	%*t*
TS1	1969	Apr.–Aug.	59	617				84	25	206	61	50	15	0	0
		Sept.–Dec.	40	628	25	64	11	125	34	202	59	21	6	2	1
	1970	Jan.–May	49	666	28	62	9	132	36	202	56	18	5	13	4
	1971	Sept.–Oct.	18	604				101	37	149	54	22	8	3	1
	1972	July–Oct.	20	665	29	54	17	111	41	107	40	7	3	45	17
	1973	Jan.–Apr.	15	664				196	56	132	38	16	5	4	1
		May–July.	20	644				102	36	146	52	7	2	25	7
	1974	June–Aug.	8	647	25	57	19	154	43	162	45	5	1	36	10
		Sept.–Nov.*	50	617				137	51	76	28	0	0	59	22
TS1A	1971	Sept.–Oct.	20	637				145	47	147	48	13	4	4	1
	1972	July–Oct.	20	652	35	48	18	140	54	63	24	15	6	42	16
	1973	Jan.–Apr.	15	615				117	32	192	53	11	3	44	12
		May–July	10	540				108	44	109	45	5	1	23	10
RS2	1970	Jan.–Apr.	22	610	36	56	7	131	47	139	50	5	2	2	1

* Data collected by J. J. Raemaekers.

3.4. Amount of Time on Different Foods

Siamang are unusual among hylobatids studied so far in their high intake of young leaves; this probably relates to their larger size, smaller territories and to the need for ecological separation between closely related species. Young leaves, leaf shoots and stems, with occasional mature leaves account for about half of feeding time among siamang; scores range from 24 to 61% in the various samples (Table II). Fruits account for about 40% of feeding time, with scores varying between 25 and 56% according mainly to the time of year and whether or not the samples were taken during the fruiting season (Medway, 1972). Flowers and buds, and insects occupied 5 and 6% of feeding time respectively. These long-term figures contrast with behaviour in 1969–70 when only 32% of feeding time was spent eating fruit, 58% on leaves, 9% on flowers and buds and 2% on insects. Fruits were relatively scarce during this period following their superabundance in 1968 (Chivers, 1974: 125).

Feeding visits to fruiting trees were either very long (up to 3 hr for some figs) or very short (a few minutes for some small berry-bearing trees). From 1969–70 feeding visits for fruit and leaves both lasted for about 27 min on average; the fewer bouts for flowers and buds tended to last a little longer, and those for termites and caterpillars were about

II

groups in two localities in Peninsular Malaysia during nine observation periods from 1969–74

			Ranging						
Total			no. ha	quadrats	Travel time	Day range	Night posn.	Cumulative range	
(min)	%AP	no. visits	total	different	(min)	(m)	shift	ha	quadrats
346	56	10·7	7·7	6·8	86	808	294		39
355	57	12·1	7·1	6·4	79	725	257		38
365	55	16·7	11·6	10·9	121	1358	320		40
275	46	12·5	11·6	9·8	78	1016	257	18·0	33
270	41	15·2	13·5	10·2	142	1483	235	30·5	42
348	52	8·5	7·3	5·9	88	696	230	16·4	29
280	43	8·4	9·1	8·0	81	790	303	28·5	43
357	55	10·3	10·0	9·0	114	1053	341	14·0	35
280	44		9·2	7·8	125	815	315	37·8	54
309	49	12·6	10·1	8·1	63	835	293	18·2	36
260	40	11·3	12·8	10·4	138	1356	314	21·4	36
364	59	10·6	5·3	4·5	66	497	184	11·3	24
258	48	7·5	5·0	4·8	60	400	205	12·5	23
276	53	12·0	7·0	5·7	84	778	193	14·7	20

half as long, averaging 14 min. Similar results have been obtained subsequently (Chivers *et al.*, 1975).

3.5. Food Selectivity and Diversity

Siamang inspect food carefully, apparently for ripeness; unripe food is left untouched for subsequent visits. It is also noticeable that siamang rarely visit the same tree more than once in a day, although they may visit as many as 30 (the average is 12 food trees per day). If there are several trees of the same species with food, the siamang may visit them all in one day, particularly if the amount of food in each is limited. Thus the daily behaviour of siamang is characterized by selection for variety, perhaps to yield a balanced intake of nutritional constituents.

Little variation in techniques, heights and sites of feeding has been seen between groups and populations. In each sample at Kuala Lompat there was a marked degree of similarity between the two study groups in terms of proportion of the alert period spent feeding and daily activity pattern (Chivers *et al.*, 1975). There was less correspondence, however, in the relative intakes of fruit and leaves. This presumably reflects differences in vegetation and floristic cycles between the two areas. The 1970 dry season is the only time for which comparable data are available for two populations. At this time the lowland group

(TS1) was active for longer each day, feeding for 90 min more on average, and eating less fruit and more flowers and insects than the highland group (RS2).

While we have a full record of the trees utilized by siamang, there is as yet no overall estimate of potential foods in the area. I suspect, however, that primates living in small groups in small home ranges have such an intimate knowledge of the resources that, through their behaviour, they provide as good an indication of the abundance and dispersion of foods as any "objective" method. The behaviour of siamang *may* show where food is, where food is not, and where food is going to be . . . and in what abundance.

Estimates of food availability independent of behaviour will confirm the extent to which primates with patterns of grouping and ranging similar to siamang are *fully* exploiting available foods to obtain a balanced diet. This hypothesis would not apply to periods of food excess (in terms of diversity of tree species yielding foods rather than amounts of particular foods). At such times only can preferences for particular foods be investigated satisfactorily.

4. TEMPORAL PATTERNING OF FOOD CHOICE

4.1. Diurnal Variation in Food Choice

At any given time the daily activity, in particular the day range, of a siamang family group is clearly orientated towards one or more food trees; these are referred to as "primary food sources". These are usually fruiting trees, often figs (*Ficus* spp.), although some trees with leaf shoots can have the same attraction. They are visited at least once a day, usually in the morning, for between one and three hours for as long as food is available (often up to 10 days, although there will be infrequent visits beforehand as fruit start to ripen or as young leaves bud).

"Secondary food sources" are trees visited frequently, usually for shorter visits, in one or more observation periods; "tertiary food sources" provide food more easily for longer periods; that is, siamang feed in them later in the day during several months, mostly on vine leaves. These principal food trees are 7% of the food trees visited by TS1 in 1969 and 1970, which accounted for 30% of feeding visits and 40% of feeding time; during the 14-month study 80% of food trees were visited five times or less.

Thus, while there was an initial subjective element in the recognition of principal food trees, and in their classification as primary, secondary or tertiary, this classification can be backed up objectively—primary sources are rich sources of food in the short-term, secondary sources are also of short-term importance but are less productive, and tertiary sources are reliable sources of nourishment over several months. During 14 months of study at Kuala Lompat species of *Ficus* figured among the principal food trees as follows:

	Primary	Secondary	Tertiary
Number of tree species	31	53	32
Fig trees with fruit (%)	55	23	16
Fig trees with new leaves (%)	10	15	3

These trees occupy an unique place in the diet of siamang since the amount of time spent feeding therein is disproportionately larger than the number of trees and frequency of visits (Chivers, 1972: 120).

Daily patterns of food use can be recognized. During the course of the day, time spent eating fruit decreases, and the time spent eating new leaves increases (Fig. 6). The proportion of time spent eating fruit in each hour decreased from about 70% after dawn to about 20% by mid-afternoon, with an increase in leaf-eating from about 30 to 70%. There is an increase in fruit-eating, especially in some seasons, at the end of the day before the group settles for the night. At Kuala Lompat in 1969 and 1970 in the first quarter of the day 41% of feeding bouts were on fruit and 45% on leaves, but in the last quarter only 25% were on fruit and 68% were on leaves; the frequency of bouts on other food categories decreased only from 11 to 7% (Chivers, 1975). Consumption of leaf stems and shoots and of flowers, buds and insects varied little throughout the day.

Decrease in fruit-eating as the day passes is correlated with a decrease in the extent and rate of ranging (see below and Chivers, 1975). It is possible that fruit-eating at the start of the day provides an immediate source of energy for subsequent activity, restoring any energy debt that may have accumulated overnight (MacKinnon, pers. comm.). Fruit-eating at dusk would serve to build up energy reserves for the night. Suspensory behaviour, more important in fruit- than leaf-eating (see above), is energetically costly (Ellefson, 1974; Fleagle, 1974), especially for a large hylobatid such as the siamang. Since fruit-eating requires more energy expenditure and movement in the terminal branches than leaf-eating, in the absence of a midday siesta the necessary nutritional constituents in leaves (Hladik *et al.*, 1971a) are more easily obtained later in the day when the siamang are more fatigued.

It has been indicated above that within days the emphasis is on diversity of foods. Thus, at Kuala Lompat only about 14% of feeding

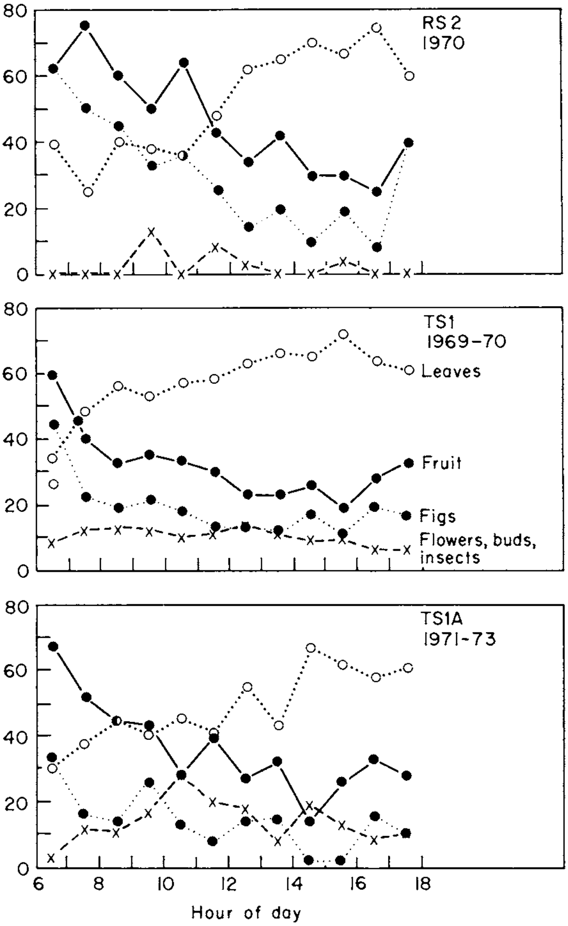

FIG. 6. Hourly pattern of feeding on different food categories (fruit, leaves, figs and flowers/buds/insects) during the day for RS2 in Ulu Sempam in 1970, for TS1 at Kuala Lompat in 1969–70 and for TS1A during 1971–73.

visits were visits to the same or different trees for the same foods (Table III). This is an underestimate because it is often difficult to determine whether leaves eaten in one tree are of the same species as those eaten in another. By contrast, over periods of 10 days the same foods are consumed on at least 50% of visits on average.

4.2. Variation in Food Choice Between Days

There is usually little change in diet between days (or groups of days), partly because the siamang adopt a routine for exploiting the available

TABLE III

Some aspects of food selectivity and diversity by the siamang group TS1 at Kuala Lompat

Year	No. of days	No. of feeding visits	Visit duration (min)	Feeding visits/ day	% Visits to same foods each day				
					fruit	new leaves	flowers and buds	insects	total
1969	59	608	31·7	10·3	23	42	34	2	9
	40	484	30·5	12·1	49	46	6	0	15
1970	49	820	21·8	16·7	42	39	1	18	18
	148	1912	27·1	12·9	40	41	9	10	13
1971*	18	225	22·0	12·5	69	15	15	0	6
1972	6	101	17·5	16·8	27	7	0	66	15
1973†	15	127	41·1	8·5	67	25	0	8	19
1974	8	144	19·9	18·0	33	17	6	44	13
‡	47	597	24·8	12·7	50	17	4	29	12
Total	195	2509	26·6	12·9	42	36	8	14	14

Year	Months	No. of food trees	No. of feeding visits	% Repeat visits to same trees	% Visits to same foods over 10 days				
					fruit	new leaves	flowers and buds	insects	total
1969	Apr.–Aug.	381	608	37	29	51	19	1	45
	Sept.–Dec.	281	484	42	48	48	4	0	47
1970	Jan.–May	441	820	46	47	39	3	11	56
148 days		1103	1912	42	42	45	8	5	50

* Data collected by F. P. G. Aldrich-Blake.
† Data collected by J. R. and K. S. MacKinnon.
‡ Data collected by J. J. Raemaekers.

food resources at any given time (Table II). This may involve circling the territory in 1 day or, more often, in 2–3 days. This pattern shifts gradually as new foods become available.

Analysis of data from Kuala Lompat (1969–70), in which the pattern of days of high activity (with a prolonged alert period and high scores for feeding and travel) is investigated, reveals that on average 2 days with long alert periods tend to be followed by 2 days with short ones. Furthermore, 2–3 days of intensive feeding were followed by 1–2 days with reduced feeding, whereas 1–2 days of increased travel were followed by 3–4 days with less movement. This suggests that following a day of increased movement about the home range, there follow 2–3 days with long alert periods and much feeding.

Any variation in food choice between consecutive days would probably relate to the rate at which supplies were replenished in particular trees. Trees with a large, fast-ripening crop are likely to be visited daily, whereas those with smaller crops ripening more slowly are visited less often. This is reflected by differences in ranging patterns whereby the home range may be covered in 1 day or in 3 or more days (see below). However much behaviour varies between consecutive days a routine is adopted, an equilibrium established, over periods of 5–8 days (Chivers *et al.*, 1975).

5. SEASONAL VARIATION IN FOOD CHOICE

In the Malay peninsula the period from January to April is usually very dry and hot. From October to December it is usually very cloudy and wet; the intervening period, May to September, is more variable although it is usually wetter in May and June and drier in September (Dale, 1959, 1960, 1964; Chivers, 1974: 24). In the 1969–70 study data were analysed in terms of three seasons—"intermediate", wet and dry. Subsequently, the latter part of the "intermediate" season has been referred to as the fruiting season (Medway, 1972; Whitmore, 1975; Chivers *et al.*, 1975).

Fruit are more abundant from July to September inclusive, although some food species, such as figs, fruit at other times of year. Flowers are most abundant in the latter part of the dry season, and new leaves during and after the November and May rains. It has still to be determined when insects are most abundant; siamang have been recorded eating caterpillars at the end of most dry seasons, and termites during fruiting and dry seasons. Floristic cycles may not be clearly reflected in the feeding behaviour of siamang (Fig. 7) because they select a balanced diet at all times of year (Chivers, 1974; Chivers *et al.*, 1975).

Though little seasonal variation was evident in the amount of time spent feeding on different parts of trees, use of tree species differed between months. The leaves of a common small tree *Sloetia elongata* are consumed in considerable quantities when available each wet season and at the end of the dry season. At the latter time flowers appear (in the form of catkins) and these are consumed avidly, especially when there is a scarcity of fruit at this time of year. It is at the end of the dry season that several other tree species produce new leaves and flowers, e.g. *Koompassia excelsa*, *Shorea leprosula*, *Xylopia caudata*, *Cassia nodosa*, *Dillenia reticulata* and species of *Cynometra*. *Dillenia* is untouched by siamang, but is fully exploited by the leaf monkeys, *Presbytis* spp. Species of Leguminosae are major sources of food for primates, and they tend to have a fairly rigid, synchronized annual cycle.

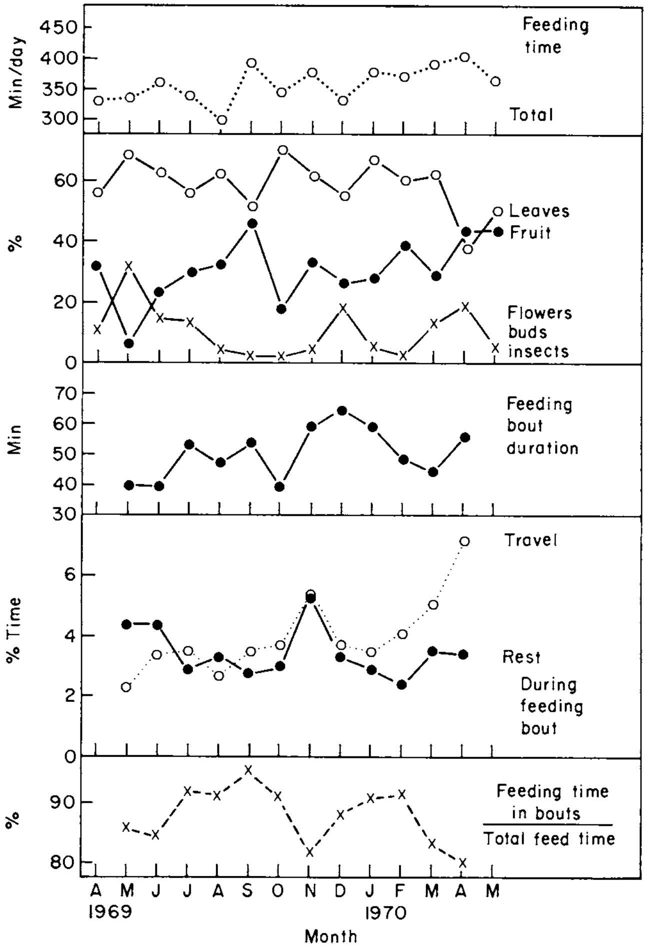

FIG. 7. Seasonal variation in food choice and feeding behaviour by TS1 at Kuala Lompat in 1969–70.

A little later in the year, from July onwards, the fruit of *Maranthes corynbosum*, *Randia scortechinii*, *Dracontomelum mangifera*, *Aglaia* spp. and *Eugenia* spp. are regularly available. Every other year, or at longer intervals, the fruit of *Sapium baccatum*, *Nephelium* cf. *lappaceum*, *Baccaurea kunstleri*, *Bouea oppositifolia*, *Knema laurina*, *Antidesma coriacea*, *Dialium platysepalum*, and species of *Chisocheton*, *Pentaspadon*, *Nauclea*, *Garcinia* and of Rubiaceae are much consumed. At these and other times the leaves and fruit of vine species, such as those of *Gnetum*, *Combretum*, *Derris*, *Vitis* and *Connarus*, are important food sources.

The year-round availability of figs has already been referred to; in any month at Kuala Lompat there is almost always one large tree in fruit in the home range of the siamang, and often several. If anything there is a tendency for figs to be scarcer in what is the fruiting season for other tree species, that is, from July to September. The lack of synchrony within some fig species, such as *Ficus virens*, is striking. Since this species fruits twice a year, it does not require many specimens for fruit of this species to be available at most times of year. Some of the 12 or so other species of fig found in the Krau Reserve fruit annually, but not always at the same time of year and not often in synchrony, e.g. *F. sumatrana*, *F. consociata* and *F. stupenda*.

In Ulu Sempam, figs were even more important as sources of food; the extended fruiting period of two specimens of *Ficus heteropleura* (a stalked fig) provided food throughout the 1970 dry season. Otherwise the siamang fed in succession on the fruits of *Ficus pellucidopunctata*, then *F. stupenda*, *F. virens* and *F. sumatrana*, and finally *F. dubia* and *F. consociata*. Other fruits consumed were of species of *Memecylon*, *Aglaia* and *Bouea*, while the new leaves of *Ficus caulocarpa* and then of *Cynometra inaequifolia*, and the stems of a species of *Connarus*, were very important food sources (Chivers, 1974: 105).

Time spent feeding on different tree species varied far more between sample periods than did the time spent eating different food categories; overall feeding time varied less as a proportion of the alert period than in absolute terms; and time spent eating different food categories varied less as a proportion of the alert period than in absolute terms (Chivers *et al.*, 1975). This degree of constancy in siamang feeding behaviour suggests an ability to overcome local and temporary inadequacies of certain foods and to achieve a balanced diet by using most of the plant forms (each of which is usually more abundant at different times of year) and by obtaining fruit from tree species exhibiting different, often asynchronous, cycles—annual, biennial, sporadic and endogenous (modified from Medway, 1970).

6. FEEDING AND RANGING

At Kuala Lompat the home range can be divided into a higher, drier north-west part and a lower, wetter (with seasonal flooding in places) south-east part. The vegetation appears to vary with soil type (Chivers, 1974: 94). The tendency of the siamang to concentrate on the north-west in each dry season, and in the south-east during each fruiting season, appears to be related to a spatial variation in foods.

In Ulu Sempam the home range of the siamang group saddled a ridge, and extended down one side a considerable distance, being intersected by several gullies. The variation in soil type in these different parts presumably determines the distribution of tree species in each. On almost all days the siamang ranged onto the ridge top and well down the slope, thereby exploiting such spatial variation as existed in tree species bearing food.

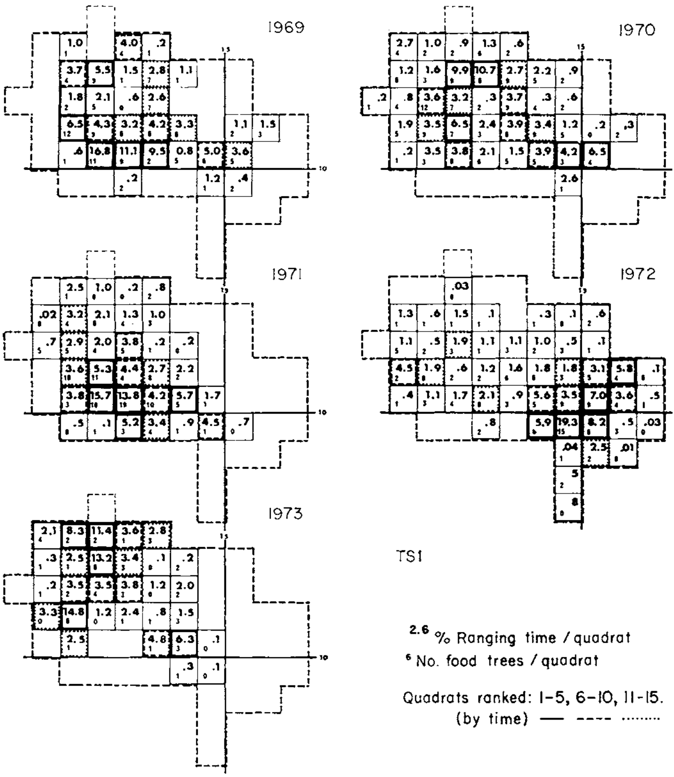

FIG. 8. Differential use of the home range by TS1 at Kuala Lompat during five observation periods.

There is a high correlation between feeding and ranging behaviour. Over the last few years 80% of TS1's alert period has been spent in the central 45% of their home range where 75% of the food trees are to be found (Fig. 8). During a 10-day period about two-thirds of this home range was visited, but 77% of the time was spent in 22% of the area.

At any given time a siamang group combines two patterns of ranging: (i) intensive use of a small (usually central) part of the range where food is temporarily abundant, and (ii) frequent visits to most other parts of the home range (a) to look for future food and (b) to maintain the exclusiveness of the group range or territory.

This pattern seems to vary little over time; only occasionally will more or less time be spent foraging or patrolling. Hence there is little seasonal variation in the way a group's time is distributed across the home range. Day range, however, either increases in length at some times (Fig. 9) so that the range is circled in one day rather than in three or four, or becomes more circuitous so that some parts of the home range are not visited for long periods. It is not yet clear whether ranging is more localized when food is more abundant or more scarce. If

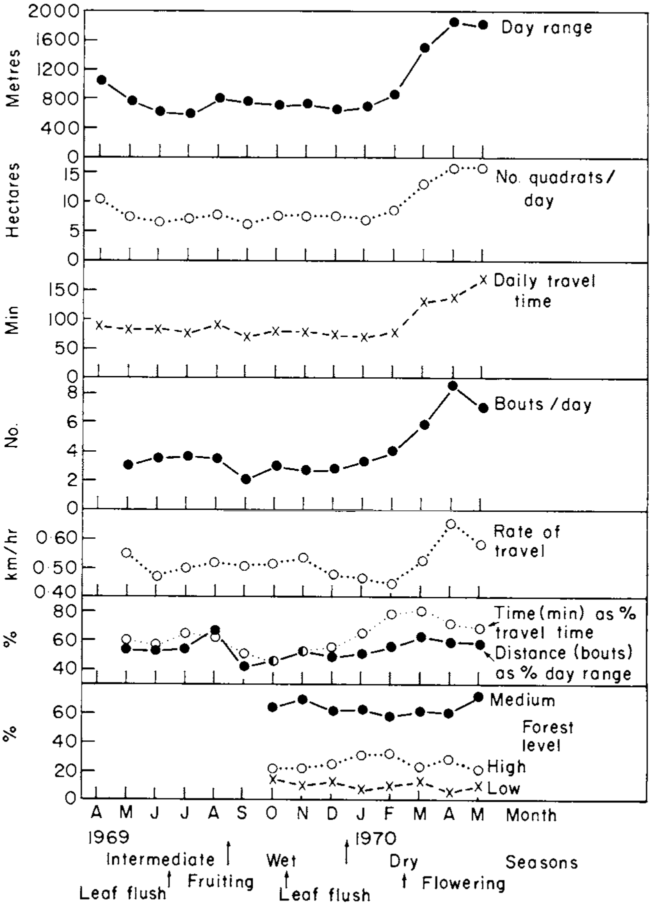

FIG. 9. Seasonal variation in ranging behaviour by TS1 at Kuala Lompat in 1969–70.

siamang are not the eclectic feeders one supposes them to be, food abundance might be characterized by more localized ranging. It seems more likely that when food is abundant siamang range more widely consuming a more varied diet, and when scarce they conserve their energy by less ranging and consume a less varied (and possibly less nutritious) diet.

7. AGE/SEX VARIATION IN FEEDING

Results are based mainly on observations of TS1 at Kuala Lompat, but there are sufficient observations of other groups to indicate that certain generalizations are justified. Adult females feed faster than adult males and for about 30 minutes longer each day. This appears to be related to her more active role in group leadership about the day range and to the high energetic costs of gestation and lactation. Subadults feed in a similar way to females, sometimes feeding faster and for longer each day. Juveniles also eat almost as much as females, but infants eat much less.

Adult siamang appear to occupy the most favourable feeding sites in each tree, in terms of density of food and ease of access. Younger animals are forced to indulge in more suspensory behaviour to obtain less accessible foods. As the bout progresses and individuals move about the tree, so the younger animals eventually gain access to the sites used by the adults. Individual distance is greater during feeding than in many other activities and less tolerance is shown to the proximity of others. The adults are most tolerant of each other and the infant and tend to feed closest together, but juveniles and subadults are "encouraged" to feed on the opposite side of the tree, or to wait until the adults have finished if it is a small tree.

The foods eaten by siamang of different sex and ages are very similar, because the group moves about in a closely co-ordinated way and feeds together, usually in the same food trees. When trees are too small for amicable relations, individuals may feed in turn or may utilize more than one tree (as when feeding on vine leaves spread through two or more trees). The only time when different foods might be obtained is when the group forages in the way characteristic of smaller gibbons (Ellefson, 1974). Siamang do not often "forage"—picking food here and there as they travel between principal food trees. In any case, different foods are no more likely to be consumed during such behaviour than would be ingested by those individuals feeding more than the others each day.

8. FEEDING BEHAVIOUR AND SOCIAL ORGANIZATION

The close relation between feeding and social behaviour is perhaps best illustrated by the observation that when ranging is increased in time and extent, and when feeding is increased in time and variety, group life is much enhanced in terms of play, calling and reproductive behaviour.

Hylobatids are unusual among primates, and unique among apes, in the way they live in monogamous family groups. Gibbons are morphologically adapted to suspensory behaviour for exploiting the small branch niche; Ellefson (1974) suggests that this might reduce their efficiency in moving long distances. Furthermore, the smaller gibbons especially require large quantities of fruit, which are widely and irregularly dispersed through the tropical rain forest. These smaller gibbons can best gain sufficient food by familiarizing themselves with a small tract of forest, thereby achieving some ability to predict the whereabouts of food at any given time, and by obtaining exclusive use of these resources by defending them against conspecifics. For these reasons male–female units are dispersed across the habitat, each utilizing a portion with great efficiency.

The larger siamang shows some variation on this pattern, since its greater size renders it relatively less mobile. It is also less specialized for fruit-eating than the smaller gibbons appear to be, and is the only species of hylobatid found sympatrically with others. Hence, different feeding strategies are presumably present to allow their peaceful coexistence. The siamang, therefore, lives in smaller territories, which are more widely spaced by the much louder group calls; they eat more leaves and are more cohesive in their group life. When food is scarce groups can range more widely—into the buffer zones which separate them to some extent from their neighbours.

These two variants of a theme are clearly most efficient ways, in terms of energetics and social harmony, for animals such as the lesser apes to be organized.

9. SUMMARY

1, 2. Data have been collected discontinuously for six years on the ecology and behaviour of siamang, *Symphalangus syndactylus*, in the lowland forest of the Krau Game Reserve, Peninsular Malaysia, with supplementary observations initially in two areas of hill forest. Observations of family groups were continuous and/or at 1-, 5- or 10-min intervals from dawn-to-dusk for periods of five to ten consecutive days. Feeding behaviour was analysed in terms of visits and time in trees yielding fruit, leaves (mature, new, shoots, stems), flowers or buds, and insects (caterpillars or termites).

3. Most food is found in the main canopy, whereas emergent trees provide sleeping and calling sites; the infrequent visits to the understorey are mostly for food. More than half the alert period was spent feeding, mostly in the morning with activity decreasing steadily after noon until the animals settle for the night well before dusk. Young leaves figure prominently in their diet; more than one-third of feeding time is spent eating fruit, mostly figs. Food is selected carefully. There is little difference between groups and populations in techniques, heights and sites of feeding, but more variation in relative intakes of fruit and leaves which presumably reflect differences in vegetation and floristic cycles.

4. Fruit is consumed more in the morning and leaves form the bulk of the afternoon diet. The daily diet is diverse; this appears to reflect the efforts of siamang to obtain a nutritional balance. By contrast, there is much less variation in diet between days in any 5- or 10-day period. Hence, siamang exploit fully available foods in a balanced way.

5. A balanced diet is obtained over longer periods by the ability of siamang to exploit fully the diversity of plant forms and floristic cycles occurring in their habitat. This is important considering their large size and small territories.

6. Ranging strategy combines elements of exploiting that part of their home range where food is temporarily abundant, and of maintaining the exclusiveness of that range and searching for future food. The relative emphasis of these factors varies with time, apparently according to the distribution and abundance of food.

7. Differences in feeding behaviour between adult males and females can be related to their different social roles. Adults have priority of access to more favourable feeding sites, and are less tolerant of their offspring during feeding bouts than during other activities. There is, however, little difference in the diets of siamang of different ages and sex, because of the high degree of cohesion of the family group.

8. For primates adapted to exploiting the small-branch niche in a habitat with a diverse flora, organization into territorial, monogamous family groups is very efficient. Each group becomes familiar with the complexities of the home range, which is maintained for its exclusive use; the long-term knowledge of feeding resources must be very advantageous. The larger siamang is more sedentary and folivorous,

and less territorial, than the smaller gibbons, but territories are more dispersed so that there is a buffer zone between neighbouring groups which either can utilize when necessary.

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Feeding Behaviour of Orang-utans of the Kutai Nature Reserve, East Kalimantan

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1. INTRODUCTION

The orang-utan (*Pongo pygmaeus*) has progressed rapidly from one of the least known of primate species to one of the most studied. Following the early reports of Schaller (1961), Yoshiba (1964) and Okano (1965), each of which was based on little or no direct observation of wild orang-utans, Davenport (1967) published a brief account of 192 hours of daylight observation of orang-utans in Sabah (East Malaysia). D. A. Horr initiated a two-year study of orang-utans in Sabah in 1967 (Horr, 1972), and in 1968 J. R. MacKinnon began observations a few miles south of Horr's location (MacKinnon, 1971, 1973, 1974, in press). I continued Horr's work starting in 1969, and then moved about 650 km south to work in east Kalimantan (Indonesia) from 1970 through 1971 (Rodman, 1973b, in press a). In 1971 B. Galdikas-Brindamour started a long-term study of orang-utans in central Kalimantan that is still in progress (Galdikas-Brindamour, 1975; Galdikas, in press), and H. D. and A. G. Rijksen began three years of research on orang-utans of north Sumatra (Rijksen, 1974; Rijksen and Rijksen-Graatsma, 1974, 1975). At the time of writing, Galdikas-Brindamour's research continues, and others continue observations of orang-utans in north Sumatra and in east Kalimantan. The various observers have accumulated more than 13 000 hours of daylight observation of wild orang-utans. This represents between 4000 and 6000 hours of feeding by the animals, and there should be sufficient material available for analysis of feeding behaviour.

The following description of feeding behaviour of orang-utans is drawn primarily from my own observations, but I will frequently refer to MacKinnon's excellently detailed description of feeding (MacKinnon, 1974). Other authors have not as yet reported on feeding behaviour in any detail, although I will refer to their occasional comments on feeding when possible.

2. METHODS

2.1. Methods of Study of Feeding Behaviour

Compared with other arboreal primates, orang-utans are easier to observe. They are large and of a colour conspicuous to a human observer. In addition they move deliberately with few precipitous actions. The observer normally contacts only one or two independent animals at a time so that selection of a focal subject is not difficult. Despite these possible advantages, there are important constraints placed on observation by the general nature of wild orang-utans. They do not live in aggregations, but rather in dispersed, small units with only a single adult or juvenile to a unit (MacKinnon, 1974; Horr, 1972; Rodman, 1973b; Galdikas, in press). It is therefore difficult to move from one subject to another at will, and each unit affords observation of a limited sample of age and sex classes. These various characteristics of orang-utans practically limit the observer to following one unit (often a single individual) for "as long as possible", for whole days, or for series of days, depending on the degree of habituation of the animal and on the endurance of the observer.

During contact with an orang-utan it is generally possible to record *transition times* of behaviours (i.e. the time at which one behaviour ceases and another begins). Transition times provide absolute durations of activities, and in the case of feeding they provide a record of the time devoted to each food species or food type. This record, coupled with estimates of rates of feeding (fruits per minute, bites per minute, etc.) and weights of items of food, allows conversion of feeding time into quantity of food consumed. Other methods are simpler and more precise in some respects (e.g. instantaneous sampling); J. Altmann (1974) discusses the various methods of recording behaviours and their advantages or disadvantages. But the record of transition times provides a complete record of activities that includes interesting items of information such as frequency and duration of feeding bouts. Both of these sorts of data are lost when a sampling technique is used exclusively.

Recording of transition times is inherently awkward when changes in behaviour occur rapidly or when behaviour is divided into numerous elements. Transition times work well for slow-moving animals and for broad categories of behaviour. It may be argued that using broad categories of behaviour is likely to lead to less information, or to less accurate information; for example, with respect to feeding, does the record of "feeding" refer to picking, handling, chewing or swallowing food? Does it refer to all of them or to some subset? Subdividing the category of feeding into these elements makes the task of recording transition times more difficult, if not impossible, and if the proportion of time spent in the various elements of feeding is of interest, transition times should not be used. On the other hand, before blindly subdividing the category of feeding, it is important to decide whether such smaller elements are of interest, or whether instead it is sufficient to know that "feeding" includes all the elements listed.

Even for broad categories of behaviour, records of transition times are likely to give less precise results than instantaneous sampling if there is some lower limit to the duration of an activity that can or will be recorded (e.g. one minute in this study). A feeding bout may be interspersed with brief bouts of resting or moving, and the record of absolute time spent feeding is likely to be an overestimate of the actual time taken. On the other hand, brief feeding episodes may be omitted from the record of travelling or resting, and the over-all picture may be reasonably accurate after all.

In my own work the record of transition times has been adequate. My assistants and I recorded transition times of major categories of behaviour that may be defined as follows:

Feeding. Picking, handling, ingesting, chewing and swallowing food.

Travelling. Moving from one feeding or resting site to another; movement within a food tree would normally be included in time spent feeding.

Resting. Not feeding, travelling or constructing a nest; a few transitory periods of play or other rare behaviours are included in the record of resting.

Nest-building. Construction of a sleeping platform from bending of branches to last apparent movement after entering the nest.

Display. Any or all of the following: Vocalizations ("smack", "grunt", "belch"), tree shaking, branch-breaking, vine rattling; in all but two instances, such display was apparently directed at the observer.

Each observer described the behaviour in diary fashion between transitions in varying detail. My wife and I described the behaviours in considerably more detail than our local assistants.

Thus observations of feeding behaviour consist of the times of initiation of bouts of feeding, their durations in whole minutes, and a set of descriptions of feeding within bouts including identification of food type and food source (if known), rates of feeding, height above ground, postures utilized, and means of support while feeding. Unfortunately only records of food type and food source were collected systematically.

Food availability was measured in two ways. In 1971 I sampled all trees above 4 cm diameter breast height (d.b.h.) in 0·012 km^2 of forest, divided into 12 samples of 0·001 km^2 apiece spaced at 0·2 km intervals along a 2·4-km transect that ran inland from the river on the north of the study area. Trees were originally identified using local names, as were food sources (this was convenient since I had access to instruction from several local experts). These names could in many cases be converted to proper Latin binomia using a tree list published by the Directorate General of Forestry in Indonesia (1971). I also received assistance from Dr Soegeng Reksodihardjo, then of the Herbarium Bogoriense, when he spent two weeks with me in the field making identifications of food trees of orang-utans.

In 1975 I was interested in the distribution of fruit in my study area. In order to sample this distribution rapidly I noted the presence or absence of fruits on the ground in each 50 m-segment along transects and paths through my study area. Obviously such a sample should be repeated regularly through one or more years in order to determine the normal distribution of fruit; obviously as well there is some relationship between fruit that falls to the ground and fruit available to arboreal frugivores. Despite these drawbacks, the method has provided interesting data regarding the relationship between distribution of primates and distribution of food (Rodman, in press b).

2.2. Study Area

The study area consists of 3 km^2 of rain forest in the Kutai Nature Reserve (0°24′ N, 117°16′ E). I have described the area in more detail elsewhere (Rodman, 1973, and in press b). Briefly, it is a section of lowland dipterocarp forest characterized by a large proportion of ironwood trees (Lauraceae: *Eusideroxylon zwageri*). It lies on the south side of the Sengata river approximately 25 km from the east coast of Kalimantan, and it is part of a large expanse of similar forest extending to the south and west. In 1970–71 this forest was nearly undisturbed for 40 to 60 km in all inland directions; by 1975 several logging companies and one oil company had cut a number of roads through the nature reserve and the timber companies had taken a substantial quantity of timber along the roads. The southern third of my original study area was logged in 1973, although the majority of the area was not disturbed.

2.3. Samples of Feeding Behaviour

As pointed out above, the nature of orang-utans places constraints on the method of observation. The six observers (four local assistants, my wife and I) logged a total of 1644 hours of observation of orang-utans distributed in months and by times of day as shown in Table I; Table I also shows the distribution of lengths of observation periods. Clearly, disproportionately many hours of observation fall into the months of March and April, 1971. Although this bias may be significant for

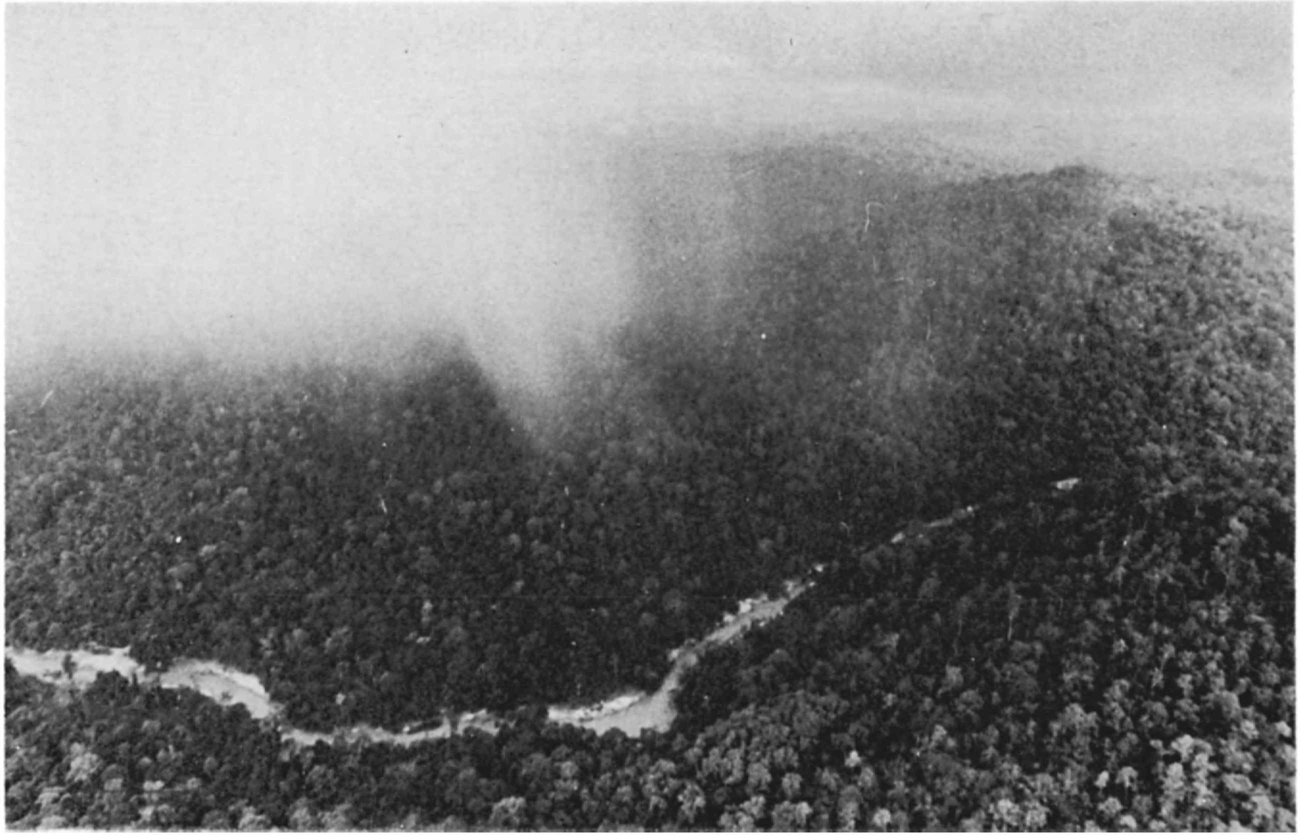

Fig. 1. Aerial view of the study area looking due south from approximately 1000 m altitude. The Sengata river runs from west to east in the foreground. The distance from east to west along the river is approximately 1·7 km.

FIG. 2. Adult male orang-utan resting about 2 m above the ground in riverine forest.

FIG. 3. Adult female and young juvenile male orang-utan.

other reasons, it is not the result of variation in the presence of orang-utans; it is instead the result of a change in priorities of research. I was collecting observations of the ecology of several primate species (Rodman, in press b) in addition to observing orang-utans, and during March and April, 1971, all efforts were put into following orang-utans. Other variations in observation time represent changes in priorities and not variation in abundance of orang-utans. The same eleven orang-utans were present throughout the study, with occasional visitors (Rodman, 1973b).

The preponderance of observation bouts of more than ten hours (Table IC) reflects the fact that it was easier to follow orang-utans for "whole" days than to switch from one animal to another. Only 42 days of observation qualify as complete days, however, since on other long days the observers missed either the first or the last movements of the day, or some interval in between.

3. FEEDING BEHAVIOUR

3.1. Feeding Techniques

3.1.1. *General postures*

Orang-utans feed mainly in or near the periphery of tree crowns, as do many, if not most, primates. Considering their large size (40 to 100 kg as adults), their postural solution to this unstable region is of great interest and awaits detailed study in the wild. A review of my film and field notes indicates that there are two principal feeding postures utilized in the tree crowns:

Upright orientation. The animal supports itself with one arm overhead and with both feet. The hand and feet grasp single branches or clusters of branches, and the second hand is free to pick food and carry it to the mouth.

Horizontal orientation. The animal grasps small branches or clusters of branches with the hand and foot of one side and suspends the body in more-or-less horizontal orientation with the hand and foot of the opposite side free for feeding. The supporting arm and leg are each extended at approximate right angles to the axis of the body.

Orang-utans also feed in "inverted suspended posture" (Mendel, 1975), supporting themselves with the two feet and hanging below the feet on fully extended legs. My impression is that this posture demands a more secure support than either of the first two, and that the support

TABLE I

Distribution of observation time

A. % of observation time by month (total time = 1644 hr)

1970 Sept.	Oct.	Nov.	Dec.	1971 Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.
0·3	2·8	3·2	2·6	7·1	2·5	26·1	29·4	4·6	12·4	9·1

B. % of observation time per hour of the day (total time = 1644 hr)

5.30–6.59	7.00–7.59	8.00–8.59	9.00–9.59	10.00–10.59	11.00–11.59	12.00–12.59	13.00–13.59	14.00–14.59	15.00–15.59	16.00–16.59	17.00–18.30
6·7	8·2	8·4	8·5	8·7	8·5	7·9	7·8	8·2	8·5	8·7	9·9

C. % of observation bouts by duration of contact ($n = 193$ bouts, time in min)

000–059	060–119	120–179	180–239	240–299	300–359	360–419	420–479	480–539	540–599	600–659	660–719	720–780
1·0	3·1	8·3	5·7	7·3	5·2	4·6	3·6	5·2	2·6	7·2	14·5	31·6

must be a nearly horizontal limb or branch. This posture is relatively rare.

I have not observed an orang-utan to feed while supported by a single arm as I have frequently observed Bornean gibbons to do. My impression is that the normal postures not only give multiple points of support, but also leave the animal in a position that would result in some angular fall if one support were to give way, rather than leading to an immediate vertical drop placing the full weight of the animal on the remaining support. It is perhaps for this reason that the inverted suspended posture is rare since the points of support given by the two feet are rather close together. It is safe to say that except in the case of feeding on some types of bark (described below), suspension is nearly invariably part of the feeding posture.

3.1.2. *Feeding on fruit*

Perhaps the most striking characteristic of frugivory by orang-utans in my study area is that they normally swallow the seeds of the fruit rather than discard them. As a result it is common to find faecal depositions of such seeds far from the parental trees. Two extremely important fruiting species in my study area are *Dracontomelon mangiferum* and *Koordersiodendron pinnatum*, both of the Anacardiaceae. Each is characterized by a fruit of 2–3 cm in diameter with a large stone. Orang-utans would feed for hours at a time on these two species, discarding the skins and swallowing the rest. During the summer of 1975 (July–August) I found numerous depositions of *K. pinnatum* in sunny spots that were sprouting shortly after passing through orang-utans; my impression was that these seeds sprouted more rapidly than those dropped from the mouths of gibbons or squirrels (*Ratufa affinis*) who fed in the same trees, but this relationship must be investigated more carefully. It is important to note that MacKinnon (1974) observed orang-utans in Sabah to discard the seeds of *D. mangiferum* after scraping the flesh from the stone with the molars. Although I occasionally observed an orang-utan to drop a seed of this species directly from the mouth, and although an animal would often depart from a tree of this species while grinding a last stone in the molars, these were exceptions rather than the rule in my study area.

The strength of orang-utans doubtless assists them in reaching fruit from the periphery of trees while not actually moving into the peripheral branches. They may bend or even break branches to bring the food closer. Branch-breaking while feeding is a common behaviour, but not an easy one to interpret since at least one of the habituated orang-utans in my study area broke off branches of fruit trees *after* stripping them of fruit rather than before.

3.1.3. *Feeding on leaves and leaf shoots*

Feeding on leaves requires no unusual techniques by orang-utans. The leaves chosen appear to be young leaves that occur in the periphery of tree crowns or on vines in the canopy. Thus the postural problems of reaching leaves are similar to those of reaching fruit. In the case of small leaves such as those of some fig trees, orang-utans remove the leaves from twigs directly with their incisors. After collecting several leaves they chew and swallow. In the case of larger leaves the animals pick one or two leaves with a hand before biting off part of the leaves with the teeth.

There may have been some selectivity of parts of leaves at all times, but such selectivity was most apparent in feeding on the bases of the leaves of two species of palms. Orang-utans commonly fed on the bases of the leaves of *Pandanus epiphyticus* which grows in the crotches of large trees. The leaves are deep green, up to 1·5 m long, approximately 6 cm wide with thorns arranged about 2 cm apart along each edge. Orang-utans grasp a leaf and pull it from the plant, then bite off the soft white base of the leaf and discard the remainder. A second palm grows only in the deep forest of the study area at least 1 km from the main river, though it is unclear what factors limit its distribution. Its base may be on the ground, but it characteristically develops a trunk up to 5 m in height from the top of which spring the leaves. The young leaves grow out of the base (top of the trunk) in clusters that will eventually radiate from the end of a thick stem that grows up behind them. Local people are fond of the heart of the palm, and they will eat it raw or cooked after cutting the plant from around it. Orang-utans cannot reach the heart of the plant, but when the leaf clusters are young, orang-utans will pull a whole cluster from the plant and chew off the bases of the leaves. These taste much the same as the heart. At times discarded leaves lie at the base of nearly every accessible palm in the study area, although I have only observed an orang-utan feeding on one once. Accessible palms are those that grow close to the ground or that grow beneath a stronger tree from which an orang-utan may reach down to the top of the trunk.

The latter palm is interesting because it is abundant in a part of the forest not favoured by orang-utans, where fruit is relatively scarce. This palm and *Pandanus epiphyticus* are not available as food to other primates or other animals. As a result the leaves of these palms give an indication of the presence of orang-utans when found lying on the ground.

3.1.4. *Feeding on bark*

Orang-utans of this study area feed on a variety of species of bark in several ways. Bark of a few strangling figs is gnawed from the distal twigs; this was a principal food when fruit was scarce. A second technique involves stripping the bark from large limbs or the trunk (commonly of dipterocarps, but also of others such as *Kompassia excelsa*). The bark may be stripped directly with the teeth; it may be split open with the teeth and then stripped with the hands; or it may be stripped entirely with the hands. Most barks taken this way are not eaten entirely; instead the cambium layer is stripped out and chewed for several minutes after which the fibres are discarded. Some bark is consumed whole (e.g. *Artocarpus* sp.).

3.1.5. *Feeding on flowers and buds*

Techniques of obtaining these plant parts are essentially the same as those used to obtain fruits.

3.1.6. *Feeding on insects*

Two techniques are used to feed on termites or ants; neither is as delicate as termiting by chimpanzees. The most common method (all but three observations) is to take insects directly from the surface of a limb with the lips. The other method probably depends upon finding the proper kind of nest; I have only seen it three times. The orang-utan breaks off a section of a termite nest, bites into it, and then picks insects from the nest with the lips and tongue.

3.2. Feeding Heights and Feeding Sites

The postures described above appear to serve well for a large animal that feeds near the lateral periphery of tree crowns. Orang-utans of this study spent the majority of their time in the middle canopy where most of the vegetation occurs, from 20 to 30 m high (Table II). The adult males each fed and travelled on the ground for a fair proportion of travel time. Although two habituated females did descend to the ground on one occasion apiece, there was a sex difference in the use of the ground level and in use of other strata above the ground (Section 7.3 below). My observations of any animals on the ground may have been biased, due to less-than-perfect habituation of the animals, and there is some indication that this is true in the comparison of total time in the lowest stratum with proportion of first contacts on the ground. The latter proportion is higher (Table II), and it may be that the animals were avoiding the observer subsequent to first contact.

TABLE II

Utilization of vertical strata of the forest while feeding

	Height (m)								
	0–4	5–9	10–14	15–19	20–24	25–29	30–34	35±	*n*
Males:									
% records	12·5	11·5	15·4	16·3	17·3	19·2	3·8	3·8	104 records
% time	3·6	5·0	11·7	20·3	19·1	32·9	2·8	4·6	3743 minutes
Females:									
% records	1·4	3·2	5·0	25·9	37·2	23·0	3·2	1·1	282 records
% time	0·6	1·5	2·4	27·3	34·5	26·3	4·2	3·2	12947 minutes
All animals									
% records	4·4	5·4	7·8	23·3	31·9	21·2	3·4	1·8	386 records
% time	1·3	2·2	4·5	25·7	31·0	27·8	3·9	3·5	16690 minutes
% First contacts	7·3	4·9	2·4	24·4	29·3	14·6	14·6		41 contacts

3.3. Feeding and Diurnal Pattern of Activity

Habituated animals spent 45·9% of their hours from 5.30 to 18.30h feeding. There were two feeding peaks during the day: one in the quarter-hour from 7.00 to 7.14h during which 65·0% of observation time was spent feeding; and one from 16.15 to 16.29h, when 66·9% of observation time was spent feeding (Table III). Feeding occupied little time in the early morning and in the late evening when the animals were normally in their night nests, and there was a midday minimum from 12.30 to 12.45h when they spent only 28·5% of observation time feeding.

The remainder of the day was spent in resting (39·2%), travelling between trees (11·1%), building nests (1·0%) and displaying at the observer (2·7%). Resting and displaying varied approximately inversely to feeding, and nest building occurred nearly exclusively after 17.30h. Travelling had a more interesting pattern related to the diurnal variation in food choice described below (Section 4.2). The proportion of travelling remained nearly constant from 5.45 to 14.00h (with a slight decrease from 12.15 to 12.30h) but increased rapidly just after 14.00 to reach a peak from 16.45 to 17.00h.

As discussed above, an undue proportion of the data on these habituated animals was gathered in only two months, and these were months when a single species of fruit dominated the diet of all orang-utans in the study area. I have therefore reviewed the features of the diurnal activity pattern of orang-utans during March and April, 1971,

TABLE III

Diurnal pattern of activity (as % time spent)

	Hour of day											
	6.00–6.59	7.00–7.59	8.00–8.59	9.00–9.59	10.00–10.59	11.00–11.59	12.00–12.59	13.00–13.59	14.00–14.59	15.00–15.59	16.00–16.59	17.00–18.00
Feeding	56·3	60·1	45·0	42·4	39·7	33·8	30·8	42·1	48·2	51·9	63·2	51·1
Resting	34·5	30·2	44·8	47·7	50·3	53·5	59·8	47·3	34·6	26·1	17·8	26·4
Travelling	8·5	9·2	8·8	8·2	8·5	10·4	6·5	8·0	15·5	20·6	16·2	14·1
"Nesting"	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	1·5	6·8
Displaying	0·7	0·5	1·4	1·7	1·5	2·3	2·9	2·6	1·7	1·4	1·3	1·6
Observation time (min)	5198	6549	6695	6753	6808	6503	5940	6119	6481	6498	6847	6353

and during all other months; with minor exceptions the data give the same picture at all times.

3.4. Amount of Time on Different Foods

Orang-utans of this study spent an average of 53·8% of their time feeding on fruit, 29·0% on leaves, 14·2% on bark, 2·2% on flowers and 0·8% on insects. These figures are the averages for 12 months (Table IV). It is important to notice in Table IV that the proportions of food types taken during August, September and October, 1970, are the proportions of food types taken at first contact with feeding orang-utans instead of proportions of time spent feeding. Theoretically the two figures should be the same if first contacts are an unbiased sample of behaviour of the animals, but it is possible that some bias enters if, for example, orang-utans are noisier when feeding on bark than when feeding on leaves, so that an observer is more likely to spot an orang-utan feeding on bark. Although such bias may have entered later in the study when I was attempting to find and follow orang-utans, during the months in question orang-utans were no more interesting to me than any other primate species. I therefore am confident that, barring sampling error associated with small sample sizes, these proportions may be considered equivalent to proportions of time spent feeding on different food types in subsequent months of the study.

3.5. Selectivity

3.5.1. *Selectivity of food parts*

Orang-utans selected parts of some leaves—usually the leaf base or the petiole—and took only bark from limited areas of some trees. For example, only the bark of distal twigs (and on one occasion from the stilt roots) was taken from strangling figs. The method of taking only the base of a palm leaf has been described above (Section 3.1).

3.5.2. *Selectivity of food items within a single source*

Choices made by an animal within a tree are difficult to measure, and I have only indirect evidence for selectivity of foods within a fruit tree. In the case of leaves observers frequently noted that the animals were taking pale green leaves, and this suggests that they were selecting new leaves; this was particularly true of leaves from vines. Selectivity of fruit may be inferred from the fact that an orang-utan was never observed to exhaust the fruit in a single tree during an extended bout of feeding.

Some evidence of selectivity was provided by two orphan orang-

TABLE IV

Percentage feeding time on different food types by month

	Aug.*†	Sept.*	Oct.*	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.
Fruit	85·3	33·3	73·7	89·0	12·8	40·0	81·8	60·7	66·2	38·0	38·7	25·7
Leaves	14·7	33·3	26·7	5·3	20·6	38·1	18·2	19·5	25·5	44·0	46·4	55·6
Bark		22·2		5·7	66·6	21·9		17·3	2·3	4·8	13·1	16·0
Flowers		11·1							4·8	10·7		0·2
Insects								2·5	0·6	2·5	1·8	2·5
Total time (min.)	(34)	(9)	(19)	813	384	2964	888	10 564	11 833	928	7330	4318

* Proportions of time spent feeding are estimated by the frequency of feeding on food types when orang-utans were feeding at first contact; the number of contacts is given in parentheses in the place of total minutes of observation.

† Observations made in August 1975, are included in the data.

utans who lived around the camp. The older one, who had not had much human contact, would reject ripe bananas in favour of bananas we found too green to eat. Both orphans sniffed and otherwise inspected any new food item and normally rejected it. I suspect that orang-utans are similarly selective of fruit in a fruit tree; it is likely that females are more selective than males (Section 7.3).

3.5.3. *Selectivity of food sources*

My judgements of selectivity of food sources are based on the relationship between food sources of the orang-utans and the frequency of appearance of those sources in the 0·012 km² sample of the forest described above. I will use the varieties of plants recognized locally to make judgements about the frequency of various plants in the sample, and I will refer to these as "varieties". Most of these have been identified to the generic or species level, and in general a local plant variety refers to a true taxon in the Linnaean system. The major exceptions in this respect are members of the commercially useful dipterocarps. The local people recognize several varieties of plants within subspecific groups of these trees.

Orang-utans fed on 44 varieties of trees of which 82% occurred in the sample and on 12 varieties of vines of which 42% occurred in the sample. The mean number of trees per variety in the entire sample was 4·1 and the mean number of vines in the entire sample was 4·9. The mean number of trees per variety fed upon by orang-utans was 6·3 and of vines per variety fed upon was 4·9. It is interesting that "edible" varieties are more common than the average variety in each case. When the parts of plants taken are considered the picture is different. Fruit sources are rarer in the sample than the average variety ($\bar{x} = 3·1$), while sources of leaves and bark are more common than the average variety ($\bar{x} = 7·0$). The relative abundance of sources is thus not correlated with the apparent preference for food type of the animals. When only fruit sources heavily used by orang-utans are considered, the picture is clearer. *Koordersiodendron pinnatum*, *Dracontomelon mangiferum* and *Dillenia borneensis*, each a principal food source at some time of year, average 2·7 trees apiece; a fourth principal source of fruit, *Jarandersonia* sp., does not appear in the sample. It seems therefore that preferred fruit sources of the orang-utan are rare in the study area.

3.6. Dietetic Diversity

Orang-utans were observed to take food from trees and vines of 56 local varieties; these correspond to at least 50 different taxa, most of which are distinct species. The animals fed on an additional 29 unidentified trees and vines so that it is possible they fed on as many as 80 different species. On the other hand, there is a proliferation of local names for the genus *Shorea* from which the animals took bark and leaves, and the number of true species of this genus utilized by orang-utans is not known. The animals took fruit from only 22 varieties of trees and vines, and these correspond to no more than 30 species. Of these, only the fruits of *K. pinnatum*, *D. mangiferum*, *Dillenia borneensis* and *Jarandersonia* sp. were utilized extensively; together feeding on these varieties accounted for more than 50% of time spent feeding on fruit. The bark and leaves of a few strangling figs and of several varieties of the genus *Shorea* and the genus *Uncaria* constituted "permanent" food sources to which the animals turned between times of availability of the principal fruit sources. This is similar to the use of permanent food sources described by Galdikas (in press). It is interesting that flowers were taken from only a single species of tree during the year (*D. borneensis*).

My observations of dietetic diversity contrast markedly with those of MacKinnon (1974). In Sabah, orang-utans took some part of 105 species of plants, and took fruit from all but eight of these species. Such a remarkable difference in feeding ecology should provide explanation —or clues to an explanation—of other interesting differences between the orang-utans in Sabah and those in my study area. The life patterns of orang-utans in this study area appeared to be related to reliance on a few fruiting species each represented by several individual trees within a small area, and it would not be surprising if ranging and many other patterns related to feeding differed in areas where such reliance was not practical.

4. TEMPORAL PATTERNING OF FOOD CHOICE

In order to describe diurnal variation in food choice I have considered only days of observation beginning earlier than 6.30 and ending after 17.30h with no gaps of observation longer than one half-hour. I have counted the frequency of days on which a particular food type (fruit, leaves, bark, flowers or insects) was taken at least once during an hour of the day. The data are presented in Table V. Thus, for example, orang-utans took some fruit between 6.00 and 6.59h on 61·1% of observation days.

There is clearly variation in food choice through the day as shown by the ratio of periods in which leaves, bark, flowers or insects were eaten to periods in which fruit was eaten. The ratio is low in the morning

TABLE V

*Diurnal variation in food choice**

	Hour of day											
Food	6.00–6.59	7.00–7.59	8.00–8.59	9.00–9.59	10.00–10.59	11.00–11.59	12.00–12.59	13.00–13.59	14.00–14.59	15.00–15.59	16.00–16.59	17.00–18.00
1. Fruit	61·1	52·8	45·8	31·9	26·4	27·8	33·3	38·9	40·3	30·3	52·8	48·6
2. Leaves	19·4	22·2	27·8	25·0	26·4	27·8	19·4	31·9	29·2	38·9	26·4	22·2
3. Bark	2·8	1·4	8·3	4·2	4·2	11·1	13·9	9·7	12·5	19·4	12·5	8·3
4. Flowers	0·0	1·4	2·8	1·4	1·4	1·4	0·0	0·0	2·8	5·6	2·8	1·4
5. Insects	1·4	2·8	2·8	2·8	2·8	1·4	0·0	2·8	4·2	0·0	1·4	2·8
6. (2 + 3 + 4 + 5)	23·6	25·0	41·7	33·3	34·7	41·7	33·3	44·4	48·6	63·9	43·1	34·7
7. 6/1	0·4	0·5	0·9	1·0	1·3	1·5	1·0	1·1	1·2	1·6	0·8	0·7
Travel	8·5	9·2	8·8	8·2	8·5	10·4	6·5	8·0	15·5	20·6	16·2	14·1

* The figures given are percentages of hours on days of observation starting before 6.30 and ending after 17.30h, with no more than half-hour gaps, when subjects took the food type indicated. The total number of observation days is 71; i.e. $n = 71$ in each case.

(high fruit, low other) and at the end of the day; it is higher from 9.00 to 15.59h when there is a greater tendency for the animals to take other foods than fruit. The ratio peaks from 11.00 to 11.59h and from 15.00 to 15.59h, and these two peaks correspond to similar peaks in proportion of time spent travelling. This correspondence provides an explanation of the diurnal variation in choice of food types.

The daily activity pattern of orang-utans consists of an early morning feeding bout in one tree, rest, movement to another principal fruit source, and a late afternoon feeding bout in that fruit source. It appears that while travelling from one principal fruit source to another the orang-utans forage on various "miscellaneous" food items encountered along the way. D. A. Horr (pers. comm.) has called these foraging periods "shopping expeditions", and they are most obvious in the afternoon; note that travel time is highest during the last four hours of the day and that the maximum of travel time (15.00 to 15.59h) corresponds to the highest ratio of feeding on other foods to feeding on fruit. It seems that the major foraging expedition terminates in another principal fruit source in the evening more often than not, and that the diurnal cycle begins again in this tree early the next day. Such a pattern carries the animals from one fruit source to another on a regular basis.

There appeared to be no shorter-term patterns of food choice, although I occasionally suspected that the animals moved from a fruit tree to a leaf source in somewhat rhythmic pattern. In October, 1970, for example, a female and adolescent fed heavily on the fruit of *Dillenia borneensis*. One tree of this species stood adjacent to a mature *Ficus albipila* from which orang-utans commonly took leaves and bark throughout the year. During two mornings of observation the orang-utans fed in the fruit tree, but moved regularly to the other tree for a bout of leaves, then back to the fruit tree for more fruit, etc. I suspected that this might be a normal pattern, the leaves serving as "roughage" for the relatively soft fruit, but subsequent observations rarely revealed such a pattern. Perhaps it occurs when a fruit tree is located conveniently close to a leaf source.

5. SEASONAL VARIATION

No other observer of orang-utans has published phenological data or productivity data from a study area, and unfortunately I have not gathered such observations. Consequently it is impossible to discuss variation in feeding behaviour in relation to total food availability. Variation in availability of fruit may be inferred from, although not demonstrated by, variation in dietary proportions of orang-utans.

Table IV shows proportions of foods taken in each month by orang-utans. There is considerable variation in the proportion of fruit taken, and there are some correlated variations in feeding behaviour. Considering only the three habituated females (two mature adults, one juvenile) and comparing March and April, 1971, with May, June and July, 1971 (when the proportions of fruit were higher and lower respectively), two of the females showed *increases* in feeding time associated with lower proportions of fruit in the diet. The third female showed no difference in activity profile, and none of the females showed changes in travel time or day range. The difference in feeding time by the two females was accommodated by a decrease in resting.

MacKinnon (1974) observed more regular variation in fruit eating through the year, and his data indicate a true fruit season (inferred from the proportion of fruit in the diet) from July through November with a non-fruit season from December through June (my interpretation of Fig. 19a in MacKinnon's 1974 paper). Activity profiles of orang-utans in MacKinnon's study differed markedly in the two seasons, and the change is in the opposite direction from that suggested by my observations: feeding time *decreased* and travel increased in the non-fruit season relative to the fruit season. Galdikas (in press) comments that day ranges were shorter in her area when the animals fed on seasonal foods (i.e. fruit or flowers) than when they fed on permanent food sources (i.e. leaves and bark). This pattern resembles MacKinnon's rather than mine.

6. SPATIAL VARIATION

The distributions of all five common primate species in the study area are related to their diets and to the availability of fruit relative to other foods (Rodman, in press b). There are two major habitat zones in the study area, one of which is flooded intermittently and one of which is not. It is predicted on theoretical grounds that the flooded zone, which is a temporally heterogeneous habitat, will be populated by r-selected plant species that produce fruit at a relatively high rate. The rest of the study area ("deep forest") is a stable forest in which K-selected plants should be favoured, and such plants theoretically should put more resources into vegetative structures (leaves, for example) relative to reproductive structures (fruit). In 1975 I tested the prediction as described above (Section 2.1). There was at least one fruit on the ground in 48·9% of 50-m segments in the flooded zone ($n = 47$), and at least one fruit on the ground in only 33·5% of segments in the deep forest zone ($n = 158$). There was a clear difference in distribution of fruit in the predicted direction.

The relative density of orang-utans in the two habitat zones is best indicated by an index of the frequency of contacts per area surveyed; I have used 0·04 km^2 cells as the unit of area. The mean index of frequency of contacts with orang-utans in cells of the flooded zone was 3·07 (contacts per walk through a cell × 100) and the mean index of frequency of contacts in the deep forest was 0·24. Not surprisingly, these highly frugivorous animals use areas of high fruit abundance more intensely than other areas.

There is no difference in proportions of food types taken by orang-utans in the two zones of the study area. Instead the intensity of utilization differs in a manner suggesting that areas of use are chosen according to the abundance of preferred food (fruit) available. The distribution of orang-utans and their patterns of life in any small area of their geographical range should therefore be variable, depending on the ambient distribution and abundance of fruit trees, and on the temporal distribution of fruit. Other observers have found somewhat different patterns of life in other areas of Borneo; it seems likely that the differences will ultimately be attributable to variation in fruit distribution among the areas.

7. AGE/SEX VARIATION

7.1. Proportion of Time Spent Feeding

My observations were of a small number of habituated orang-utans and a slightly larger number of others. I observed only one habituated adult male supplemented with observations of two additional unhabituated adult males. My sample size of habituated adolescent animals is also one, with no supplemental observations. For some comparisons I have added observations of the adolescent female to those of the two mature females. I have no presumptions about the strength of conclusions based on such small samples, but the differences among the animals appear to be related to age/sex variation in ways that are interesting and may or may not be supported by more extensive observations in the future.

I have limited analysis to observations taken during March and April, 1971, because most observations of the habituated adult male were made in those months. This limitation has an advantage in that the resource base for the male and females was similar: all four were using

TABLE VI

Sex difference in activity patterns of habituated subjects, March and April, 1971

	Activity					
	Feed	Rest	Travel	F/T	Mean no. feeding bouts per day*	Mean duration of feeding bouts (min)
Females:						
Jfa	42·1	42·0	12·6	3·3	—	—
Afd	31·4	55·7	10·6	3·0	—	—
Afa	47·5	36·3	13·1	3·6	—	—
ALL	40·3	44·7	12·1	3·3	7·2 ($n = 14$)	35·7 ($n = 287$)
Male (BC)	57·0	32·6	9·3	6·1	6·9 ($n = 7$)	50·1 ($n = 161$)

* Number of feeding bouts on whole days of observation, from first to last movement.

the same region of the study area and feeding on a single principal fruit source, *D. mangiferum*.

Comparison of activity profiles is presented elsewhere (Rodman, in press a). Briefly, the adult male spent a larger proportion of time feeding than any of the females (Table VI). The mean number of feeding bouts per day was the same for the male as for the females, but this implies that the mean length of feeding bouts was greater for the male than for the females, as it was.

The difference in feeding time is to be expected not because the animals are male and female, but because the male is considerably larger than the female. Given similar rates of feeding on similar foods, the male must spend more time feeding to support his greater metabolic costs.

Although feeding time alone appears to be related to size differences —and therefore to sex differences—among the adults, the relationship of feeding time to travel time shows even greater sex difference. The male spent less time travelling each day than any of the females so that the ratio of feeding time to travel time is considerably greater for the male than for the females.

MacKinnon (1974) has analysed activity patterns of orang-utans in Sabah and in Sumatra, and his observations differ from my own in the total ratio of time spent feeding to time spent travelling; the ratio is smaller in his sample. The sex difference occurs in the same direction in his sample, but it is not nearly as marked as in my own observations. MacKinnon includes subadult males in the comparison without separating them from adult males, and since subadult males are smaller than mature adult males, it is not surprising that the feeding to travelling ratio differs less between males and females in his analysis.

7.2. Feeding Sites

The pattern of utilization of vertical strata for feeding is different for males and females, as shown in Table II. In general, feeding is distributed more evenly through strata for males than for females, but the striking sex difference is in utilization of the lowest strata (0–14 m). Males used this region 4·5 times as much as females (based on total time). This difference appears to be entirely consistent with observations made by Galdikas (in press) who reports a similar differentiation of male and female feeding despite the fact that both males and females used the lower strata, including the ground, to some extent.

7.3. Foods Eaten

Considering only the months of March and April, 1971, there is a sex difference in proportions of food types taken by the habituated adult male and by the others (Table VII). Although all four habituated orang-utans (and several others) fed predominantly on the fruit of a single species and in the same trees of that species during these months, the adult male took considerably less fruit and considerably more bark than the three females. The difference in feeding on bark is interesting since bark seems to be a food with low energetic yield for a high cost of procurement. Bark of most species eaten appeared to be difficult to obtain relative to fruit, and it is perhaps not surprising that the larger, presumably stronger, male utilized it more than the females. On the other hand, fruit appeared to be abundant, and it is perplexing that the male did not feed more heavily on it. He appeared to be taking less of the most "preferred" foods and more of the least preferred foods relative to the females.

TABLE VII

*Proportions of food types taken by habituated subjects, March and April, 1971**

	Fruit	Leaves	Bark	Flowers	Insects	Time (min)
Females	67·1	23·2	4·9	2·8	1·9	13 660
Male	58·6	22·0	16·5	2·1	0·8	8665

* Percentages of total feeding time spent on each food type.

There is a high degree of ecological divergence between adult male and female suggested by these observations. The significance of such divergence to the social system is discussed below (Section 9).

8. INTERPOPULATIONAL VARIATION

8.1. Stability and Size of Home Ranges

Orang-utans of my study lived in ranges averaging 0·42 km^2 ($n = 6$), and their ranges were constant during the 15-month study. The ranges of two adult males were similar in size to those of four adult females, although two other males passed through the study area for brief periods of time on one occasion each; the latter observations suggested to me that there were different classes of males in the adult population: a resident class and a nomadic class (Rodman, 1973b). Galdikas (in press) reports a very similar pattern except that ranges of adults were much larger; ranges of five females were 5–6 km^2 in area, and those of two resident adult males were similar in size to the females' ranges. MacKinnon (1971) originally reported that orang-utans in his area were highly nomadic, but later (1974) he modified this assessment to suggest that a few animals may have been resident in very large home ranges; these ranges were large relative to his 5-km^2 principal study area.

8.2. Day Ranges

The mean day range of animals in my study was 305 m ($n = 76$). Galdikas (in press) reports an average day range of no more than 800 m. The relationship between home range area and length of day range is roughly similar in the two studies if linear measurements are expected to vary as the square root of a related area. MacKinnon (1974) observed a day range of approximately 500 m.

8.3. General Comparisons: Climate and Topography

Despite an overall similarity in life patterns of orang-utans in the various study areas, there are considerable differences in details of ranging patterns. These probably are accounted for in large part by differences in the resource bases in each area, and differences in resources may be related to local climate and topography. For example, there is little seasonal variation in weather in the Kutai area (Rodman, 1973b), while there are distinct monsoonal seasons in Sabah and probably in Galdikas' area since both lie on or near the coast a few degrees from the equator. Greater seasonality of weather should lead to temporal clumping of fruit, and it seems logical that if fruit is clumped in time an animal will need a larger range to maintain a minimal resource base than if fruit is spread evenly through time. Topography in Galdikas' area is uniform (Galdikas, in press) whereas there is marked relief in both MacKinnon's area and in my area. Such relief may easily introduce spatial patchiness in habitat due to variation in soils and exposures. The following assessment should be examined critically, but at present it seems reasonable to suggest that the "extreme" pattern of animals in MacKinnon's area is due to a combination of high seasonality and variable terrain; that the "intermediate" pattern in Galdikas' area is due to uniform substrate in a seasonal area; and that "extreme" conditions in my area are due to a non-seasonal climate in a study area which covers a "good" patch in a spatially patchy terrain.

9. FEEDING BEHAVIOUR AND SOCIAL BEHAVIOUR

9.1. General Aspects of Social Behaviour

Orang-utans are invariably highly solitary compared with other diurnal primates. Their social system fits the scheme presented by Jolly (1972b) in which degree of aggregation is related to patterns of search, distribution of food and mode of predator defence. The principal food source is fruit which is distributed in small, discrete patches (trees) relative to the size of an individual orang-utan. In the absence of predation such a resource base favours solitary animals rather than aggregates. The resource base thus explains why females do not remain in aggregates (i.e. why mother–offspring bonds do not persist). Given this distribution of females, males are faced with a problem of finding mates while competing with other males for access to them. The male pattern of behaviour may be explained as a solution to the problem through competing for space in which females reside rather than attempting to associate with females directly, except for mating (Rodman, 1973b). Strong competition among males for females tends to promote size dimorphism, the males being larger (Trivers, 1972), and the size difference may lead to ecological differentiation as described below.

9.2. Activity Budgets

The relationship between individual activity profiles and solitary behaviour is discussed in detail elsewhere (Rodman, in press a). Briefly, the large adult male is limited to his activity pattern by energetic constraints, and the female derives no benefit from association with the male. On the other hand the female may benefit from increased selectivity of foods by travelling more and feeding less at each site than the male (the benefit is presumed to be increased vigour of offspring as a result of better foetal nourishment or improved quality of milk produced). The differences in activity patterns serve to reinforce spatial segregation of adult males and females.

9.3. Ecological Segregation

Males differ from females in utilization of vertical strata of the forest (Section 3.2 above). Galdikas (in press) observed similar spatial segregation, and she states, "Ground foraging seemed to be a normal part of each habituated male's daily routine but was much rarer even among the most habituated females". My observations suggest that males and females differ in degree of selectivity of food sites and of food at food sources as well as in proportions of various food types chosen (Section 7.3). If fruit is considered to be the preferred food, it appears that the male was taking less of preferred foods. Assuming such a pattern is characteristic of male orang-utans, it is interesting to speculate on selective pressures that might lead the male to such apparent sacrifice. If it is correct that selection favours females who maximize the quality of their diets, and if resident males are most likely to be the fathers of young born within their ranges (limited observations by Galdikas, in press, tend to support this assumption), then it is to the resident males' advantage to avoid competing with females for preferred foods in order to maximize survival of their own offspring. There is, of course, no reason why non-resident males should avoid competing with females, but as Galdikas (in press) has argued, the system of male–male competition will tend to exclude transient male competitors from female ranges. An interesting prediction of this line of thought is that an adult female should be able to exclude a resident male from favoured food sources (although it is not predicted that she will always try to do so) because it is to the male's advantage to defer to his offspring's mother's dietary quality. I have observed a single incident in which an adult female drove a resident male from a fruit tree. It is also interesting that if this chain of reasoning is correct, resident males may "emigrate" in times of scarce preferred resources thereby reducing competition with females. Galdikas (in press) describes changes in male presence that are correlated with changes in availability of fruit; she comments that,

> . . . the central study area seemed devoid of males during mid-1973 when only minor fruit crops were available and the females were subsisting on unusually large amounts of bark. Perhaps significantly, it was during this one time that there was even an absence of resident males.

Similarly, the habituated resident male in my study area occupied part of his range in the deep forest zone where there is less fruit (Section 6 above) except during March and April, 1971, when fruit was particularly abundant in the flooded zone. Perhaps coincidentally, the latter zone was the area of most intense occupation by female orang-utans. Unfortunately these observations may be explained by an entirely opposite line of reasoning: perhaps in time of scarce preferred resources males move off to more fruitful ranges while the females are left with what they can find, as Galdikas (in press) has suggested. Existing data do not allow a choice between the two arguments, although the former explanation, which assumes "altruistic" motives on the male's part, appeals more to me than the latter, which assumes entirely the opposite male motivation.

10. SUMMARY

1, 2. The nature of orang-utans influences the observer to follow a subject for extended periods of time rather than switching from subject to subject, and to record transition times of behaviours as the primary data. Transition times are useful if behavioural categories are sufficiently large and if the animals are slow moving, but the resulting record may be less precise than one provided by a sampling method. In this study food availability was measured by enumerating trees and tree species in a small sample of forest and by counting fruits on the ground in the study area. The study area consisted of 3 km^2 of lowland dipterocarp forest. Observations of feeding behaviour were unevenly distributed through the year, evenly distributed through the day and taken primarily in bouts of more than ten hours duration.

3. Techniques of feeding almost invariably involved suspension by two or more appendages in the middle canopy of the forest, near the periphery of tree crowns. Orang-utans appeared to disperse some fruit species since they swallowed the seeds. They utilized several foods, such as the leaves of two palms and bark of dipterocarps, that are not available to other animals as food. Most feeding took place in the middle canopy from 20 to 30 m high but there were sex differences in utilization of strata. Orang-utans spent 45·9% of their waking hours feeding, with peaks of feeding in the early morning and late afternoon. They

spent 39·2% of their time resting, 11·1% travelling, 1·0% building nests, and 2·7% displaying at the observer. Travelling occupied more time in the afternoon than in the morning with a peak in the mid-afternoon. The animals were primarily frugivorous, but fed on a large proportion of leaves, some bark, and a few flowers and insects. The animals were selective of parts of some leaves; apparently selective of fruit in a fruit tree; and selective of food sources in the forest. Their preferred food sources were less common than the average variety of tree or vine in the forest sample. They fed on at least 50 species of plants, but their dietetic diversity was lower than that of orang-utans observed by MacKinnon (1974) in Sabah.

4. There was diurnal variation in food choice: orang-utans took less fruit relative to other foods in the middle of the day and in the early afternoon, and this variation in food choice was correlated with the diurnal pattern of movement from one food source in the morning to another in the evening. There is little evidence of other temporal patterns of food choice.

5. Seasonal variation in food supply of orang-utans has not been studied, but there are some correlations between dietary variation and variation in other feeding behaviour. In this study, time spent feeding increased for two of three animals when fruit consumption was lower. In other studies feeding time decreased with lower fruit consumption (MacKinnon, 1974) or travel time increased (implied by Galdikas, in press).

6. Availability of fruit apparently varied between two habitat zones in the study area, but dietary proportions did not vary between the two areas for orang-utans. Intensity of utilization by orang-utans was higher in the zone of higher fruit abundance.

7. A habituated male spent more time feeding each day than any of three females. He fed in the same number of feeding bouts for a longer time at each food source. The difference is probably related to size differences between adult males and adult females. MacKinnon's (1974) data show a similar sex difference in pattern of feeding and travel, but the difference is smaller. Males utilized the lower 14 m of the forest 4·5 times as much as females, and the habituated male took more bark and less fruit than females when all fed on the same abundant fruit.

8. Home ranges of six adult orang-utans in this study area averaged 0·42 km^2 and were stable through the 15-month study. Galdikas (in press) found a similar pattern, but with much larger home ranges of 5–6 km^2 in central Kalimantan. MacKinnon (1974) observed animals in Sabah whose home ranges were very large or who appeared to be nomadic. Day ranges in this study area averaged 305 m, and in

Galdikas' area averaged no more than 800 m. The author provisionally attributes the variation in ranging patterns to variation in seasonality and in topography among the three study areas.

9. Social behaviour is related to feeding behaviour in that the dispersal of orang-utans in minimally small "foraging units" is to be expected of an animal feeding on small patches of resources without threat of predation. Male patterns of behaviour are further determined by their competition with other males for dispersed females. Differential activity patterns of males and females contribute to segregation of the sexes. The habituated male in this study appeared to utilize resources in different proportions to the females, choosing a less "preferred" diet. This difference, if it is characteristic of male orang-utans in general, can be interpreted as a choice by breeding males that limits competition with females—and thus with the males' own young—for preferred resources. Some data are presented relating to this hypothesis, but alternative hypotheses cannot be rejected.

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14

Feeding Ecology of Free-ranging Mountain Gorilla *(Gorilla gorilla beringei)*

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1. INTRODUCTION

In contrast to the other apes, which range in parties of changing composition and size (chimpanzees and orang-utans), or in small family groups (gibbons and siamangs), most gorillas live as members of comparatively stable groups, usually with an adult sex ratio of more than one female per male (Hamburg and Goodall, in press).

Published data on the feeding behaviour of gorillas in the wild is sparse. Schaller (1963) remains an invaluable reference work on the East African gorilla populations: eastern lowland gorilla (*Gorilla gorilla graueri* Matschie) and mountain gorilla (*Gorilla gorilla beringei* Matschie) (see Groves, 1970). Other work has also been done on the eastern populations: Donisthorpe (1958) and Kawai and Mizuhara (1962) provided data on diets; Kawai and Mizuhara (1962), Casimir and Butenandt (1973) and Fossey (1974) gave details of ranging patterns and their relations to food distribution. Donisthorpe, Kawai and Mizuhara, Schaller, Fossey, and Harcourt worked mainly in the Virunga volcanoes. Casimir and Butenandt worked in the Mt Kahuzi region. Schaller (1963) has given a preliminary map of the distribution of the East African gorilla populations.

Data on the West African gorilla populations, western lowland gorilla (*Gorilla gorilla gorilla* Savage and Wyman), are even more scarce. Sabater Pi (1966) provided details of diets; Jones and Sabater Pi (1971) provided details of diet, activity patterns and range sizes.

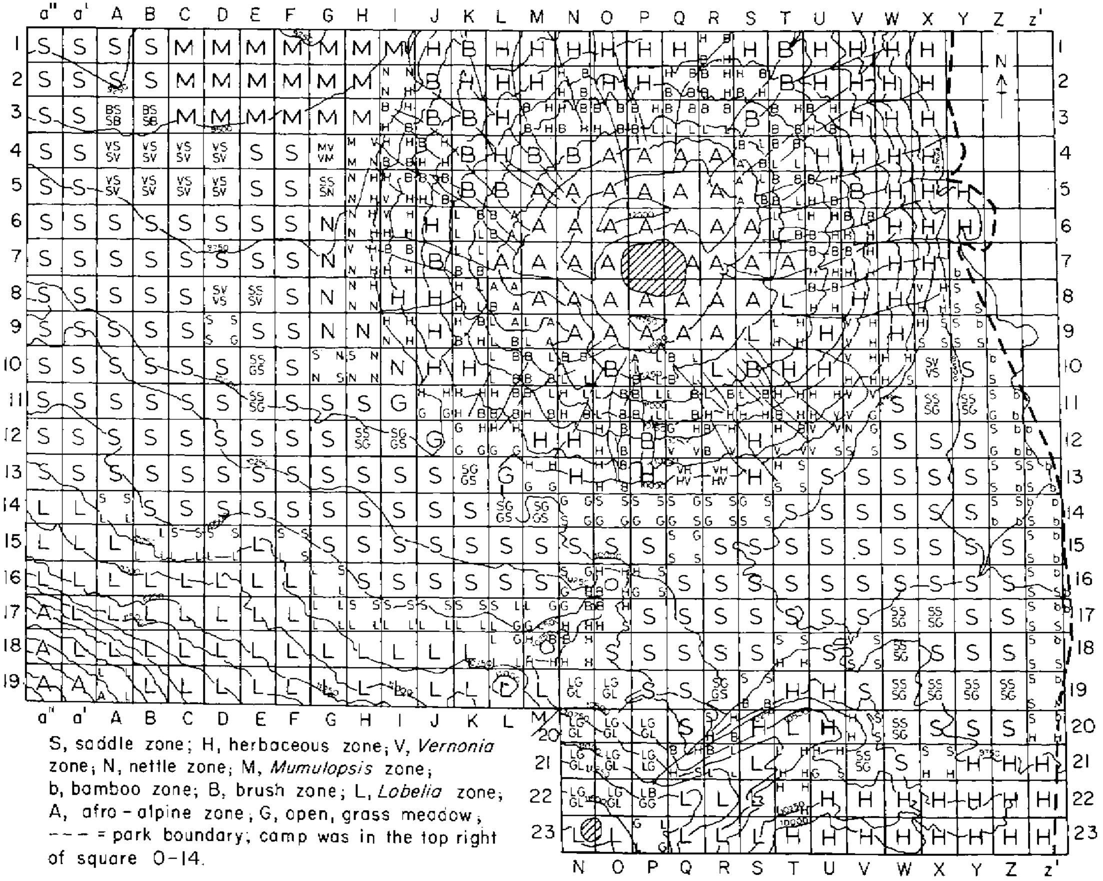
FIG. 1. Adult female in herbaceous vegetation.

This chapter and papers by Caro (1976); Elliott (1976); and by Fossey (1971, 1972a, b, 1974) are all based on data collected within the same study area, and the same group reference numbers are used in all.

2. STUDY AREA AND METHODS

The study area was approximately 25 km^2 and was centred on the base of the southern slopes of Mt Visoke within the Virunga volcanoes. Part of the area lay within the Parc des Volcans of Rwanda and part in the Parc des Virungas of Zaïre at approximately 30° E and 1° S. The main vegetation zones within the study area were *Hagenia-Hypericum* woodland and an afro-alpine zone. The study area was subdivided into a number of more definitive zones (see Fig. 3). More detailed descriptions of them

FIG. 2. View from 3100 m on west slopes of Mt Visoke. Herbaceous zone in foreground; saddle zone in middle ground (mostly *Hagenia* trees visible); afro-alpine zone and meadows on mountain in background.



S, saddle zone; H, herbaceous zone; V, *Vernonia* zone; N, nettle zone; M, *Mumulopsis* zone; b, bamboo zone; B, brush zone; L, *Lobelia* zone; A, afro-alpine zone; G, open, grass meadow; --- = park boundary; camp was in the top right of square O-14.

FIG. 3. Vegetational zonation in the study area.

may be found in Schaller (1963), Fossey (1974) and Lind and Morrison (1974).

Saddle zone. The saddle terrain was a comparatively flat area between the mountains of Visoke, Karisimbi and Mikeno. It was interrupted by hills and ridges, most of which were less than 30 m in height. For the most part, the saddle zone, characteristic of most of the saddle terrain, consisted of dense, lush ground cover and many *Hypericum* and *Hagenia* trees. The zone supported an abundance and variety of vines and gorilla food items not found in other zones.

Herbaceous zone. Found on the lower slopes of Mt Visoke and Mt Karisimbi at an altitude of approximately 3000 m, and on the steeper slopes of the saddle. It consisted of a fairly dense ground cover of both gorilla food and non-food plants with only a minimal amount of *Hypericum*, *Hagenia* and *Vernonia* trees.

Vernonia zone. Distinguished by a dense growth of *Vernonia* saplings and trees which grew in small areas of the saddle terrain and on the lower slopes of Mt Visoke around 3000 m. The ground cover within the zone itself was usually similar to that of adjacent areas, but in some areas the *Vernonia* were so dense that ground cover was almost absent.

Nettle zone. Found mainly around the base of the western slopes of Mt Visoke, though nettles were found scattered throughout the saddle and herbaceous zones. The zone consisted of a very dense growth of the nettle, *Urtica*, and the *Galium* vine.

Mimulopsis zone. Within the study area this zone was found only in the northern section of the saddle terrain. It was distinguished from other zones by the sometimes dense patches of shrub growth of *Mimulopsis*, which the gorilla did not eat.

Bamboo zone. Found mostly in the eastern part of the study area near the boundaries of the park, although there were a few isolated clumps in the saddle terrain and low on Mt Visoke. Stands were seldom more than 3–5 m in height and were interspersed with patches of herbs, shrubs and vines.

Brush zone. Found on narrow ridges and steep slopes, i.e. mainly in the most ravined parts of Mt Visoke. The ground cover consisted of tough shrubs with very few herbaceous plants. Two tree species, *Pygeum* and *Rapanea*, were more characteristic of this zone than any other.

Lobelia zone. Found between 3500 and 3700 m on the mountain slopes. It was characterized by a dense growth of giant *Lobelia*, stunted trees, and sparse ground cover.

Afro-alpine zone. This zone, which was usually found above the lobelia zone and up to the mountain summits, and the *open*, *grass meadows* contained very little gorilla food.

Cultivation abutted the south-eastern boundaries of the Parc des Volcans.

There were a number of other herbivores in the area; elephant, buffalo and, in particular, cattle were probably the ones which most affected the gorillas and their habitat. Gorillas avoided the areas trampled by these animals until regeneration had occurred (see also Schaller, 1963; Jones and Sabater Pi, 1971). Man was and is the only important predator. Though gorillas have been killed in the Virunga volcanoes (Fossey, 1972a; Harcourt and Groom, 1972; Groom, 1973), they are not killed for food there, so they are not hunted as extensively as in other parts of Africa (Schaller, 1963; Jones and Sabater Pi, 1971).

Eight groups, consisting of approximately 65 animals, at an estimated population density of 1·5–2 animals per km^2, were found within the study area, but only two groups used it permanently. Over a period of seven years (September 1967 to September 1974) observations were concentrated on these two groups (groups 4 and 5). Observations were also made on other groups (particularly groups 8 and 9) when they were encountered in the study area. The compositions of the four most studied groups are summarized in Table I. The frequency and length of observational periods ("contacts") varied from 0 to 25 per month, and from under 1 to over 8 hr per day. During the last two years of the study, daytime activities were recorded at quarter-hourly intervals (Table VII; Fig. 4). Activities recorded were as follows. (a) *Eating*, behaviour involving the collection, preparation, and ingestion of food. (b) *Stationary*, most sedentary activities, i.e. mainly resting. (c) *Locomotion*, any travel from one point to another. (d) *Play*, the activities classed as play were judged subjectively, but most authors agree that play is usually an easily distinguishable behaviour. The activities included are essentially those described in Loizos, 1967. (e) *Other*, copulatory behaviour, non-play displays. It was often possible to judge activities of obscured animals from sounds alone, but records from such judgements were not used since moving and feeding animals would have been overrecorded compared to stationary ones. Observations were not distributed evenly throughout the day. In order to obtain figures for daily activities of individuals, the unevenness was corrected by taking the mean of the percentage of records for each activity per four-hour period. Figures for group activities were calculated by taking the mean of the individuals' corrected per cent of records.

In the same quarter-hourly scans, the positions of all possible individuals were mapped and the overall group activity was recorded. (The activities of group members were more or less synchronized, so it is legitimate to speak of "group activities".) To compare interindividual

TABLE I

Group compositions

	Sb	Bb	F	yA	J	I	Total
GROUP 4							
Start							
Sept. 67	3	1	4	4	—	2 (4)	14
Sept. 70	1	—	7	—	2 (3)	3 (1)	13
Sept. 72	1	—	3 (4)	2 (1–3)	2 (1–3)	2	10
Sept. 74	1	1	2	2	2	1	9
GROUP 5							
Start							
Sept. 67	2 (3)	1	5 (4)	—	4 (5)	3 (4)	15
Sept. 70	2	—	5	1 (3)	3	2	13
Sept. 72	1	1	6	2	2	4	16
Sept. 74	1	1	4	—	3	2	11
GROUP 8							
Start							
Nov. 67	2	1	1	2	—	—	6
Sept. 70	1 (2)	3	— (2)	—	— (1)	—	4
Sept. 72	1 (2)	1	1	1	—	— (1)	4
June 74	1	—	2	—	—	—	3
GROUP 9							
Start							
Dec. 67	1	1	5	2	—	4 (1)	13
Aug. 70	1	1 1*	5	—	4	2	13
Feb. 74	1	1 1*	3	2	—	3	11

Sb: silverback (male of 11 + years); Bb: blackback (male of 8–11 years); F: adult female (8 + years): yA: young adult (6–8 years); J: juvenile (3–6 years); I: infant (0–3 years). The upper age limits to most of the classes are higher than those given in Schaller (1969) and Fossey (1972b), which are now considered to be underestimates.

* Blackback or female. Bracketed numbers are counts in the intervening period which exceed the unbracketed counts.

spacing during resting periods with that which occurred during travel–feeding periods, a sample of records of group 4 taken during 22 days in November, December 1973 and February 1974 was selected (Tables X and XI). Only those records of distance when the group activity was unmistakable were used. Also, no more than two quarter-hour records per group activity per day, and very few consecutive records were used.

The recording of feeding was not as systematic. Both authors concentrated on observations of social behaviour, so feeding behaviour was less precisely recorded. The records consisted of: (a) the individual and its food; (b) in the last two years, other food species available. "Food species" were defined as such if the previous five years of the study had shown the gorilla habitually fed on them. A food species was defined as *available* if it was within arm's reach of the subject. In the first five years of the study, intervals between records varied widely and were often less than a quarter-hour for any particular individual, but in the last two years they were never less than a quarter-hour for any particular individual. The more commonly eaten foods were probably underrecorded and the less common ones overrecorded. Data from the first five years form the basis of Table II and Figs 5 and 6, and data from the last two years, Tables II, III, IV, V and VIII, and Fig. 5.

In the analysis of activity and feeding records, we distinguished between the six age/sex classes in Table I. Since the methods of quantifying feeding measured time of intake, not amount of intake, "% of feeding time" is synonymous with "% of records" throughout the chapter. Also, for activities, "% of the day" is synonymous with "% of corrected records".

To measure the animals' movements, a contoured map (Fossey, 1974) was gridded with squares of side 0·25 km (0·0625 km^2) and the positions of groups and their trails were assigned grid references. Prior to September 1972, only groups, not their trail as well, were recorded within the square in which they were found. Summing squares in which just groups were found (=contacted) underestimated range sizes. Therefore range sizes are here presented as a total of both the squares in which a group was contacted plus the squares in which the groups' trails were found (p. 434 and Table IX). A comparison of the two methods of recording showed that contact evidence alone gave a good idea of range usage patterns (Figs 7 and 8), though with two main disadvantages [see (c) and (d) below]. Because of the slope and irregularity of the terrain, the map squared areas do not correspond to ground areas. This discrepancy was partly corrected by finding the median change in altitude along one side of 21 squares in the steeper parts of the study area (127 m). Trigonometry showed that one side of the squares was, therefore, 280 m, not 250 m, which gave a ground square area of 0·07 km^2 for the steeper parts of the terrain. No corrections were made for the ravines. Day journeys (Altmann and Altmann, 1970) were estimated from routes drawn on the map. The main disadvantages to the methods were that: (a) ground area was still underestimated; (b) there were areas within some squares which were not used; (c) using only squares in which groups were contacted overestimated use by lesser studied groups of squares near camp; (d) squares of lesser studied groups which overlapped those of the more studied groups were over-recorded; (e) day journeys were underestimated since the drawn routes were "smoothed".

Chi-squared tests were used in Sections 3.3 and 7; Mann-Whitney U tests in Sections 5 and 6; two-tailed values of "P" are shown.

3. FEEDING BEHAVIOUR

3.1. Feeding Techinques

The animals usually fed while seated and the food was normally collected before it was eaten. Juveniles and infants were noticeably more careful of spined and stinging plants than were adults. Rarely were all parts of any plant eaten, except for the most common food plant, the *Galium* vine. Preparation techniques varied according to the part of the plant eaten. This was especially noticeable when one part, for example the stem, was separated into its different subparts, e.g. epidermis and interior, which were then eaten separately.

Collected food was often wadded before it was eaten. *Leaves*, (e.g. thistle, *Urtica*) were usually picked separately, or stripped off by running the hand up the stem. Juveniles and infants, who took less leaves at a time than did adults, sometimes stripped the leaves downwards. *Fruits*, (e.g. *Rubus*) were picked off separately by hand or mouth. *Insides of stems*, if the outer portion of a stem could not easily be removed (which was generally the case with woody stems, e.g. *Senecio*), the interior was exposed by breaking the stem, gripping the jagged ends with teeth and hands and stripping the stem open, and then gnawing out the interior. The outer portions of softer stems (e.g. celery, *Laportea*) were removed prior to eating by stripping or peeling off the leaves by hand and then by peeling off the exterior with fingers and/or teeth. *Roots and stem bases*, if it was possible to pull a plant out of the ground (e.g. celery, *Cynoglossum*), this was done and the base and/or roots then eaten. At times it was evident that considerable force was exerted when pulling. If a plant could not be pulled up (e.g. *Senecio*), the gorillas often dug around the base until the roots were exposed. The interiors of smaller roots were sometimes separated from their exteriors by being pulled through the teeth, which action left the bark in the mouth and the interior in the hand. Then either or both were eaten. Hard roots were gnawed. *Wood and bark*, either broken off the tree by hand or mouth and the chunks then chewed, or the tree was gnawed directly. *Grubs*, obtained from split stems, underneath bark slabs, or from the surface of leaves by either fingers or mouth. *Dung*, deposited in the hand or picked off the ground, and then nibbled. *Water*, drunk by bending down to the water's surface and sucking.

3.2. Feeding Activity

Gorillas normally rose between 6.00 and 6.45h and night-nested between 18.00 and 18.45h. Only in exceptional circumstances did

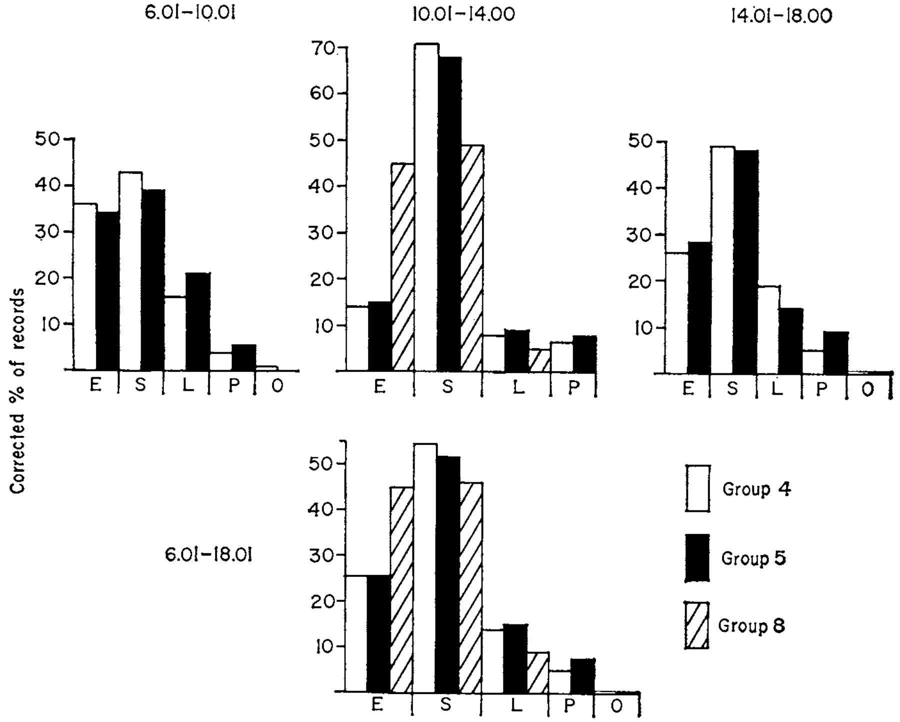


FIG. 4. Diurnal activity patterns of groups. E: eating; S: stationary; L: locomotion; P: play; O: other activities. The numbers of records for the four periods, given chronologically are: group 4—543, 2670, 559, 3772; group 5—553, 2250, 511, 3318; group 8—209, 307.

groups move during the night. Groups 4 and 5 had similar activity patterns and spent about 25% of the day feeding (see Fig. 4). Group 8's markedly higher proportion of the day spent feeding was possibly inaccurate because lack of data prevented correction for unevenness of observations through the day. The data show, though, that group 8 did not have the marked midday rest periods shown by groups 4 and 5. Neither group always had a midday rest period, and on some days there was no discernible group resting period at all. Most of the activity records of groups 4 and 5 were taken when their compositions were similar; this could have been part of the reason for the similarity of their activity patterns.

Climate affected activity patterns. In rain, animals sat huddled and almost motionless; on sunny days, adults tended to rest longer, basking in the sun. Whether they then compensated for this inactivity by increased locomotion, or feeding, during the rest of the day is not yet known.

3.3. Food Selection

The gorillas did not eat all of the plant species within their range, and some of the most common ones, such as balsam (*Impatiens*), were not seen to have been even sampled, although other herbivores ate them. The 42 species (18 families) shown in Table II are all wild species. No reports were heard from the Rwandans of gorillas feeding on their crops, though group 5 occasionally entered the cultivated areas. A few food species formed the bulk of the feeding records (see Tables II and III). Sixty per cent of feeding records were for the three most commonly eaten species and 20% for the next six most common. Because of

TABLE II

Numbers of plant types in diet

Plant type	In diet Very common	Common	Uncommon
Tree		1	7
Shrub		2	1
Herb	2	2	15
Vine	1		4
Grass		1	2
Epiphyte			2
Fungus			2
Total	3	6	33

recording bias (p. 422), the actual figures were, perhaps, nearer 70 and 25% respectively; i.e. 95% of feeding time spent on 21% of all food species. Leaves, shoots and stems (*Galium* included) formed the bulk of the gorillas' diet: 85·8% of all records. Wood accounted for 6·9%; roots, 3·3%; flowers, 2·3%; and fruits, 1·7%. Grubs and dung were also eaten and the gorillas occasionally drank. Feeding time was probably roughly proportional to intake for the more commonly eaten items. This was not the case with the less commonly eaten ones (wood and roots) since much time was sometimes spent obtaining a small intake.

Donisthorpe (1958), Kawai and Mizuhara (1962), Schaller (1963) and Jones and Sabater Pi (1971) also reported that a few species comprised the bulk of the diet. Schaller (1963) estimated that the four most commonly eaten species comprised 80% of the daily diet of his study groups. Jones and Sabater Pi (1971) estimated that two species of *Aframomum* comprised 80–90% of the yearly diet of their western gorilla study groups. All reported that the gorillas were predominantly folivorous rather than frugivorous. Western lowland gorilla probably ingest more fruit than do mountain gorilla (cf. Sabater Pi, 1966).

Group differences in the amount of time spent feeding on certain foods (see Table III) were commonly associated with obvious differences in the amounts of those foods within their ranges. For example, there seemed to be more thistle than celery in group 4's range while the

TABLE III

Percentages of feeding records for the more commonly eaten species

		Group 4		Group 5		Group 8	
Galium (vine)		29·8	59·8	27·1	57·8	23·7	69·5
Thistle		21·0		10·5		37·3	
Celery		9·0		20·2		8·5	
Vernonia (tree)		4·6	20·1	5·4	21·1	—	8·5
Urtica	nettle	6·5		—		—	
Laportea		7·0		4·5		3·4	
*Rubus** (shrub)		2·0		5·3		5·1	
Bamboo (grass)		—		6·0		—	
Others		20·1		21·0		22·0	
n =		817		669		62	

* Two species were eaten.

reverse was true in group 5's range; thistle comprised 21% of group 4's records and celery, 9%, whilst thistle made up 10·5% of group 5 records and celery, 20·2%.

Individuals usually did not eat all food species available at any one feeding spot. Thus Table IV shows that of the 120 records made of two simultaneously available species, only 28 were of both being eaten; of the 34 records for three available species, only three of all of them were being eaten. Age/sex classes differed in their degree of selectivity ($P<0{\cdot}001$ for a comparison of one, as against more than one species being eaten). The silverback showed the least selectivity; this was perhaps related to his spending more time per feeding spot than did any other animal (see Section 5).

If feeding time on a particular food was proportional to the abundance of that food (see above), it would seem that selection within the diet did not occur. However, records made when more than one food species were available showed that some of the less commonly eaten species were usually chosen over some of the more common ones (Table V). For example, thistle and celery (about 10–20% of the diet) were each chosen about three times more often than *Galium* (about 28·5% of the diet). A further indication of choice was noted in that thistle leaves were usually eaten before the stems: 28 records for leaves first as against 13 for the stems first (records from 8 days over 28 days in May and June 1974). We think that the reason for this temporal selectivity was that if they ate the stem first, then the leaves became unusable: to eat the stem, they stripped off the leaves, and discarded food was rarely eaten.

Individuals and groups often moved to new feeding spots when there

TABLE IV

*Records of numbers of food species eaten at any one feeding spot, compared with numbers available**

Number eaten Number available	1 2	2 2	1 3	2 3	3 3
Age/sex class					
Sb	10	7	2	3	—
Bb	10	3	4	—	—
F	27	15	7	7	2
Imm	45	3	8	—	1
Totals	92	28	21	10	3

The figures are numbers of records taken during 8 days over 28 days in May and June, 1974.
* i.e. within animal's reach.

TABLE V

Choice of food species in relation to other foods available

	Thistle	Celery	*Vernonia*	*Urtica*	*Laportea*	*Rubus*	Bamboo
Galium	20* 56	19* 56	22 18	116* 37	54* 26	8 6	2 8
Thistle		29 17	2 4	12* 2	56* 20	— 2	— —
Celery			3 5	11 2	40* 12	3 7	— 2
Vernonia				— —	5 —	— —	— 2
Urtica					3 8	— —	— —
Laportea						— 5	— —
Rubus							1 —

The top left of each pair of figures is the number of times the row plant was eaten, when the column plant was available. The bottom right of each pair of figures is the number of times the column plant was eaten when the row one was available. The records are for groups 4 and 5 combined: combined, because all choices for each were in the same direction, and most choices for each had similar ratios.

* Indicates the largest differences.

was still seemingly abundant food remaining in their previous area. The immediate cause of such movement might have been that collection was becoming inefficient: animals were spending too much time reaching for plants further from them, having cropped the closer ones, or were crossing each others' feeding paths too often. The benefits of such movements could have been threefold: (a) to maintain the efficiency of collection; (b) to leave plants for regeneration; (c) to stimulate regeneration. Rearden (1974) and Vesey-Fitzgerald (1969, 1974) also suggest the last benefit.

Gorillas built most of their nests from non-food species even when food species were available (Table VI). Of 598 nests examined, 585 were built of non-food species. Of 196 built near a substantial number of food species, 185 were built of non-food species. Females with infants tended to select non-food areas for nest building more than did others. The cause of such selectivity in this area was probably that food plants

TABLE VI

Extent of use of food species in nests

	Nests built with food species		Nests built with non-food species		Nests built with mixture	
	+	−	+	−	+	−
Females + infants	0	0	27	100	0	0
Others	2	0	158	300	9	2
Totals	2	0	185	400	9	2

Nests were counted as being built with a "mixture" if there was a ratio of less than 1 : 1·5 (40 : 60%) by volume (visual estimation) of food and non-food species in them. If the ratio was more than this, then the nests were counted as being built of food, or non-food, species depending on the direction of the ratio. " + ": nests built near a substantial number of food plants. " − ": nests not built near a substantial number of food plants.

were unsuitable nest material. In other areas, where food plants were suitable nest material (e.g. Rio Muni) nests were made of them (Jones and Sabater Pi, 1971). Since most gorillas built a nest every night, the selection of non-food plants for nesting material possibly resulted in considerable "saving" of food.

4. SEASONAL VARIATION

(See also Section 6.3.)

There was a marked seasonal variation in rainfall with a major wet period occurring from March to May and a major dry period from June to August (see Fig. 5b). (For most months the total rainfall differed widely between years, so summing the feeding records for seven years probably obscured some year by year seasonal differences.) Seasonal variation in the diet was evident (Fig. 5a): records for *Galium* decreased from a peak in July to a low point in October, while those for celery, thistle and *Vernonia* rose more or less irregularly over the same period. *Galium* records rose markedly in November, at which time those for thistle and *Vernonia* dropped. Records for celery were highest around both wet periods, while those for wood were highest in the wettest period only. *Pleopeltis* records were clearly highest during the three months before the wettest period and were very low at all other times. Records for bamboo were highest in June and December with a gradual increase over each of the preceding three months.

With the exception of bamboo shoots, the availability of particular

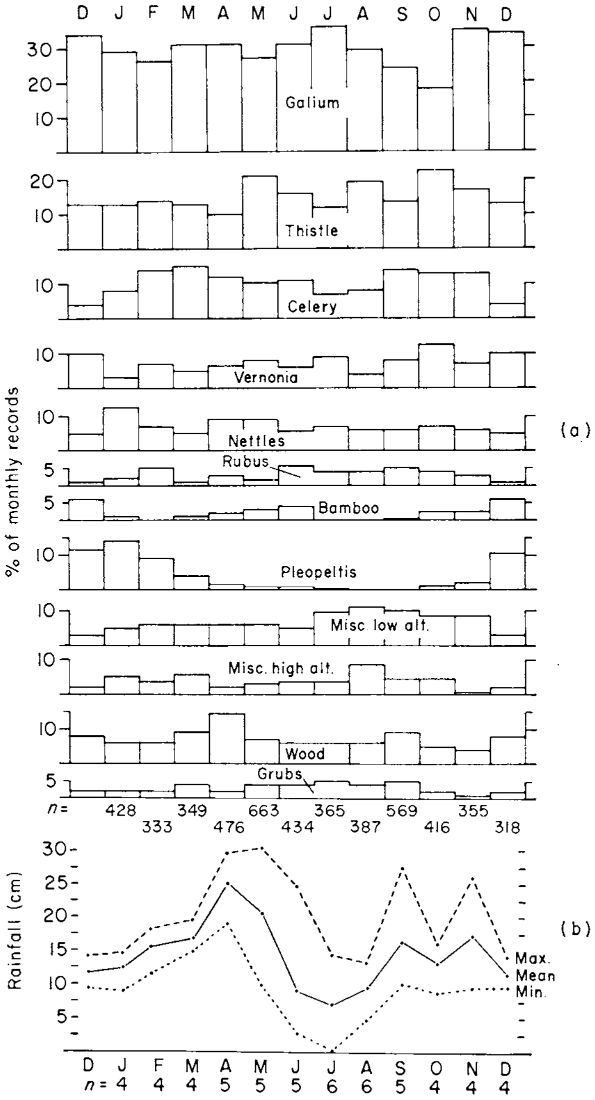


FIG. 5. Seasonal variation in (a) diet and (b) rainfall.

plant foods did not appear to change through the year. However, the amount of flowers, fruits, and shoots of both food and non-food species, in addition to the general "lushness" of the vegetation, did change. This undoubtedly altered the nutritional qualities of the plants and, presumably, the gorillas changed their diet accordingly.

Donisthorpe (1958), Kawai and Mizuhara (1962), and Casimir and Butenandt (1973) have all reported seasonal variation in bamboo intake. Donisthorpe (1958) and Kawai and Mizuhara (1962) reported it as having been eaten mostly in June; Casimir and Butenandt (1973) reported October. The last two references have reported bamboo as comprising more than 90% of the diet at the peak of the shooting season (gorillas fed on the shoots far more than on the leaves). Correlated with the increase in bamboo consumption there was a decrease in intake of other species. Donisthorpe (1958) reported celery as one such example. Sabater Pi (1966) found that fruit consumption by western gorillas increased during the fruiting season to more than 50% of their diet.

5. AGE/SEX VARIATION

Although individual differences in feeding behaviour were sometimes marked (see Table VII), consistent differences between the various age/sex classes were found. In groups 4 and 5, silverbacks spent the most time eating, infants the least, and the other four classes were intermediate (Table VII). Also, both silverbacks of group 8 spent more time eating than did either female. The differences in the amount of food consumed were greater than the figures indicate since the size of each mouthful of food was roughly proportional to the size of the animal. In addition, the

TABLE VII

Age/sex variation in % of day spent eating

	Sb	Bb	F	yA	J	I
Median %*	35·3	28·3	29·7	27·1	25·5	11·4
Range	34·2 to 36·5	28·2 to 28·5	15·6 to 35·7	22·4 to 30·3	14·5 to 29·3	7·7 to 23·5
Number of individuals	2	2	8	5	6	3

* The figures are the medians of the corrected per cents of records for each individual in groups 4 and 5, the range of which percentage is shown in the second row of the table.

group 4 silverback's median time per feeding spot was significantly higher than that of the other individuals: 8·5 min ($n = 16$) as opposed to a range of 2·5 to 4·0 min ($n = 14$–21) with $P < 0·04$ for all silverback–other individual comparisons. (The records are from 8 days over 28 days in May and June, 1974.)

The difference between the silverbacks' and others' time spent feeding is small so, however real the difference, a chi-squared test would not show it as significant. It is suggested that the difference is real because only one animal in one group had a higher figure for time eating than did the silverback of that group and it is difficult to think of any sampling error that would cause this result: bias introduced by silverbacks spending more time per feeding spot than others (and so being more likely to be recorded eating) was counteracted by the same bias for their stationary and locomotion records. Silverbacks were about twice as heavy as other adults (Schaller, 1963, pers. obs.). Perhaps this difference was the reason why, despite a smaller body surface to weight ratio, silverbacks needed to spend more time feeding than did other adults. The silverbacks' larger size also meant that acceleration and deceleration took more energy. Therefore, it was presumably more efficient for them to have a few, long eating periods rather than many, short ones. Also, because their arm reach was greater, they had more food available to them, thus they could afford to spend longer in each feeding spot (R. W. Wrangham, pers. comm.).

Differences in diet also existed between the classes (see Fig. 6). In Fig. 6, the foods in the left column of histograms were the most commonly eaten, and those in the right were the least commonly eaten. Because of the bias in our recording (underrecording of the more commonly eaten foods), the records in the two left columns should be increased compared to the one(s) in the right. Immatures fed more on *Vernonia*, *Pleopeltis*, wood and grubs than did adults, but less on *Galium*. Infants fed less on celery, and silverbacks more on thistle than did other classes.

Immatures (young adults to infants) spent more of their feeding time up trees than did adults and particularly when feeding on *Galium* (Table VIII). Three reasons are suggested for this: (a) there were many trees that would bear an immature's weight and not an adult's; (b) adults most often climbed trees only to obtain fruits, which were rare in this area; (c) immatures often climbed trees for non-feeding activities initially; these could later lead to feeding.

In general, immatures fed less on the most commonly eaten species than did adults. The immediate causes might have been different for each species. For example, infants might have fed less on celery than did

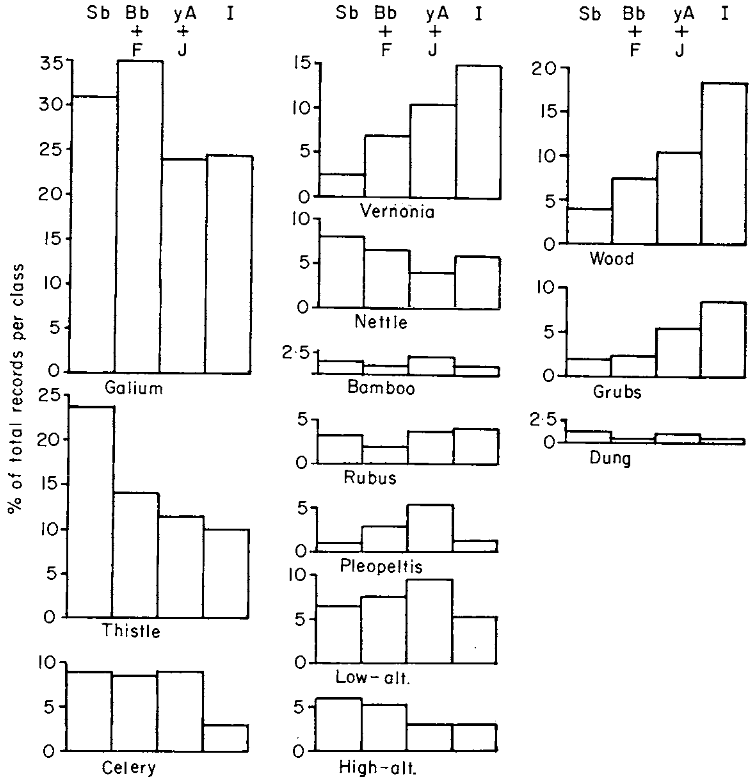


FIG. 6. Age/sex class variation in diet. The total number of records for each class are: Sb: 734; Bb: 594; F: 692; yA: 308; J: 600; I: 310.

TABLE VIII

Percentages of total feeding records which were of individuals feeding up trees

	All foods (excluding dung)	*Galium*
Adults	3·6%	2·4%
Total *n*	853	266
Immatures	18·2%	24·7%
Total *n*	686	147

The figures are the means of the % of the three classes in each age category.

other classes because of the difficulties involved in pulling the plant free from the soil (celery was usually pulled up before it was eaten); immatures might have fed more on *Vernonia* parts and *Pleopeltis* because these items were abundant up trees. Whatever the immediate causes, one of the effects of the generally different diet and feeding sites between adults and immatures could have been to maintain competition at a low level. The chances of competition for the most common food, *Galium*, would have been reduced, since the immatures ate less *Galium* than did adults, and also ate more of their *Galium* up trees (see also Kummer, 1971—baboons).

It is not known how important grubs were in the gorilla diet, but the observation that immatures ate more than did adults agrees with the results of a number of other studies (see Schoener, 1971) concerning predominantly herbivorous species, in which immatures ate more animal protein than did adults.

6. FEEDING BEHAVIOUR AND RANGING BEHAVIOUR

There was no substantial evidence that groups defended areas. If lone silverbacks did so (Fossey, 1974), the defended area was small compared with the total area used, and the defence was temporary: other groups could visit the defended area when the lone silverback was not there. In this chapter the term "range" means the area used by a group, or lone animal, over a given period with no implications of habitual use during normal activities (Burt, 1943).

The *yearly range sizes* (between October 1972 and September 1974) of the two most studied groups were: group 4, 4·9 km² and 4·0 km² in the two consecutive years; group 5, 8·1 km² and 7·7 km². Estimates by other observers of the yearly range sizes of their most studied gorilla groups were quite different: Schaller (1963) reported about 20 km² ($n = 2$); Jones and Sabater Pi (1971) reported 6–12 km² over a period of 6–9 months ($n = 3$); Casimir and Butenandt (1973) reported about 30 km² ($n = 1$). All of these observers used contact evidence equivalent to that of this study (see p. 422); how they then calculated the given range sizes was not stated. Since Schaller's study area was adjacent to that of this study, it might have been expected that our estimates of range sizes would have been more similar despite his groups having been larger (18 and 20 animals), and their ranges less encroached upon. When this study's method of measuring range size from contact evidence alone was applied to the map area in Schaller (1963), a figure of 10 to 12 km², as opposed to 20 km², was obtained as the range size for his two most studied groups. Although Schaller allowed for irregular terrain and also used data not shown in his book (pers. comm.), it is suggested that his final estimate of 10 to 15 miles^2 (25–38 km^2) was too large. Jones and Sabater Pi (1971) seemed to have multiplied the sides of the quadrangle which covered their few observations, and this possibly resulted in an overestimate. Casimir and Butenandt (1973) seem to have summed squares in which nests were found and then to have multiplied the resultant figure (approximately 12 km^2) by 100/40 because they found only 40% of nest sites; this method probably also resulted in an overestimate. It is suggested that gorilla yearly range sizes vary between areas and that they are from 4–5 km^2 to 20–25 km^2. Yearly ranges shifted. For example, the five-yearly range size of group 4 (Fossey, 1974) was about twice its yearly size. Casimir and Butenandt (1973) also reported shifting yearly ranges.

Table IX shows the *monthly range sizes* of a number of groups and two lone silverbacks; the medians range from 0·66 km^2 to 1·98 km^2. It appeared that the monthly range sizes of groups were positively correlated with group size (and therefore, presumably, with total food requirements): significant differences were found between the range sizes of groups 5^a and 5^b; 5^a and 4; 8 and 4, 5^a, 5^b. However, the monthly range sizes of two newly formed groups were smaller than the median monthly range of an established group of the same size. Also,

TABLE IX

Monthly range sizes of groups and lone silverbacks between October 1972 and August 1974

	Groups						Lone silverbacks	
	5[a]	5[b]	4	8	S[c]	N[c]	S	B
Median no. of animals	15	10	10	3	3	3	1	1
Median range size (km^2)	1·98	1·45	1·52	1·06	0·66	0·79	1·65	0·99
Max. range size (km^2)	2·51	3·37	2·51	1·45			2·24	
Min. range size (km^2)	1·45	0·99	0·86	0·40			1·25	
No. of months	7	10	18	7	1	1	1	1

[a] Group 5 before June 1973.
[b] Group 5 after June 1973.
[c] Newly formed groups: the range sizes are those of the first month after formation of the group.
Two females joined silverback S to form group S.

the range of one of the two groups was well outside the silverback's normal range. Judging from groups' effects on the vegetation, it seemed likely that the larger groups' minimum monthly ranges could not have been as small as those of the smaller groups' without causing serious damage to the vegetation. Lone silverbacks had monthly range sizes as large as those of established groups (Caro, 1976). Monthly ranges shifted, sometimes markedly, and usually there was no discernible consistency in the pattern of movement. Schaller (1963) and Casimir and Butenandt (1973) both implied that monthly ranges shifted. (Through most of their paper, Casimir and Butenandt used the term "core-area" to mean what we would call "monthly core area", i.e. the area in which about 50% of each month's night-nests were most densely distributed.)

Over an 8-month period (October 1972 to May 1973), the median *length of day journeys* per month of groups 4 and 5 were 295 m and 360 m respectively. The figures are underestimates (see p. 423) and should be nearer 350 m and 450 m. The daily variations were usually from about 100 m to 2·5 km, and once 6 km. Individuals in the groups travelled farther than the group as a whole; some perhaps twice as far during a normal day's movement. Over seven months in 1973, Elliott (1976) found that the mean day journey of group 8 was 522 m (median: 434 m) (83–1342 m; $n=41$). For three months in early 1974, Caro (1976) found that the mean day journeys of two lone silverbacks were 460 and 385 m ($n=35$ and 91 respectively). Elliott and Caro estimated the day journeys by pacing. The above day journeys are similar to those given by Schaller (1963) who reported a range of means per group from 337 to 663 m. Casimir and Butenandt (1973) gave a mean (and median) day journey of about 900 m. Jones and Sabater Pi (1971) reported mean day journeys of about 1 km in Rio Muni, with the length varying with the density of *Aframomum* thickets. With an estimated mean group diameter of about 50 m per day, and a day journey of about 400 m, the daily range of gorilla groups was about 0·02 km^2. Monthly range sizes did not vary with season or with zone. Day journeys might usually have been longer in the alpine zone and slightly shorter in the wettest season. Because of the variation and inconsistency in ranging patterns, the positions and sizes of yearly ranges could not be estimated from even 6-month range positions and sizes (cf. Wrangham, this volume).

The ranges of the groups overlapped (Fig. 7). The portrayals of the ranges of group 5 from 1967 to 1972, and groups 8 and 9, were biased by the two disadvantages [(c) and (d)] given on p. 423, especially regarding the positions of their core areas. The groups actually spent far more time than was indicated farther away from both camp and group 4's range.

The portrayed ranges of groups 4 and 5 from 1972 to 1974 were accurate samples because, for the most part, the groups were followed wherever they were in their range (see also, Fossey, 1974). Group 8's range extensively overlapped those of groups 4 and 9 because group 8 persistently followed these two groups (Fossey, 1972a). The ranges of many other groups and lone animals also overlapped those of the main study groups; it seemed unlikely that there were any exclusively used areas within any groups' yearly range. Group 4 overlapped with the ranges of at least four other groups plus three lone silverbacks; group 5 overlapped with at least five other groups and three lone silverbacks; and group 8 with at least three groups and two lone silverbacks. It was possible that some lone silverbacks spent most of their time within their "parent-group's" range (Caro, 1976).

The "main core areas" and "core areas" (Fig. 7) were, for the most studied groups, the areas of "heaviest regular use throughout the entire period of observation" (Kaufmann, 1962); for the lesser studied groups they were simply the areas in which the groups were found the most frequently. Figure 7 indicates that core areas and even main core areas overlapped though a group's core areas were visited only infrequently by other groups. Of all previous studies of gorillas' ranging habits, only Jones and Sabater Pi (1971) have reported that ranges did not overlap.

It may be seen from Fig. 7 that (a) core areas were not necessarily in the range centres; (b) there could be more than one main core area; and (c) core areas were mostly low on the mountain slopes. Comparison of Fig. 7 with Fig. 3 shows that most of the core areas were in the herbaceous zone (between 1972 and 1974: 77% of group 4's core area and 45% of group 5's). It appeared that the saddle zone, rather than the herbaceous zone, offered a more abundant food supply to the gorillas; but it was used less, probably because of human interference. Both Schaller (1963) and Casimir and Butenandt (1973) reported core areas in the yearly range and Casimir and Butenandt (1973) implied that the core areas contained abundant food.

Despite the shifts of yearly ranges, group 4's main core area has always been in about the position shown in Fig. 7, and there were few indications that the position would change. Group 5, however, never visited its main core area on the mountain during the last five months of the study period and may have been in the process of changing its ranging pattern.

Figure 8 shows the extent of differential use of the ranges: 50% of the time was spent in about 17% of the range; 62% of time in 25% of the range; and 83% of time in about 50% of the range. Figures for lone

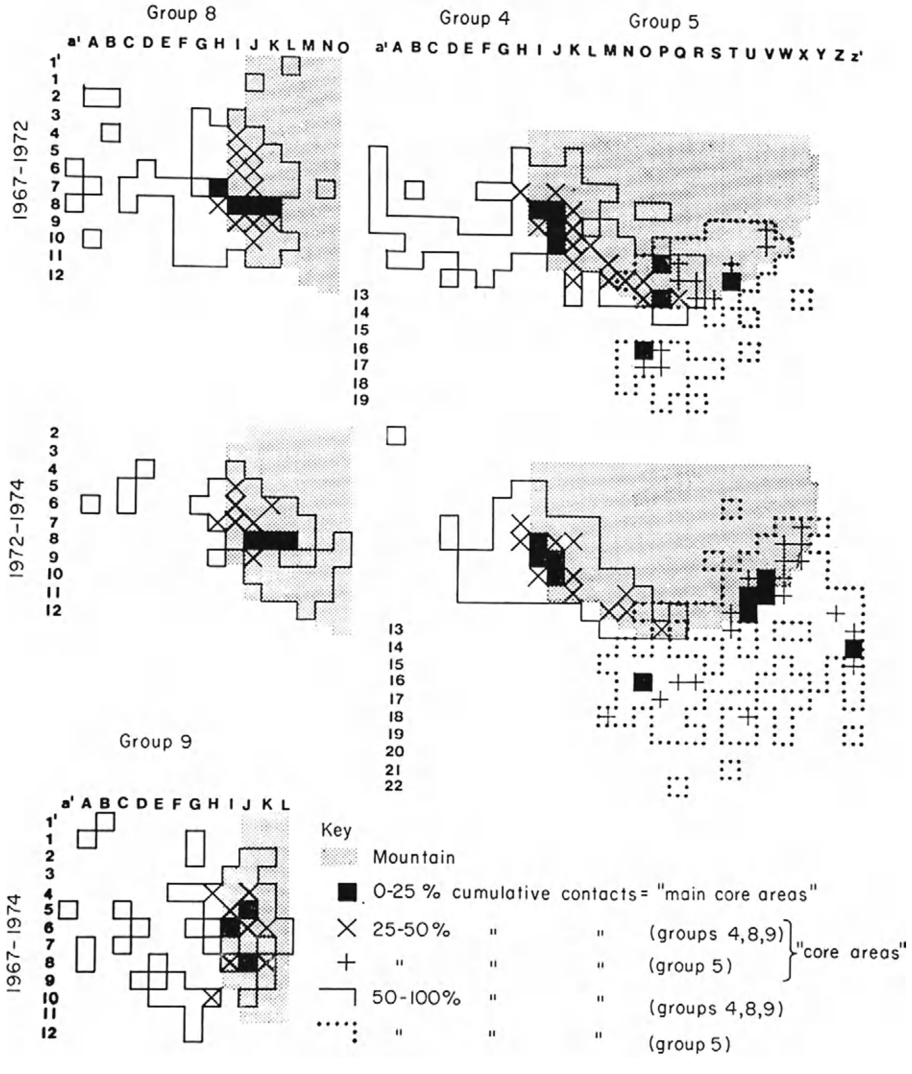


FIG. 7. Time spent by groups in different areas of their range. The figure shows the cumulative number of contacts with each group in the different squares. The two black squares in the overlapping area of group 4 and 5's ranges in 1967–1972 are group 4's. The number of contacts on which the ranges are based are:

1967–72: group 4—598; group 5—232; group 8—263.
1972–74: group 4—337; group 5—354; group 8—146.
1967–74: group 9—99.

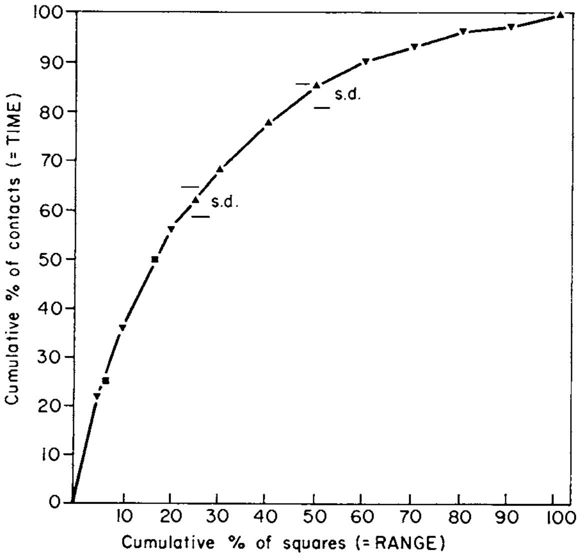


FIG. 8. Distribution of groups' time over their range. The points are records for one group over one period from the same data as formed Fig. 7. The standard deviations are for records for the groups and periods shown in Fig. 7. The standard deviations for the 25 and 50% cumulative contacts figures are too small to show.

silverbacks were similar (Caro, 1976). The small standard deviations indicated that the extent of differential usage of even segments of ranges (only part of group 9's range was within the study area) was similar to that shown over the entire range.

The only evidence indicating that movements between zones were affected by food preferences was that provided by group 5's movement to the bamboo zone between September 1972 and September 1974. They were contacted in this zone from April to June and October to January. The data suggested that these were also the months in which the bamboo shoots were most abundant. The amount and quality of food species varied across zones and grid squares. It was found that the gorillas did not use all parts of each zone, or even each square, equally, and it is suggested that the pattern of movements was perhaps closely related to food distribution. Such a correlation may have been responsible for short-term, diurnal, and between-day, variations in the diet. Ranging patterns were also related to past movements, since gorillas tended to avoid areas which they had recently used. This was most clearly shown whenever group 4 travelled around the bottom few hundred feet of the mountain: their return routes were usually either higher or lower than the outward routes, and thus were made through unused vegetation. Kawai and Mizuhara (1962), Schaller (1963) and Casimir and Butenandt (1973) all reported that gorilla movements were related to bamboo shoot abundance. Sabater Pi (1966) reported that the spatial pattern of fruiting (of two species in particular) determined the ranging patterns of some western gorillas. Jones and Sabater Pi (1971) suggested that the daily ranging patterns of their study groups were related to the distribution of *Aframomum* thickets: *Aframomum* was both the main food and the main night-nesting material.

7. FEEDING BEHAVIOUR AND SOCIAL BEHAVIOUR

Feeding individuals stayed further from their neighbours than did non-feeding ones: adults were seen on their own (more than 10 m from other adults) more often during travel-feeding periods than during resting periods (Table X), and most nearest neighbour distances were higher during travel-feeding periods (Table XI). Adults dispersed more than immatures (Table XI): all adult–adult median nearest neighbour distances were higher (most significantly so) during travel-feeding periods; immature–immature distances were not.

It is suggested that the animals, by feeding far apart, kept the chances of competition for food low, and certainly kept them lower than they would have been if the animals had fed at the rest period interindividual distances. Adults fed further apart than immatures, possibly because adults, who used more space and ate more food than did immatures, were potentially more severe competitors with each other than were immatures.

Agonistic encounters over food were so rare that even silverbacks, the class that supplanted others by far the most frequently, probably gained

TABLE X

Records (in percentages) of different numbers of adults within 10 m of each other during rest periods and travel-feed periods

	Nos. of adults within 10-m diam.					
	1	2	3	4	5	*n*
Rest period	33·9	40·3	19·3	4·8	1·6%	62
Travel-feed period	64·1	30·1	2·9	1·9	1·0%	103

The distribution of the records between the two periods was significantly different ($P<0{\cdot}001$).

TABLE XI

Records of distances to the nearest member of each class during travel-feed periods and rest periods

		Distances (m)					
Classes	Periods	0–5	6–10	11–15	16–20	>20	Totals
Sb–Bb	Rest		3	*3*		n.s. 4	10
	T–f			3	1	*11*	15
Sb–F	Rest	12	*9* †	4	2		27
	T–f	4	5	2	*4*	9	24
F–Bb	Rest		1	7	*3* ‡	6	17
	T–f			3	1	*11*	15
F–F	Rest	*8*	3 ‡	2	1		14
	T–f	2	4	*3*	2	5	16
Sb–imm	Rest	21 n.s.	*13* n.s.	7	1	2	44
	T- f	9	*13*	4	3	2	31
Bb–imm	Rest		11	*7* *	12	3	33
	T–f		1	2	4	*24*	31
F–imm	Rest	*32* *	17		1	1	51
	T–f	7	9	*10*	7	11	44
Imm–imm	Rest	*22* n.s.	10	2		1	35
	T–f	*13*	2	3	1	1	20

Median distances are *in italic*; symbols are placed between the distance categories chosen for comparison.
* $P<0{\cdot}001$.
† $P<0{\cdot}01$.
‡ $P<0{\cdot}05$.
n.s. = not significant.

no significant advantage, in terms of food intake, from their dominant position. However, in areas where food was less abundant, they might have done so. The nature of the encounters ranged from fighting, through pig-grunting (Fossey, 1972b), to just staring, with occasional supplantings. If food sources were localized (e.g. a single bamboo clump), agonistic interactions were more severe and often involved more than two animals (cf. Recher and Recher, 1969—birds; Chalmers, 1968b and Southwick, 1972—primates).

8. INTERTROOP AND INTERPOPULATION VARIATION

Group size, composition and diet differed between populations as well as between groups. If the parks were divided into two sections, each containing three of the six largest mountains, then the median group size in the western section (study area location) was significantly larger than that in the eastern section ($P<0{\cdot}01$): in the western it was 10 (range, 2–20; $n=17$) and in the eastern it was 5 (range, 2–9; $n=11$) (Fossey, 1972b; Harcourt and Groom, 1972; Groom, 1973). Schaller (1963) reported similar differences from samples in the two sections. There appeared to be less food and cover and more human intrusion in the eastern section than in the western one. All three factors were possible causes of the smaller group size in the former.

The main components of the gorillas' diet in the eastern section of the parks were bamboo, *Pychnostachys*, *Vernonia*, *Cynoglossum* and *Basella* (Donisthorpe, 1958; Kawai and Mizuhara, 1962; Schaller, 1963). These species differ from those reported for the western section (see Section 3.3; Schaller, 1963). This interpopulation difference in diet is greater than the intergroup difference shown in Table III. In addition, differences between the entire Virunga population and other East African populations were greater than between the two Virunga populations (Schaller, 1963). A few of the differences did not appear to be associated with the different plant distributions, but were possibly "cultural" i.e. the same species was present in two areas but eaten in only one (Schaller, 1963). A few such differences have been observed within the study area. For example, *Pychnostachys*, a fairly commonly eaten shrub in the eastern section of the parks in 1971 (pers. obs.), was also found in group 5's range, but there were no signs of it ever having been eaten. It was rare in group 4's range, but a juvenile was once seen to eat it.

9. DISCUSSION

In descriptions of activity patterns or feeding behaviour of groups or populations, it has often been the practice to combine the records from all age/sex classes. There are, however, objections to such a procedure: it disguises differences between age/sex classes and gives misleading results if, as is usual, the different age/sex classes are not equally represented, either in the population or in the records because of their different visibilities (see Chalmers, 1968b; Aldrich-Blake, 1970b). In addition, the differences between even adjacent groups and populations reported here enforces the point that generalizations based on the study of only a few groups or populations should not be accepted without question. Fossey (1974) described how one group's interactions with other gorillas disrupted that group's normal ranging patterns. Our data on the ranging of newly formed groups—different from that of established groups and the previous ranging of the new group members —demonstrates again that determinants of ranging patterns, even of non-territorial species, should not be sought only in terms of available resources, but also in terms of social factors. Struhsaker (1974) makes the same point: he found that diversity of ranging patterns was correlated with frequency of intergroup encounters.

The montane forest habitat provides an abundance of food for folivores, especially those which, like the gorilla, eat both mature and young leaves. However, a possible inference from the fact that some less common, and less commonly eaten, species were usually chosen over some more common ones (p. 428) is that, were the rarer more common, they would have been eaten more. This could imply that some foods were not, in fact, abundant and that animals were being forced to eat less preferred items (see also e.g. Klein, 1970). The above argument does not apply if the less eaten species were chosen simply because of their relative novelty.

Since no analysis was made of the chemical composition of any plant, we can only assume that the animals selected plants and plant parts with the highest usable nutrient content. The fact that other herbivores ate some plants not eaten by gorilla suggests that nutrients were present in those plants, but were less economically usable by gorilla, perhaps because of the presence of antinutritive substances (e.g. Gontzea and Paraschiva, 1968) and/or toxins (e.g. Freeland and Janzen, 1974). The plants eaten by the gorilla were not necessarily completely free of these substances, but concentrations of them might be expected to be low, since their breakdown requires energy (Freeland and Janzen, 1974). Another explanation is that nutrients were present and usable in the uneaten plants, but the eaten plants contained more useful amounts and combinations of them. That the latter explanation might sometimes be the case is suggested by the facts that the gorilla occasionally ate small amounts of the very common, but rarely eaten, species (e.g. *Conyza*), and that some uneaten species were eaten in other areas (e.g. *Pychnostachys*). If the nutrients in the uneaten plants were totally unusable, it can be assumed that the gorillas would not eat them. However, if they were only less usable than in the more commonly eaten plants, then it might be worth the gorillas' while occasionally to test the nutritive value of the uncommonly eaten plants (Freeland and Janzen, ibid.). If the plants were common in the range and found to be valuable, then the rewards of testing would be great.

Brambell (1972) reported that gorillas, which he thought were purely herbivorous, do not have a distinct fermentation chamber in their gut, so seemingly are unable to synthesize a number of essential nutrients (among them vitamin B_{12}) that are present in animal matter but not in plant matter. The data presented here show that gorillas do, in fact, eat animal matter, deliberately and inadvertently, probably in sufficient quantities to provide at least their vitamin B_{12} requirements. Dung was probably eaten too infrequently for this purpose (see Oxnard, 1969).

Because members of a group spend more time closer to each other than do members of a scattered population, the former are potentially more severe competitors with each other than are the latter, though competition could be reduced if dispersion varied with resource density (Schoener, 1971). Why, then, do gorillas live in relatively stable groups? There are two main lines of argument. First, food is abundant enough for the disadvantages of potential increased competition to be overcome by the advantages of prolonged association. These might include, for example, advantages resulting from the socialization process (Poirier, 1972), particularly those resulting from play, which might make a group-living animal better able to survive and reproduce than a non-group-living one (though see Baldwin and Baldwin, 1973b). Denham (1971) seems not to have taken these advantages into account in his theory of social organization. This is perhaps why gorillas do not fit neatly into his scheme. For example, his predicted adult sex ratios in the group (equal) and degree of sexual dimorphism (moderate) do not agree with what is found: 1 male to 1·5 females [or 1 : 2·3 if only fully mature males (silverbacks) are counted]; and marked sexual dimorphism. The second argument is that feeding efficiency is actually increased by group-living: (a) aggregations of feeding animals might indicate good food sources and so attract other animals (Krebs, 1974). Essentially, the searched area is increased. (b) Younger animals (including adults) might benefit from the experience of older ones, not only in the finding of rare resources (Rowell, 1969; Kummer, 1971), but also in the finding of the best ones. (c) Vesey-Fitzgerald (1969, 1974) and Cody (1974a) have respectively shown that buffalo and finches can effect long-term regulation of movements to allow optimal regeneration of plants between visits. If gorillas lived in a scattered population at a similar density as at present, they would have to live in extensively overlapping ranges, because ranges with little overlap would not provide each animal with a sufficient variety of food. Because of extensive range overlap, attempts at such regulation by members of a scattered population would be vitiated by frequent uncoordinated visits to the area by other individuals. The advantages to group living would then be that only as members of groups could the animals co-ordinate their movements to prevent unregulated visits to areas and, at the same time, to decrease overlap between ranges, and thus ensure that the most used areas (perhaps the areas most susceptible to misuse) are infrequently visited by strange gorillas. The consequent advantage of long-term assurance of a good food supply to group members would outweigh the disadvantages of possible immediate competition caused by their feeding comparatively close together. S. A. Altmann (1974) pointed out that this immediate competition could be decreased if the animals avoided one another's feeding paths, by moving parallel and in-line, and maintaining their distance from each other. Gorillas, however, did not so move and therefore crossed each others' feeding paths. For the gorilla, we do not think that advantage (a)—attraction to feeding aggregations—operates: first, there was no evidence that it did; and second, it would not be expected to do so, because the vegetation is so dense that differences in the sizes of aggregations are difficult to detect. We can only suggest that advantage (b)—benefit from experience of older animals—operates, but there is evidence that advantage (c)—co-ordinated regulation of movement—does (p. 439). We suggest, therefore, that the main advantages to a gorilla in group-living are those that arise from, (i) the development of a number of stable social relationships, and (ii) the co-ordination of ranging patterns to allow optimal resource use.

10. SUMMARY

1, 2. Though information from a number of groups is presented, most of it is from two groups, which varied from nine to 16 members.

3.1. Rarely were all parts of any plant eaten, and preparation techniques varied according to the part, rather than the species.

3.2. The gorillas were diurnal. They tended to have morning and afternoon travel-feeding periods separated by a midday resting period. Groups spent about 25% of the day feeding. Climate affected activity patterns.

3.3. The gorillas were selective in the choice of their diet of 42 plant species; grubs, gorilla dung and water were also consumed; no cultivated plants were eaten. Seventy per cent of feeding time was spent on 7% of the diet (three species). Leaves, shoots, and stems formed 85·8% of the diet; fruits only 1·7%. Differences between groups in the amount of time spent feeding on certain foods were related to differences in the amounts of those foods between their ranges. Individuals usually did not eat all food species available at any one spot, and they showed preferences for a few of the less commonly eaten species. Animals often moved to new feeding areas when there was still seemingly abundant food in their previous area. It is suggested that the move maintained efficiency of collection, prevented overcropping, and stimulated regeneration. Gorillas built most of their nests from non-food plant species, probably because food species made unsuitable nesting material.

4. There was seasonal variation in rainfall; correlated variations in the diet were presumably due to changing nutritional qualities in the vegetation, although bamboo shoots were the only food items which obviously changed in amount through the year.

5. Silverbacks spent the most time eating, infants the least, and the other four classes were intermediate. Immatures spent more of their feeding time up trees than did adults. There were differences between classes in their diets; it is suggested that the different diets and feeding sites of adults and immatures might have maintained a low level of competition between them.

6. The gorillas lived in overlapping home ranges; core areas were seldom entered by strange gorilla, though there was no overt territorial defence. Yearly range sizes varied with time and place, and shifted from year to year. In the study area, they were 4–8 km^2; in other areas, perhaps up to 25 km^2. It is suggested that some previous figures of range sizes were overestimates. Monthly range sizes of established groups varied proportionately to group size, but newly formed groups had abnormal ranges. Lone silverbacks had monthly ranges as large as those of established groups. Median day journeys of groups and lone silverbacks varied from 100 m to 2·5 km, but were mostly about 400 m. In some other areas, day journeys were usually about 1 km. The home range was used unequally—50% of the time in 17% of the range—and the most used parts (core areas) offered the best combination of food and safety. Ranging patterns were probably related to food distribution, but usually not overtly so; they were sometimes obviously related to social factors.

7. Feeding individuals stayed further from their neighbours than did non-feeding ones, and feeding adults stayed further apart than did feeding immatures. Agonistic encounters over food were so rare that status could rarely be related to priority to food.

8. In addition to much intertroop variation (mentioned throughout the chapter), there was interpopulation variation. For example, the median group sizes (10 and 5) in two sections of the park were significantly different. The smaller group size could be related to a poorer habitat. Interpopulation differences in diet were mainly due to different food distributions, but some might have been cultural.

If misleading generalizations about group activity patterns and diets are to be avoided, students should take into account, (a) differences between age/sex classes, and (b) differential representation of the classes in the records. In addition, since even adjacent groups may differ markedly, generalizations about populations must be based on the study of a number of groups. Because ranging patterns are affected by social factors, these, as well as resource distributions, should be considered in studies of ranging behaviour. Though gorillas lack a distinct fermentation chamber, and, therefore, cannot synthesize some nutrients that are found in animal material only (e.g. vitamin B_{12}), we suggest that they eat enough grubs to offset the lack. Preferences shown by the gorilla for a few of the less common, and less commonly eaten, species over the more common ones might indicate that the preferred species were in short supply, unless they were preferred simply because of their relative novelty. It is suggested that the advantages to gorillas of group living are mainly those that arise from (a) the development of a number of stable social relations, and (b) co-ordination of ranging patterns to allow optimal use of resources, particularly in terms of stimulation and maintenance of optimal growth of food plants.

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15

Feeding and Ranging Behaviour of a Mountain Gorilla Group (*Gorilla gorilla beringei*[a]) in the Tshibinda–Kahuzi Region (Zaïre)

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[a] The precise taxonomic position of this population is still unclear and may need further revision (Groves, pers. comm.). In this paper the most common nomenclature is used.

1. INTRODUCTION AND METHODS

1.1. Introduction

True "mountain gorillas" (*Gorilla gorilla beringei*) are found only in two regions of central Africa—the Virunga volcanoes and the Kahuzi region (Groves, 1970). The range of the Virunga gorillas is dominated by large areas of *Hagenia–Hypericum* woodland (Robyns, 1947) (Spinage, 1972) which was much more extensive until recently. The range of habitat occupied by the Kahuzi gorillas, and that of *Gorilla gorilla graueri*

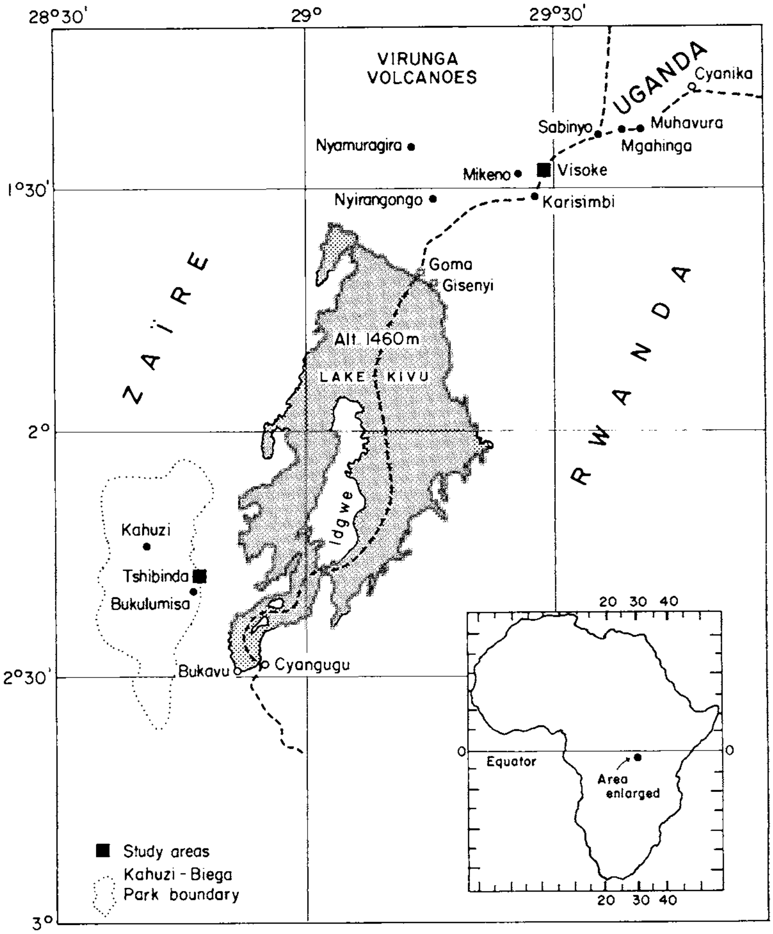

FIG. 1. Geographic regions and study areas.

(Groves, 1970), is far more variable and is probably more similar to the habitat occupied by gorillas during the Pleistocene when montane forest covered all areas over 500 m. This paper is concerned with the feeding and ranging behaviour of one group of *Gorilla gorilla beringei* which inhabits the Tshibinda–Kahuzi region of Zaïre.

1.2. Study Area

The main study area was around Tshibinda in the Kahuzi-Biega National Park. This lies approximately 100 km south-west of the Virunga volcanoes and is in the Kivu province of Zaïre (Fig. 1). The altitude of the study area was 2000–2500 m and the terrain consisted of many hills covered in various subtypes of montane forest. Several large, flat areas were covered by *Cyperus* swamps. Ten natural vegetation types were recognized (Lambinon, Marius *et al.*, pers. comm.). These are listed in Table I together with data on altitude and dominant species. An eleventh vegetation type—cultivation—was also recognized. This bordered the study area along its eastern boundary and consisted of tea and coffee plantations together with crops of beans, potatoes, bananas, manioc and maize.

Additional notable natural vegetation included tree ferns (*Cyathia manniana*) on wet slopes among the primary forest regions; *Usnea* lichen was common on many trees in the primary montane forest—especially near the swamps; *Myrianthus holstii* trees were found in localized patches amongst a mixture of old secondary/primary forest within the study areas. Large areas of ferns *Pteridium africanum* were also prevalent, especially in regions which had been repeatedly burned and cleared for cultivation. Such areas were most extensive on the south-western borders of the park near the village of Nyakalonge. Vegetation types 1–6 (inclusive) are *primary* forest types while vegetation types 7–10 (inclusive) are *secondary* vegetation types.

Temperature records at Lwiro (1680 m) show a mean minimum value during the period 1953–70 of 12·4° C, and a mean maximum value of 24·6° C. Temperature records at the highest station, Mt Bukulumisa (2100 m), during 1971 show a minimum value of 9·9° C and a maximum value of 19·2° C. During the same period the relative humidity varied between 46% (at 15.00h in August) and 82% (at 6.00h in May). The amount of precipitation increases with increased altitude, from an annual mean from 16 years of 1590 mm at Lwiro, to one of approximately 2300 mm per year in the region of Mt Bukulimisa. Most rain fell in March/April and in September–December (Meteorological records—IRSAC, Lwiro).

TABLE I

Major vegetation types in the Mount Kahuzi region

Vegetation type	Altitude	Dominant species	Other characteristic species
1. High montane forest (primary)	2000 to 2400m	*Podocarpus* sp. *Ficus* sp. *Chrysophyllum longipes* (Engl.) *Parinari* sp. *Carappa grandiflora* (Sprague) *Symphonia globulifera* L.F.	*Albizzia gummifera* (Gmel) *Newtonia buchanani* (Bak) *Strombosia grandiflora* (Hook) *Pteridium africanum* (Alston) is common in the undergrowth
2. Bamboo forest	2350 to 2600m	*Arundinaria alpina* (K. Schum)	*Polyscias fulva* (Hiern) *Conophyryngia johnstonii* (Stapf) *Pannicum* sp. (in dry areas) *Brillantaisia* sp. (in wet areas)
3. Swamp forest	2250 to 2350m	*Xymalos* sp. *Draecona* sp. *Halophyllus* sp. *Rapania pulchra* (Gilg and Schellenb.)	*Symphonia globulifera* L.F. *Syzygium guinense* (D.C.) *Coffea* sp. *Alchornea hirtella* *Toxocarpus racemosus*
4. Cyperus swamp	2200 to 2250m	*Cyperus latifolius* (Poir)	*Rapanea pulchra* (sapling) *Hypericum lanceolatum* (Lam) (saplings) *Maytenus acuminatus* (L.F.)

5. and 6. Heath types (N.B. *not* present in study area)	2600 to 3300m	*Erica arborea* (L) *Senecio* sp. *Lobelia* sp.	*Alchemilla* sp. *Deschampsia* sp.
7. Mixed secondary montane forest	2000 to 2400m	*Myrianthus holstii* (Engl.) *Neobotonia macrocalyx* (Pax) *Dombeya goetzenii* (K. Schum) *Vernonia* sp. *Hagenia abyssinica* (Gmel) *Alangium chinense* (Lour)	*Urera hypselodendron* (Wedd) *Basella alba* (L) *Serichostachys scandens* *Cissus* sp. *Lactuca* sp.
8. Open vegetation dominated by *Hagenia abyssinica*	1800 to 2100m	*Hagenia abyssinica* (Gmel) (N.B. this formation is much smaller than that seen in the Virunga)	*Pteridium* sp. *Graminae*—many sp.
9. Meadows	2300m	*Imperata* sp. *Pennisetum purpureum* (K. Schum)	*Hyparrhenia* sp. *Setaria megaphylla*
10. Herbaceous (N.B. at roadsides and in recently cleared areas)		*Vernonia* sp. *Maesa lanceolatum* *Pennisetum purpureum* (K. Schum) *Brillantaisia* sp. *Lobelia* sp.	*Urera hypselodendron* (Wedd) *Basella alba* (L) *Helichrysum* sp. *Clematis* sp. *Cissus* sp.

After Marius, 1973.

1.3. Field Methods

Data were collected from trail signs and direct observation on both unhabituated and habituated gorillas (Goodall, 1974). Particular family groups were studied over periods ranging from one to seven months—the longest period being spent with one group in the Tshibinda area, and this became the "main study group". It was composed of one silverback male, one blackback/silverback male, three blackbacked males, four adult females, three subadults (unknown sexes), two juveniles, five infants, plus one semiperipheral silverback male. At the start of the study the group had been partially habituated by intermittent contacts made by Monsieur Adrien Deschryver (Conservateur—Parc National du Kahuzi-Biega) during the previous three years. The group was followed by the present author, almost on a day-to-day basis, during April–October (1972).

Each day's trail made by the group during the study period was followed and paced. If a day was missed from field work then the entire gorilla trail—from the place they were last seen to their present position—was followed and recorded the next day. In this way 209 of the total 213 day journeys were recorded accurately. Four further trails in the bamboo forest were so criss-crossed that it was impossible to record their exact route. The location of all 213 night nest-sites was also recorded. The gorillas' daily routes were carefully mapped onto a transparent overlay superimposed upon stereoscopic aerial photographs of the study area (scale 1 : 28 000). This method enabled the locations to be pin-pointed usually to within 100 m on the ground. The daily routes were later transposed onto detailed vegetation maps (scale 1 : 28 000). These were divided into one-centimetre square quadrats (280 × 280 m on the ground) for the purposes of calculating the home range sizes of the main study group and the relative cover of the various vegetation types within the home range, Table IIa. The number of visits paid to each vegetation type by the group throughout the study period was recorded daily, and monthly summaries were prepared, Table IIb.

Prolonged visual contacts with the group (i.e. of more than 15 minutes duration) were not possible each day. This was due mainly to the problems, and the real dangers, involved in making extremely close contact with partially habituated gorillas in areas of dense vegetation. During the seven-month period, 103 prolonged visual contacts were made providing 273·4 hours of detailed observation time as follows:

April 41·24 hr (11); May 50·19 hr (16); June 39·33 hr (17); July 50·07 hr (13); August 38·06 hr (17); September 30·33 hr (13);

TABLE II

(a) *The relative percentage cover of each vegetation type (1–11) in the home range of the main study group (Tshibinda–Kahuzi)*

	Primary vegetation types				Secondary vegetation types				
	1	2	3	4	7	8	9	10	11
% cover in home range	11·8	5·8	2·1	11·6	62·6	0·2	3·1	2·8	0
		(31·3)					(68·7)		

(b) *The numbers and percentages of crossings of each vegetation type within the home range area of the main study group*

		Nos. primary vegetation types				Secondary vegetation types					
Month	%	1	2	3	4	7	8	9	10	11	Totals
Apr.	no.	8	1	2	3	29	0	0	12	0	55
	%	14·5	1·8	3·6	5·5	52·7	0	0	21·8	0	
May	no.	3	2	2	2	31	3	0	15	0	58
	%	5·2	3·4	3·4	3·4	53·4	5·2	0	25·9	0	
June	no.	24	5	9	13	26	2	1	20	0	100
	%	24·0	5·0	9·0	13·0	26·0	2·0	1·0	20·0	0	
July	no.	18	2	1	6	31	4	3	22	1	88
	%	20·5	2·3	1·1	6·8	35·2	4·5	3·4	25·0	0·2	
Aug.	no.	24	8	9	14	29	4	2	19	0	109
	%	22·0	7·3	8·3	12·8	26·6	3·7	1·8	17·4	0	
Sept.	no.	26	21	12	21	25	0	0	8	0	113
	%	23·0	18·6	10·6	18·6	22·1	0	0	7·1	0	
Oct.	no.	24	31	1	19	27	0	0	5	0	107
	%	22·4	29·0	0·9	17·8	25·2	0	0	4·7	0	
	Totals	20·2	11·1	5·7	12·4	31·4	2·1	1·4	16·0	0·2	(630)
	%		(49·4)					(51·1)			

October 23·35 hr (16) (N.B. the number in brackets refers to the number of prolonged visual contacts, numerous other brief encounters are not included).

Plant samples were identified at the herbarium in IRSAC (Lwiro). Those intended for nutritional analysis were dried for several hours at 96° C, cooled in a desiccator and then sealed in separate polythene bags. They were later analysed for crude fibre content, total nitrogen and gross energy content. Monthly summaries of all data were prepared and the feeding and ranging behaviour of the gorillas were analysed in relation to these (Goodall, 1974).

2. FEEDING BEHAVIOUR

2.1. Dietetic Diversity

At least 104 food plants, comprising 42 families, were eaten by gorillas of the two Kahuzi-Biega study areas. Only two of these lacked personal verification (they were pointed out by pygmy trackers). The remainder were either observed to be eaten or found as food remnants on the gorilla trail, or both. The main study group ate over 160 parts of at least 78 of the known food plants in the Tshibinda area. The complete list of food items comprises 33 vines, 25 herbs, 20 trees, 13 shrubs, six grasses, four ferns and three semiparasites. Further details, including a complete species list, are given in Goodall (1974). From data collected via trail signs and visual sightings the food plants were given a rating for degree of relative importance in the diet and classified into the following groups:

1. *Main food items* (*****)	Plants with a wide and plentiful distribution, eaten throughout the year but with some seasonal variation in amount, e.g. *Urera hypselodendron*, *Basella alba*, *Taccaza floribunda.*
2. *"Preferred" food items* (****)	Plants with a very patchy distribution, often rare; these are almost always eaten when they are encountered, usually in great quantities, e.g. *Achyrospermum omicranthum*, *Galineria coffeoides*, *Coffea* sp., and species of semiparasitic *Loranthus.*
3. *Occasional food items* (** and ***)	Plants which may have either a wide or a patchy distribution but may or may not be eaten when encountered, e.g. *Hypoestes* sp., *Piper capense*, *Hagenia abyssinica.*
4. *Rarely eaten food items* (*)	Plants with varied distribution but only seen to be eaten on one or two occasions, e.g. *Albizzia gummifera*, *Sericostachys scandens*, *Begonia* sp., *Dombeya goetzenii.*
5. *Seasonal food items* (*****)	Plants which are eaten in large quantities when they become seasonally abundant, e.g. fruits of *Myrianthus holstii* and *Syzygium guinense*, bamboo shoots (*Arundinaria alpina*).

Although the main study group had opportunities to eat eggs or helpless chicks of several species of birds, I found no indication that these were ever eaten. In fact on several occasions intact eggs and squabs were found on or at the side of the trail left by feeding gorillas. While chimpanzees in the study area frequently dug open the underground nests of *Trigona* bees and ate honey, grubs and adult bees, the gorillas were seen to pass near to, and even over, nests of these stingless bees without attempting to feed. No traces of animal matter of any kind were ever found in the many samples of dung which were analysed.

2.2. Foraging and Feeding Techniques

In general the group was spread out while foraging, the maximum spread depending upon the local vegetation types and the food items being eaten. When feeding on *Ensete* sp. (the wild banana) most of the group concentrated around one or two of these large trees for periods up to one or two hours until the plant was almost completely demolished. While foraging in either old secondary forest or bamboo forest, the group often spread out over distances of up to 200 m, and sometimes split into two subgroups.

Animals from the main study group were seen to feed in almost every conceivable position, from sitting on the ground to hanging in the trees by one foot and one hand, partly upside-down and anything up to 40 m above the ground. The feeding posture adopted was greatly influenced by the food item being consumed and the local vegetation type. For example, the herbaceous vine *Basella alba*, one of the main food items in Kahuzi-Biega, usually occurred in great quantities in open areas associated with *Pteridium* ferns and other low herbaceous growth. Gorillas would typically sit down, reach out with one or both hands and pull in patches of this vine which were entangled in the nearby vegetation. Leaves were then either bitten off directly or a number were collected manually and then placed in the mouth. The leaves of many vines, particularly *Urera hypselodendron*, were collected by rapidly pulling the stem between clenched fingers and the resulting bunch was then eaten (cf. Casimir, 1975) although sometimes they were discarded and only the bark was eaten. This behaviour emphasizes the importance of visual verification of all food items, for many can easily be missed by reliance on trail signs alone. Feeding animals sometimes stood bipedally to reach up and pull down low hanging vines from nearby shrubs. When feeding intensively the gorillas often pushed leaves rapidly into the mouth with one hand while collecting more with the other hand. The bark of woody vines such as *Urera hypselodendron* was either bitten off directly with the incisor teeth or scraped off while the vine was pulled between clenched teeth. Large quantities were eaten by all gorillas except suckling infants.

A marked vertical distribution of feeding animals was often observed, especially in secondary forest regions, with the largest silverback usually feeding on the ground and the rest of the group feeding above ground. Some independent infants climbed highest (up to 40 m), while juveniles were seen to climb higher than females, and the females higher than males—though one very large blackbacked (almost silverbacked) male was frequently seen at heights of up to 35 m. However, when feeding on the leaves of semiparasitic *Loranthus* sp. or the fruits of *Myrianthus* or *Syzygium*, all animals were seen to climb and even the largest silverbacked male, who must have weighed at least 200 kg, was seen to climb over 20 m high—even among hanging vines.

Only a few herbaceous plants such as *Rubia cordifolia*, *Galium simense*, three species of epiphytic ferns, and possibly a few herbaceous vines on occasions, were seen to be eaten in their entirety. Part or parts of other food plants, such as leaves—especially upper leaves and growing tips—bark, flowers, fruits, shoot, root, pith and even dry wood, were consumed in varying quantities. While only one part was eaten from the majority of food plants, three or four parts were eaten from some of the main food items. The gorillas used their hands, lips, teeth and jaws in extremely well co-ordinated movements in order to collect, prepare and ingest food items ranging from tiny succulent fruits to tough fibrous bark or pith from mature trees. Detailed descriptions of the feeding techniques used to deal with this wide variety of food items are given by Goodall (1974).

Drinking. The gorillas of the main study group apparently obtained most, if not all, of their water requirements from the herbs and vines which were eaten during the rainy season; from the juicy *Myrianthus holstii* fruits and the saturated leaf bases of *Cyperus latifolius* during the dry season; from bamboo shoots during the latter wet part of the year and from the pith of wild bananas at various times throughout the year. However, on several occasions trail signs, especially in the swamps during the dry season, strongly indicated that gorillas had pulled vegetation aside to expose a small stream or trickle of water. On two separate occasions members of the main study group were seen to lick dew from nearby leaves while they were still in the nests early in the morning. When feeding on the pith of the wild banana (*Ensete* sp.) the gorillas were seen to ingest large amounts of the copious cell-sap present in this food item.

2.3. Nutritive Values of Vegetation Samples

A variety of vegetation collected from many parts of the study area was analysed for nutritive values in terms of gross available energy and protein. The results for 39 items known to be eaten by the study gorillas revealed gross energy values ranging from 1467–2472 kJ/100 g (dry matter) and crude protein values from 2·18–47·68 g/100 g (dry matter). The percentage of crude fibre in 22 of these samples ranged from as low as 7·41% (in new bamboo shoots) to as high as 43·07% (see Table III). The mean nutritional values of the remaining 28 samples showed no significant differences, in terms of gross available energy and protein, to the known food plants (t-test). These plants appeared to be as readily available as known food items—in many cases growing with them in mixed stands. Some were eaten by *Pan troglodytes* and several species of *Cercopithecus*. Although no crude fibre analyses were carried out on these samples it seems unlikely that these were significantly different from known gorilla food items.

It is obvious that whatever the gorillas actually gain from their food, in terms of both energy and protein, will depend not only on their intrinsic availability in various food items but also on the efficiency of the gorilla digestive system. Therefore, in order to arrive at what Mitchell (1964) calls "the truly metabolizable" energy of a diet, i.e. *net* available, various debits have to be made from the gross available values owing to losses via indigestibility, urine and the specific dynamic action (SDA) of a given ration.

According to Dr T. Lawrence (pers. comm.) the losses due to these three factors are generally in the order of 70–80%, 5–10% and 15–20% respectively. Unfortunately it was impossible to collect accurate data on each of these losses for free-living gorillas, and no animals were available in captivity which were feeding on a "wild-type" diet. However, an attempt has been made (Goodall, 1974) to estimate values of the net available energy (and protein) in the plant samples from Kahuzi.

There is a high negative correlation between the digestibility of vegetable diets and their crude fibre content. Regression curves of these relationships for various farm animals are given by Mitchell (1964). Since pigs are animals of comparable size to gorillas, and also are non-ruminants, it was decided to use the regression curve given for these animals in order to estimate the digestibility values of some of the Kahuzi plant samples. By this method it was found that they varied from as high as 84% digestibility in bamboo shoots and the leaves of the herbaceous vine *Basella alba*, to as low as 38% for the leaves of *Smilax*

TABLE III

Nutritive values of some plants found to be eaten by the main study group

Name	Part eaten	Gross energy kJ/100 g	Gross N_2 (%)	Gross protein ($N_2 \times 6{\cdot}25$) (%)	Crude fibre (%)	Digestibility (%)	Metabolizable energy/100 g	Metabolizable protein/100 g	Relative amount eaten
U. hypseledendron	Leaves	1716	2·85	17·81	14·99	75·0	1108	12·0	*****
U. hypselodendron	Bark	1800	1·87	11·68	37·93	43·0	500	6·0	*****
U. hypselodendron	Fruit	2351	4·77	29·81	25·83	60·0	1008	12·8	***
B. alba	Leaves	1802	4·82	39·06	7·29	84·0	1391	30·0	*****
T. floribunda	Leaves	2016	2·98	18·62	16·46	72·0	1209	11·2	****
T. racemosus	Leaves	2162	2·03	12·68					***
Ensete sp.	Leaves	2066	3·46	21·62	27·26	58·0	826	8·6	*****
Ensete sp.	Pith	1780	0·59	3·68	23·17	64·0	864	1·8	*****
A. alpina	Shoots	1909	7·63	47·68	7·41	84·0	1474	36·8	*****
M. holstii	Leaves	1897	3·15	19·68	24·72	68·0	994	12·0	****
M. holstii	Fruit (flesh)	2056	1·76	11·00	16·58	72·0	1233	6·6	*****
C. latifolius	Leaf base	1595	1·47	9·18	29·83	55·0	569	3·3	*****
Lactuca sp.	Leaves	1749	3·28	20·50					****
R. cordifolia	All	1601	2·26	14·12					***
E. woodfordioides	Leaves	1918	2·79	17·43	11·41	80·0	1370	12·5	****
G. braunii	Leaves	2191	2·46	15·37					****

Polypodium sp. (1)	All	1820	1·91	11·93				****
Polypodium sp. (2)	All	1911	2·44	15·25				?
P. capense	Leaves	2062	5·91	36·93	16·94	72·0	1238	22·1	***
Chrysophyllum sp.	Fruit	2472	2·45	15·31	24·9	62·0	1131	7·0	***
Shefflera sp.	Bark	1880	1·22	7·62	40·78	41·0	294	1·2	****
S. kraussiana	Leaves	2092	2·43	15·18	43·07	38·0	239	1·7	***
A. omicrantham	Leaves	1878	4·73	29·56					****
Hypoestes sp.	Leaves	1776	3·82	23·87					**
R. abyssinicus	Leaves	1875	5·24	32·75	34·39	50·0	535	9·4	****
S. guinense	Fruit (flesh)	2141	2·09	13·06	12·17	78·0	1468	9·0	*****
P. purpureum	Stem	1547	0·99	6·18					***
Brillantaisia sp.	Leaves	2099	4·62	28·87					*
T. cordifolia	Leaves	1753	2·43	15·18					***
Embelia sp.	Leaves	2040	2·26	14·12					***
G. simense	All	1698	2·29	14·31					**
M. punctata	Leaves	1793	6·77	42·31	21·17	66·0	923	21·8	**
M. cordata	Leaves	1892	3·09	19·31					**
Helichrysum sp.	Leaves	1537	3·21	20·06	21·23	66·0	790	9·7	***
Eucalyptus sp.	Bark	2031	0·35	2·18					*
I. niamiamnensis	Leaves	1746	4·99	31·18					**
A. gummifera	Leaves	2005	7·30	45·62	12·47	77·0	1346	30·6	*
S. scandens	Leaves	1870	6·57	41·10	19·09	70·0	1070	23·5	*
D. goetzenii	Leaves	2014	4·33	27·11					*

kraussiana. Assuming that these losses due to indigestibility were equal to 70% of the total losses, further allowances were made for urinary losses of 10%, and those due to SDA of 20%. Finally, deductions for such total losses were made from the gross available values for each plant sample. The resulting estimates of *net* available metabolizable energy and protein are listed in Table III.

2.4. Theoretical Nutritional Requirements and Estimates of Possible Intakes of the Study Animals

Since data are available on both the energy and protein values of all the main food items of the study gorillas, and also of many minor food items, it is possible to speculate on the daily intakes of the study animals and relate this to their theoretical nutritional requirements.

The total wet weight intake of food per day was estimated for various age/sex classes of the study animals. Based on calculations made from the daily dung output, the wet weight intakes for an adult silverback male and an adult female gorilla were estimated to be 30 and 18 kg per day respectively (Goodall, 1974). Calculations of daily intakes based on direct observations of animals feeding on single food items, such as bamboo shoots and *Myrianthus* fruits, for prolonged periods of time indicated that the estimations based on dung output were realistic ones.

Since it would obviously be impossible to simulate the actual daily "menu" of the study animals the energy and protein values for two very simplified versions have been worked out as shown in Table IV.

It can be seen that equal proportions of three main food items, *Basella* (leaves) and *Urera* (bark and leaves), would yield some 45 530 kJ and 560 g protein/30 kg wet weights. A similar amount of bamboo shoots will yield slightly less energy i.e. 44 220 kJ but double the amount of protein at 1104 g. Thus, these are possible *net available* values for an adult weighing some 200 kg. The relationship between body weight and basal metabolic rate (BMR) is discussed by Brody (1945) who suggests

$$\mathrm{BMR} = 70\,W^{0.75}\ \mathrm{kcal/day}\ (W = \mathrm{wt\ in\ kg}).$$

In a study of 120 species of zoo animals, Evans and Miller (1968) found that the voluntary calorie intakes were almost exactly twice that required for basal metabolism. Examination of Table IV shows that the estimated net available energy for both a 200 kg animal and a 100 kg animal (equivalent to an adult male and an adult female gorilla respectively) are almost three times the theoretically predicted value for their basal metabolic rate. Regarding protein levels, Bilby (1968) refers to a figure of 1 g protein per kg body weight per day being a useful

TABLE IV

Simplified menus for (A) = 200 kg animal and (B) = 100 kg animal, to show the nutritive values of each

Food item	Wet weight of intake (in kg)	Dry weight of intake (in kg)	Available water (in litres)	Net available energy (in kJ)	Net available protein (in g)
(A) 200 kg animal	(i) Three typical main food items eaten in secondary forest areas				
Basella (leaves)	10·0	1·0	9·0	13 910	300
Urera (leaves)	10·0	1·5	8·5	16 620	180
Urera (bark)	10·0	3·0	7·0	15 000	90
Totals	30·0	5·5	24·5	45 530	570
	(ii) Bamboo shoots—eaten almost exclusively when in season				
Bamboo (shoots)	20·0	2·0	18·0	29 480	736
Bamboo (shoots)	30·0	3·0	27·0	44 220	1104
*cf. Theoretically predicted values for a 200 kg animal/day =				(15 560 BMR)	(200)
(B) 100 kg animal	(i) Three typical main food items eaten in secondary forest areas				
Basella (leaves)	6·0	0·6	5·4	8346	180
Urera (leaves)	6·0	0·9	5·1	9972	108
Urera (bark)	6·0	1·8	4·2	9000	108
Totals	18·0	3·3	14·7	27 318	396
	(ii) Bamboo shoots—eaten almost exclusively when in season				
Bamboo (shoots)	18·0	1·8	16·2	26 352	662
*cf. Theoretically predicted values for a 100 kg animal/day =				(9252 BMR)	(100)
Compare					
"Guy"—220 kg adult male gorilla in London Zoo receives/day (N.B. *gross* values)				28 060	222
A 200 kg pig receives/day (N.B. *gross* values)				30 206	117

guide to the protein requirements of man. It can be seen from Table IV that the figures for net available protein for both 100 and 200 kg animals are between three and six times greater than this theoretical value.

It must be stressed here that the gorillas could do even better than these simplified estimates by eating more leaves of *Basella alba* or other similarly highly digestible items with high gross nutritive values. Examples of alternative food items like this would be the leaves of *Piper* *capense* and *Achyrospermum omicranthum*, both of which are listed as "preferred" food items, i.e. found only in some areas but usually eaten whenever found. In addition all gorillas were seen to choose mainly the upper leaves and growing tips of almost all food items. Thus they would get higher values than indicated from the plant samples which were analysed since I was frequently forced to collect older leaves from some plants in order to have sufficient for analysis.

All animals have additional energy requirements to those for BMR i.e. growth = 2–3 × BMR (Abrams, 1968) e.g. movement and lactation [though lactating females may well increase their food intake (Abrams, 1968)]. It would appear from the analyses that the herbivorous diets of the Kahuzi gorillas provide ample energy and protein to meet these requirements. In particular, the annual new shoots of bamboo have high protein levels. Since these are eaten in vast amounts during September/October it is possible that the gorillas build up reserve energy and fat levels from this item. In turn this may influence the periodicity of births—but unfortunately no evidence is available to confirm or deny this possibility.

One further aspect of the nutritional habits of free-living gorillas is that they apparently rarely drink free-standing water. It can be seen from the data presented in Table IV that an adult silverback male gets between 24 and 27 litres of water per day from 30 kg of food and an adult female gets 15 to 16 litres from 18 kg of food. Analysis of the dung showed that it contained approximately 80% water (possibly 90% when they were feeding on young bamboo shoots). Therefore, if we assume for an adult male that approximately 4 litres are lost per day in the dung, a further 4 litres in urine losses and 2 litres in evaporation losses, he still has some 14–17 litres of water available for metabolism. In these circumstances it is hardly surprising that they only rarely drink free-standing water.

3. FEEDING AND RANGING BEHAVIOUR

3.1. Home Range Size and Day Journey Length

During the seven-month period (April–October inclusive) the main study group were found to visit 256 quadrats within the study area. A further 32 quadrats, which had not been visited but were surrounded by other quadrats which had, were included in the final home range total of 288 quadrats—or 22·6 km^2. However, in the hilly terrain of this region a correction factor of × 1·5 was applied (Goodall, 1974, p. 191), giving a final value of 34 km^2. This is smaller than the 40–50 km^2

suggested by Casimir and Butenandt (1973)[a] for a neighbouring group in the Mt Kahuzi region, but considerably larger than the home range estimates for gorillas in other regions, such as those given by Schaller (1963),[b] Goodall (1971), Jones and Sabater Pi (1971) and Fossey (1974).

During the seven-month study period the trails left by foraging and wandering animals took every conceivable form, consisting of straight lines, zig-zags, curves and even ellipses and circles. In consequence the straight-line internest distances were often considerably less than the actual day journey of the group. Each day's trail was different. Occasionally the group followed old elephant tracks, and even more recent poacher's paths, through the forest. Some paths were used repeatedly—especially when the group moved from one area to another. However, the group sometimes suddenly changed direction, branched off a good trail, and made their own way through the forest. Each day journey was paced, or paced and estimated, over the whole seven-month period. Wherever possible the main trail left by the large silverback was followed, and all distances recorded are in relation to the night nest of this animal.

The total range of day journeys recorded for the main study group at Tshibinda was from 200 paces to 4850 paces (mean 1511, s.d. 837). Each pace can be taken as approximately equal to 0·7 m—thus giving a range of 140 m–3·4 km. Although heavy rain temporarily halted movements, there was no direct correlation between day journey length and rainfall. Monthly summaries of all day journeys are shown in Fig. 2 where considerable variation can be seen in the data both within and between months.

These day journeys were compared on a month-to-month basis (t-test) see Table V. It was found that:

(a) day journeys were low during April, May and June with mean values not significantly different between the three months;

(b) there was a significant increase in mean day journey from June–July ($P = < 0{\cdot}001$), which was further increased during August and September;

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[a] When calculating the home range area of Casimir's study group I believe that these authors have erroneously included data (Oct. 1971–Feb. 1972) on the movements of *another* group whose home range lay to the north. This was the group which became my "main study group" in April 1972. By calculating range size and usage almost entirely from trail signs, which were often unconfirmed by visual sightings, they are perpetuating the mistaken belief that the home ranges of the two neighbouring groups are completely interchangeable. This is not so. However, the trails of the two groups did cross on several occasions—hence the unwary tracker could easily follow the "wrong" group unless visual identifications were made.

[b] I believe that Schaller made his calculations using an incorrect scale for the aerial photographs from which he drew his maps. For further details see Goodall, 1974, p. 230.

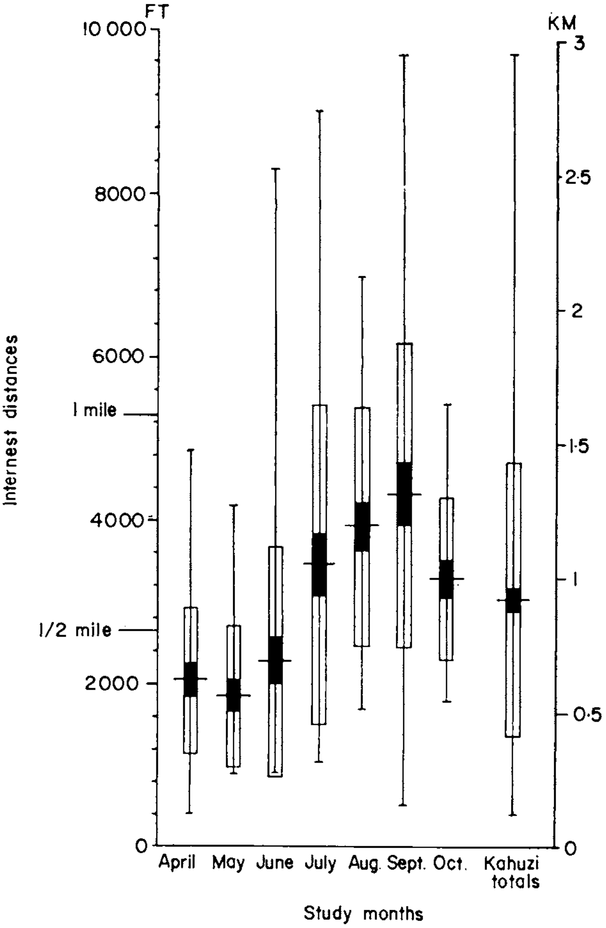

FIG. 2. Day journeys (main study group).

(c) there was a significant decrease in mean day journey length from September to October ($P = <0{\cdot}001$). However, the October mean was still higher than that in June ($P = <0{\cdot}001$).

3.2. Differential Utilization of Home Range

The main study group visited and utilized different areas within their home range at differing rates and times during the study period. The 256 quadrats which were entered within the home range received a total of 805 visits. The frequency and location of these visits are shown

TABLE V

Comparisons of mean monthly internest distances for main study group, showing the distribution of "d" and its significance value if any

	April	May	June	July	Aug.	Sept.	Oct.
April		0·78	0·76	3·62*	6·0*	5·92*	4·08*
May			1·37	5·16*	6·69*	6·46*	5·64*
June				2·7†	4·47*	4·74*	3·12†
July					1·07	1·75	0·41
Aug.						0·89	1·94
Sept.							2·59†
Oct.							

Significance values indicated are: * $P \leqslant 0·001$; † $P \leqslant 0·01$.

in Fig. 3 and the distribution of visits per quadrat in Fig. 4. It was found that:

(a) 32 quadrats inside the boundaries of the home range were *never* visited during the study period.

(b) 50% of all visits were recorded from a total of only 57 quadrats. Ten quadrats accounted for 134 entries—one quadrat alone being entered 15 times.

The study area was a mosaic of nine of the 11 vegetation types present in the Kahuzi area (see Table IIa). The home range area included 68·7% of secondary vegetation types and 31·3% of primary vegetation types. Until this area was granted National Park status (in November 1970) extensive patches of forest were subjected to "slash and burn" types of agricultural usage. They were later also used for grazing cattle (Deschryver, pers. comm.). Areas abandoned after a few years of cultivation thus formed pockets of secondary regenerating forest of varying age, species composition and physiognomy. These were particularly extensive in the eastern section (near the present park boundary). More westerly areas contained primary forest vegetation types, some of which, especially *Arundinaria alpina* and *Cyperus latifolius*, were very localized (see Goodall, 1974 for vegetation maps). The numbers of visits paid to each vegetation type are shown in Table IIb.

A comparison of the resources of the quadrats which were never visited and which were frequently visited reveals that, of the 32 quadrats which were not visited during the study period:

17 contained large areas of *Cyperus* swamp or a mixture of swamp and forest vegetation;

three contained entirely or mainly primary montane forest vegetation;

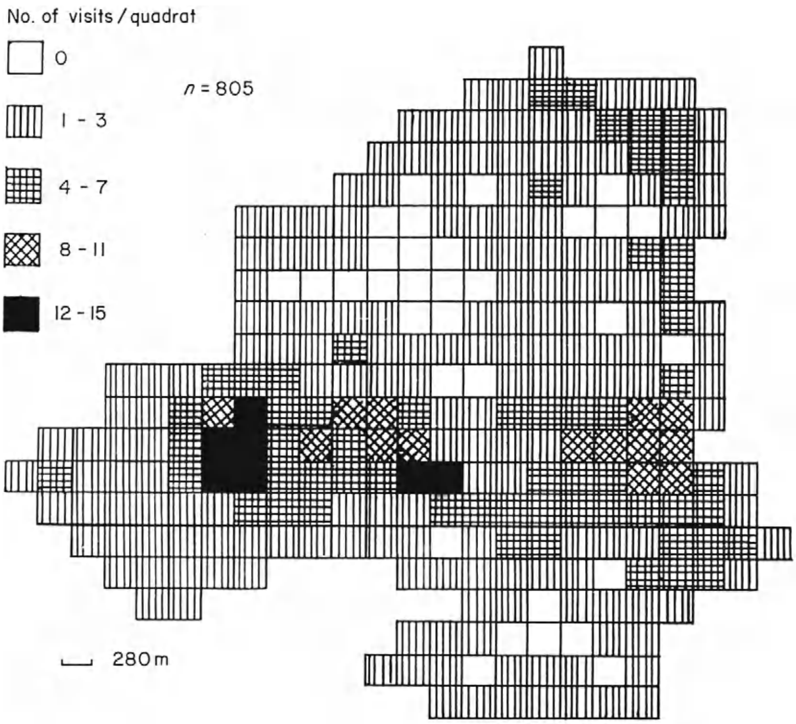

Fig. 3. Numbers of visits to quadrats in home range during seven consecutive months.

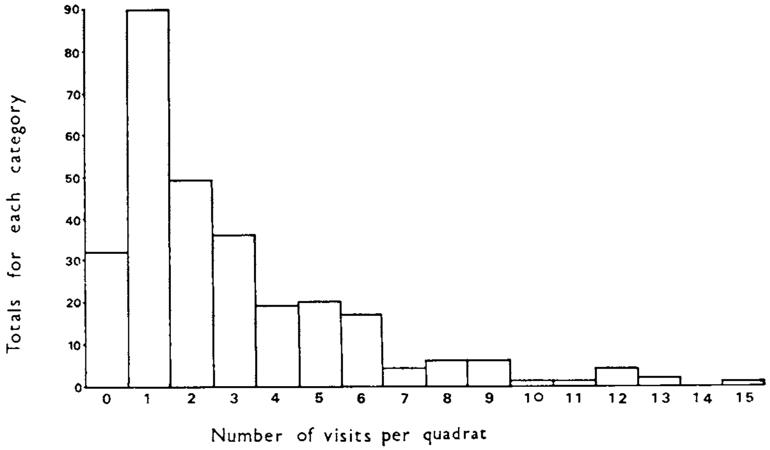

Fig. 4. Home range utilization.

five contained very large areas of young *Hagenia* trees and open, scrub-like vegetation;

seven contained secondary vegetation types.

The first 17 quadrats and the following three of the above list are situated either in the centre or near the borders of the very large *Cyperus* swamp in the north-eastern section of the home range. The five quadrats containing the young *Hagenia* trees were very poor feeding areas and were exceptionally dehydrated during the dry season. The final seven quadrats all contained secondary vegetation with an abundance of available food, but all were in the south-eastern section of the home range, across the tarmac road from the main part of the range and in an area frequently visited by another gorilla group. During the period of investigation the main study group did not spend much time in this section of their home range—despite the fact that abundant secondary growth was available during the rainy seasons.

Ten quadrats received ten or more entries. Six were in an area of bamboo forest/swamp and swamp/forest mixture, two were in an area containing swamp and several large *Myrianthus* tree "crossroads" of many previous trails of the main study group, while the remaining two contained mainly luxuriant secondary forest growth and also more *Myrianthus* tree "crossroads".

3.3. Monthly Variation of Quadrat Visits

The summaries of all monthly quadrat visits are contained in Table VI. A chi-squared test showed that the data were not homogeneous

TABLE VI

Monthly totals of visits and revisits per quadrat in their home range by the main study group

No. of visits per quadrat	Totals/month paid to each category							
	Apr.	May	June	July	Aug.	Sept.	Oct.	Totals
1	30	50	53	58	61	38	21	311
2	11	9	8	32	25	26	18	129
3		2	2	2	15	7	5	33
4			1	4	4	7	2	18
5				2	2	3	2	9
6						1	0	1
7						1	1	2
8							1	1
	41	61	64	98	107	83	50	504

($P = <0{\cdot}001$). Examination of these data shows the following monthly trends.

(a) There was a gradual increase in the number of total *visits* per month (from 52 in April), up to a maximum of 183 in August.

(b) Similarly there was a parallel increase seen in the total number of different quadrats visited per month (from 41 in April) up to a maximum of 107 in August.

(c) Both of these trends were reversed during September and especially October; during this month the total number of different quadrats visited per month [(b) above] fell to 50.

(d) There was a differential distribution of visits and revisits per quadrat per month as follows:

April, May, June: 97% of all visits were two or less per quadrat; only 3% of all visits/revisits were three or more.
June/July: 85% of all visits were two or less per quadrat; 14·1% of all visits/revisits were three or more.
September/October: 77·5% of all visits were two or less per quadrat; while 22·5% of all visits/revisits were now three or more per quadrat, up to a maximum of eight visits per quadrat.

(e) the rate of re-crossing previous trails was highest in October.

Thus the patterns of home range utilization recorded for the main study group at Tshibinda–Kahuzi can be summarized as follows.

The day journeys during the wet season months of April, May and early June were not extensive and were mainly restricted to localized areas of open secondary regenerating forests. However, with the advent of the dry season in mid-June, and the corresponding decrease in both the abundance and regeneration of food plants (especially vines) in the exposed secondary forest areas, the main group was observed to increase significantly the length of the day journeys, the total number of quadrats visited (and hence monthly home range size) and the number of visits and revisits to various quadrats. This behaviour was also correlated with the seasonal appearance of the fruits of *Myrianthus holstii* which were eaten by the study animals in vast amounts during this time.

As the fruiting season of this species came to an end in early September, the new vegetative shoots of bamboo (*Arundinaria alpina*) were appearing above the ground in increasing numbers in the localized stands of bamboo forest. The behaviour of the gorillas showed significant decreases in day journey length and monthly range size, and increases in the revisiting of localized areas of bamboo at this time. Large amounts of the fruits of *Syzygium guinense* and the basal parts of *Cyperus latifolius* were eaten near the end of October from the localized concentrations of these species which occurred in or at the sides of the swamps and near the bamboo forest.

The nesting habits of the gorillas were not found to influence their migrations, for the gorillas generally nested wherever they happened to be feeding near nightfall and used whatever vegetation was available in the immediate vicinity to construct nests—unless they were in either *Cyperus* swamp or pure stands of bamboo, in which case they would travel to the mixed forest interface to nest. Thus there were no permanent or even regularly used nest-site locations, nor were any particular types of vegetation used exclusively for the construction of individual nests (Goodall, 1974).

By November the open secondary forest areas had an abundance of new growth after the late rains and almost all the traces of heavy feeding by the main study group earlier in the year had disappeared. According to Adrien Deschryver (pers. comm.), Conservator of the Kahuzi-Biega National Park, the main study group moved back to these areas by December, thus repeating the annual cycle which, according to the most experienced pygmy tracker, has been the same pattern during the 15 years or more he has been hunting gorillas in this area.

4. DISCUSSION

4.1. Dietetic Diversity and the Selection of Food Items

Lists of gorilla food plants supplied by Schaller (1963) and Goodall (1971) indicate a food repertoire of some 40 different species for the gorillas of the Virunga volcanoes region. The gorillas of the Kahuzi region ate a much wider variety. The total of 104 food plants recorded by Goodall (1974) in Kahuzi is four more than the combined total listed by Schaller (1963) for all six geographic regions visited by Emlen and himself. In view of the far greater diversity of forest types, and therefore of different plant species, which are present in the Kahuzi region in comparison with the Virunga region, these findings are in agreement with the prediction of Levins and MacArthur (1969), i.e. that polyphagy is more likely:

(a) the greater the probability of failure to find a known suitable plant;

(b) the greater the proportion of unknown, suitable plants;

(c) the lower the proportion of unknown, unsuitable plants.

Visual sightings revealed that the Kahuzi gorillas selected their diet carefully. Some of the rampant herbs and vines grew in tangled masses, with their stems and leaves completely mixed together—yet, out of such tangles, feeding animals were observed regularly to pick out only the leaves of known food plants and to reject others either with their fingers or lips. Such careful selectivity was not confined to interspecific choice for it was also exercised within the various species. In some food plants leaves were eaten, while in others only the bark or stem was eaten. In extreme cases only some leaves (usually the younger ones) or even parts of these leaves, or the growing tips of the stems, were eaten while others were ignored. On many occasions the cambium layer was seen to be scraped out from bark of species such as *Myrianthus* or *Schefflera*. From *Hagenia abyssinica* the small side branches were split open and the inner pith was excised and eaten.

In attempting to examine the selectivity of food items by mountain gorillas, I have drawn up a list of factors which could possibly influence the food selectivity of free-living mountain gorillas as follows.

(1) *Abundance and availability* of the various plant species—including the influences of seasonality and interspecific competition.

(2) *Nutritive value* in terms of energy, protein, vitamins, trace-elements, minerals and water.

(3) *Taste* (? due to presence of plant secondary compounds, Freeland and Janzen, 1974).

(4) *Smell or odour.*

(5) *Size, shape and texture.*

(6) *Preparation* necessary to render it ready for ingestion.

(7) Physical action in the *digestive system* of the feeder.

(8) Local or group "*tradition*".

(9) *Individual* (personal) *preference.*

Each of the above factors has been discussed in detail by Goodall (1974). Whilst limitations of space available here do not permit a further full discussion, one factor—nutritive value—seems likely to be of paramount importance. Some of the main food items in the diet of the main study group were of high nutritive value, others were not. However, other highly nutritious and easily available plants were very rarely eaten—or not at all. This raises a doubt as to whether, in terms of nutritive value or "net energy/unit feeding time" (Schoener, 1971) the main study group was feeding optimally. Another way of looking at this is to ask why, in such a forest habitat, be selective at all? Would unselective feeding be more efficient?

Given the realistic possibility that at least some of the wide variety of plants in the montane forest are poisonous, then the advantages of some degree of selectivity are obvious. However, to judge food plants, or potential food plants, by a single criterion (even one as apparently important as nutritive value) may well be misleading. For example, as mentioned earlier, the net available (metabolizable) energy from the food items is greatly reduced by higher levels of indigestibility, thus the higher degree of digestibility of most leaves makes them better value for energy (weight for weight) than most of the bark that was eaten. The gross available energy of the bark of *Schefflera* sp. of 1880 kJ/100 g (dry matter) is reduced to a net available (metabolizable) energy value of approximately only 300 kJ/100 g—because of indigestibility and other losses. When one considers that the gorillas usually have to climb to reach this vine, and then expend considerable energy in removing the bark, it is not difficult to imagine that they are actually *losing* energy when they feed on this and similar food items. Add to this the very low initial gross available protein (7·62 g/100 g dry matter), which could be reduced by losses to approximately 3 g/100 g (dry matter), one wonders why the gorillas bother at all—what does *Schefflera*, and other food items with similarly low net energy and protein values, have to offer?

In the seasons when large amounts of bark were eaten, the dung was seen to consist of discrete lobes containing leaf, fruit and stem fragments, with many lobes being joined together like a string of beads, by long bark fibres. Dr T. Lawrence (pers. comm.) suggests that a large intake of bark could have a "gut full" effect i.e. not providing substantial amounts of nutritive value but avoiding indications of hunger which may come from an otherwise empty stomach. However, when gorillas were seen to feed on bark they could easily, and in most cases more easily, have fed on leaves—thus obtaining greater net nutritive values per energy output. It would appear therefore that barks of various plant species are selected by feeding gorillas, despite initial low nutritive value and subsequent indigestibility losses, and it may be that their physical action in the gut, i.e. in helping to move the food along, is a primary reason for this selection.

The relative roles played by all the above factors, and others as yet unknown, in influencing the final expression of this selectivity are far too complex to attempt any sort of order of importance. Rather they should be viewed as influencing food selectivity in a dynamic, multifactorial way—both in the daily lives of individual gorillas and their social groups, and in the longer term during the evolution of the genus. The final expression of the diet of particular gorilla groups therefore is a result of this dynamic interaction and not the result of unitory factors such as net energy gain per unit time, as implied by Fossey (1974, p. 580), (see Royama, 1970). In addition, such feeding strategies must be viewed as part of what Parker (1974) calls overall "time investment strategy". Thus these are likely to vary from region to region and even between individual animals.

The strictly vegetarian diet of gorillas has recently been doubted on theoretical grounds (T.-W. Fiennes, 1972). Analysis of the diet of various primate species in zoos (Bilby, 1968) showed that a 220-kg adult male gorilla received 5057 kcal (21 130 kJ) and 177 g protein per day in winter, and 6713 kcal (28 060 kJ) and 222 g of protein per day in summer. Much of the protein was in animal form—milk, eggs and meat. It must be stressed that these figures are for gross available value, therefore various losses would occur during digestion as outlined above. In addition there was considerable wastage of food by the captive gorilla—up to 50% in summer.

The Kahuzi gorillas are far more active than their captive counterpart and will obviously require a higher energy intake. The analyses of the Kahuzi plant samples show that the gorillas of this region can get sufficient energy and protein from a purely vegetarian diet. While it is possible that gorillas in some areas of poor forage could supplement their diet with animal protein (especially where bamboo is absent) this may be an unnecessary, or even accidental, addition to their intake. I suggest that most gorillas obtain all of their nutritional requirements simply by eating more and more vegetable matter. In their daily lives this is usually consumed in two or three extensive feeding sessions per day. Since not all group members are feeding on exactly the same diet it is possible that some are feeding sub-optimally. However, given the wide variety of possible food items available in the Kahuzi area I feel that this is unlikely since "polymorphic optima" are probably feasible. In addition individual differences in feeding habits could reduce intra-specific competition for some of the available resources.

4.2. Regional Variations and the Evolution of Gorilla Diets

It is interesting to speculate on the possible path of the long-term patterns of gorilla feeding habits. The boundaries of forest areas have in the past been in a dynamic state of movement under the influence of various factors. During the Pleistocene, the main factors influencing these movements, especially of altitudinal vegetation zones, have been climatic ones, Moreau (1966), Langdale-Brown *et al.* (1964). As a result of such movements of forest, one can now find identical species or closely related endemic species of many plants in widely separated areas, especially montane area, Langdale-Brown *et al.* (1964). While the boundaries of the various forest types have moved due to changing conditions, so the forests in particular areas have undergone various changes in floristic composition or disappeared completely.

Animal populations living in such areas could either follow the shifting forest, and thereby live in the same or similar conditions, or adapt their feeding habits to a changing flora in one area—or both. One would expect animals which were able to accomplish both alternatives to have a wide present day distribution and to be eating a wide range of food items. These are exactly the feeding patterns seen among extant gorilla populations (Schaller, 1963; Sabater Pi, 1972; Goodall, 1974) in their present day disjunctive distribution. Further, since changes in floristic composition in the geological past have taken place very slowly, one would expect to see only gradual changes in the diets of gorillas living in areas farther and farther apart. Comparisons of the lists of all known food items in the diets of gorillas (taken from the literature mentioned above and from data collected during this study) show that this is true only to a certain extent. There are apparent differences in feeding habits between gorilla populations inhabiting different regions—which have been explained as "cultural" differences by Schaller (1963). My findings in the Kahuzi region have tended to confirm Schaller's explanation.

Therefore we now have to explain how these similarities and differences could have arisen. Both similarities and differences may be due to the interaction of cultural tradition in feeding habits of particular groups with changes in the floristic composition *at a local level.* Thus the feeding habits of each group have changed and are still changing, within the confines set by nutritional needs, to suit the local condition of the forest which the group inhabits.

4.3. Home Range Utilization

Schaller (1963) states

> Except for bamboo, gorilla habitats throughout the range show no conspicuous seasonal differences in the abundance of forage. . . . The only generalisation regarding movement which can safely be made are that gorillas (at Kabara—Virunga volcanoes) travel continuously within the boundaries of their home range at irregular intervals.

A much longer study on the nearby Mt Visoke indicates that

> the presence or absence of other gorilla groups and/or individuals appeared to be the strongest determination of the range patterns of the study group, though food distribution may have played some role in movements between vegetation zones or parts of the range. (Fossey, 1974).

In the more heterogenous and seasonal forest areas of Kahuzi quite definite patterns of home range utilization by the study group were apparent within several months. Reliable local sources indicate that such patterns have been repeated for over 20 years—at least the life span of many group members. Group avoidance was also observed in the Kahuzi study area. On one occasion the main group moved directly from one side of its home range to the other during ten days of direct travel after a contact with a lone silverback. In addition there appeared to be a far lower degree of home range overlap in the Kahuzi area than Schaller (1963) observed in the Virunga volcanoes.

Thus while the presence or absence of other gorillas may be one proximate cause of some gorilla movements in Kahuzi, it is suggested that different patterns of food distribution are the most important factors. Obviously food which is available in discrete, discontinuous amounts will demand a different strategy for its optimal exploitation than food which is widespread and continuous. There will be an optimal gain per unit time spent feeding on particular food items which is directly proportional to the "search time" necessary to find them (Royama, 1970a and Parker, pers. comm.). Such different strategies of movement and range utilization by the main study group are evident from the data presented above. These also serve partly to explain why there appears to be so much wastage of food in areas of high food density, e.g. bamboo.

In addition, either directly or indirectly as a result of climatic factors, food distribution appeared to be the main ultimate factor influencing gorilla movements throughout the year. For these were not randomly distributed movements but obvious *migrations* as part of a well established pattern of range utilization. These migrations, and the fact that some paths were used repeatedly, indicated that some of the group members were familiar with the spatial distribution of their main food items. The visits they paid to the bamboo zones, and their digging for young shoots before they appeared above the ground, indicate that the gorillas also anticipated some of the seasonal changes. Overlying the climatic and resulting vegetational factors are the more recent anthropogenic influences, mainly as a result of the creation of extensive areas of secondary regenerating forest. In Kahuzi these areas provided the largest amount of gorilla foods during much of the year—especially during the rains—and their expansion has probably greatly influenced gorilla migrations in recent times.

The apparent non-territorial nature of gorillas has been the subject of considerable academic debate. In one area at Kabara in the Virunga volcanoes, Schaller (1963) found six gorilla groups utilizing the same resources. He concluded that territorial behaviour is absent in gorillas. However, territoriality may occur in the absence of active defence (Fretwell, 1972). In Kahuzi, group avoidance and the low degree of home range overlap suggest that some form of territoriality does occur.

This may be effected mainly as a result of long-range, intergroup vocalizations and chest-beat displays (hoot series and chest-beat, with or without ground thumps) by the adult male silverbacks of the various groups. What we see in the Virunga volcanoes, where there is an abundance of food all year round, is the compression of the home range, accompanied by extensive overlaps, such that apparently all that is left is the defence of the group integrity—with occasional group avoidance. Thus the differences, both in absolute home range size and patterns of home range utilization, which were observed between the gorillas of the Kahuzi and Virunga regions are, to a great degree, reflections of differences in the abundance and availability of local food resources in each region. The two primary factors influencing food abundance and availability appeared to be (a) climatic—particularly seasonal variations in rainfall, and (b) the creation of open secondary forest conditions by man. Other influences, such as the gorilla population size and its distribution throughout the region, local pressures from hunting, harassment and habitat destruction, "culture" and "traditions" within particular gorilla groups probably influence the final expression of home range size and its utilization by the animals of all regions. Since it is extremely likely that all these influences vary widely, both between and within the various geographic regions inhabited by all subspecies of gorilla, it is likely that the behaviour of the gorillas themselves will also vary under the different ecological influences.

4.4. Conservation

The biggest danger to the continued existence of gorillas in the Virunga volcanoes region is the destruction of their habitat by man. The situation in the Kahuzi region, and probably throughout eastern Zaïre, is more paradoxical. The pattern of agricultural practice in these areas has created mosaics of secondary regenerating forests, of differing ages, among vast areas of primary forest. The feeding behaviour of gorillas, evolved during extensive forest changes during the geological past, together with their peculiar anatomy, have enabled them to exploit these areas most successfully. Unfortunately this often brings them into direct conflict with villagers who may still have crops in apparently abandoned fields. Thus gorillas are accused of actually raiding the crops and are killed e.g. in some parts of the Utu region.

As a consequence of the increase in areas of secondary regenerating forest recently created by man, it is possible that the gorillas of some regions are undergoing both a population increase and a range expansion. Unfortunately there is too little data available as yet on the extent of deaths and captures. However, it is obvious from field research that the future survival of the eastern gorillas (and probably the western gorillas) does not depend on their behavioural and ecological efficiency but upon the patterns of land usage which are adopted by the people of countries like Rwanda, Uganda and Zaïre. In this respect it is most encouraging to hear that President Mbuto Sese Seko of Zaïre plans to extend their National Parks to cover 12–15% of their country. Some of these new park areas could be selected with regard to the distribution of gorillas. It would be both unrealistic and unwise to claim many of these areas as "inviolate" gorilla reserves. Since it is now clear that gorillas thrive in a wide variety of forest habitats it is this variety which should be maintained. This will call for the careful *management* of gorillas and their habitats. Thus while controlled "neglect" may be the best policy in some areas, it may be wise in other areas to create secondary/primary forest mosaics as in Kahuzi. Such management techniques would not only ensure viable gorilla populations and an expanding tourist industry, they could also greatly reduce the conflicts of interest surrounding the choice of land usage by giving the local people the felled timber—which they desperately need to build houses and for use as cooking fuel. However, it must be made clear that the wholesale creation of secondary forest is not being advocated—much more basic scientific groundwork remains to be done regarding gorilla distribution and ecology before realistic management plans can be formulated.

5. SUMMARY

As part of a comparative research programme to investigate the behaviour and ecology of mountain gorillas in different parts of their range, a partially habituated group of 20 animals was studied for seven months in the mixed montane forests of Tshibinda–Kahuzi (Zaïre) (Section 1.0). They were found to eat a wider range of food items than the mountain gorillas of the Virunga volcanoes region, and to climb expertly and frequently in order to exploit the many vegetation resources available in different forest strata (Sections 2.1, 2.2). Many of the food plants were analysed for their gross available nutritive values. Allowances were made for various losses from these gross values and estimates of net available or "metabolizable" values are given. These estimates were used to calculate the nutritive values of simplified gorilla "menus", from which it was concluded that the study animals could obtain ample energy and protein for all their requirements without eating additional animal matter (Section 2.4).

Eleven vegetation types were recognized in the study area and the relative percentage cover of these was calculated from vegetation maps prepared from aerial survey photographs (scale 1 : 28 000) (Section 1.2). The study area was divided into quadrats equivalent to 280 × 280 m on the ground. The home range of the main study group, calculated on a quadrat basis and allowing for hilly terrain, was estimated to be some 34 km^2 and is far larger than previous estimates for gorillas in other regions. The day journeys, quadrat visits and range utilization are analysed and discussed. It is concluded that differences in temporal and seasonal distribution of food resources, via climatic factors, are the most important factors influencing gorilla movements and are probably responsible for regional differences in ecology of gorillas (Sections 3.0, 4.3). It is suggested that, owing to the expansion of secondary regenerating forest areas caused by man, gorillas could be increasing their numbers and possibly expanding their range. Suggestions are made for the formulation of a "management plan" for gorilla reserves in east Zaïre, which would entail the artificial maintenance and possible increase of secondary forest mosaics inside areas of primary forest. This could provide optimum gorilla habitat and supply much-needed timber to the local population on a continuing basis (Section 4.4).

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Chimpanzees of Gabon and Chimpanzees of Gombe: some Comparative Data on the Diet

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1. INTRODUCTION

The feeding behaviour and diet of chimpanzees in Gabon (*Pan troglodytes troglodytes*), was the subject of a one-year field study in 1971–72 (Hladik,

FIG. 1. Inside the rain forest at Ipassa.

1973). A parallel study of feeding behaviour on the well known population of *Pan troglodytes schweinfurthii* in the Gombe National Park, was carried out in 1972–73 (Wrangham, 1975 and this volume). Unfortunately, the scope of the comparison of these two studies is limited by the small amount of information concerning diet (quantification and composition) available for the latter population.

2. METHODS

2.1. Comparison of Study Areas

The Gabon study was carried out at the CNRS field station of Ipassa (500 m), mainly on a 2-km-long island in the Ivindo river. Vegetation diversity in the study area is very high and over 900 plant species have been determined and listed (Hladik and Hallé, 1973). Many lianas (Fig. 1) play an important part in the production of this forest (A. Hladik, 1974), especially in fruit production. The chimpanzee population consisted of eight subadults introduced into the island from the nearby forest. The chimpanzees were well habituated and the observer could usually stand among the group when recording. Bananas were provided at an artificial feeding area and, except during the minor dry season (when the fruits were very abundant), the animals obtained about 30% of their food from this. The observations were resumed in the 1975 minor dry season and little food was provided, the animals feeding on natural fruits, particularly those of *Irvingia gabonensis*.

In contrast, the habitat at Gombe is drier and more mountainous (Goodall, 1965; Clutton-Brock, 1975a). It includes open woodland and grassland and the vegetation is less diverse (see Clutton-Brock, 1975a; Appendix II: at Gombe only nine species account for 50% of the tree population, while in the Ipassa forest, in a smaller sample, 15 species accounted for 50% of the tree population).

At Gombe, the chimpanzees obtained small amounts of bananas from the artificial feeding area (less than 20% of their food, according to Wrangham), but were not fed during Wrangham's study.

2.2. Field Methods

Individual animals were observed from dawn to dusk and their food intake recorded using the methodology described in Chapter 11. As Table I shows, the amount of time spent feeding on different foods was not closely related to their abundance in the diet.

Food samples were collected in order to calculate the weight of the

TABLE I

Comparison between the time spent feeding and the food intake by Pan troglodytes troglodytes

	Time spent			Amount ingested fresh weight		
Sample eaten	min	%		g	%	
Baphia leptobotrys (Papilionaceae) leaves	35	16·7	48·8% of the feeding time spent on leaves and bark	85	5·3	33·3% of the fresh weight ingested from leaves and bark
Hypselodelphis violacea (Marantaceae) stems	12	5·7		120	7·5	
Musanga cecropioides (Moraceae) petioles of leaves	2	0·9		10	0·6	
bark	3	1·4		30	1·9	
Pterygota bequaertii (Sterculiaceae) young leaves	12	5·7		135	8·5	
stems	3	1·4		10	0·6	
Macaranga spinosa (Euphorbiaceae) bark	3	1·4		15	0·9	
Roureopsis obliquifoliolata (Connaraceae) leaves	9	4·3		50	3·1	
Baphia sp. 1383 (Papilionaceae) leaves	4	1·9		5	0·3	
Vine (unidentified) apex	8	3·8		20	1·3	
Musa sapientum (Musaceae) banana skins	11	5·3		50	3·1	
Garcinia polyantha (Guttiferae) pulp of fruits	8	3·8	14·4% on fruits	15	0·9	62·6% from fruits
Mammea africana (Guttiferae) pulp of fruits	6	2·9		50	3·1	
Cissus dinklagei (Vitaceae) fruits	2	0·9		10	0·6	
Musa sapientum (Musaceae) banana pulp	14	6·7		920	57·9	
Macromiscoides aculeatus ant nests	64	30·6	36·8% on insects	45	2·8	4·1% from insects
Termites (including rotten wood)	4	1·9		15	0·9	
Ants (unidentified)	9	4·3		±5	0·3	

Example of 1st September 1971, from 5.40 to 18.07h.

food ingested by the chimpanzees (average fresh weight). They were preserved by boiling in alcohol or by drying in an electric oven (see Appendix III this volume).

2.3. Observation Sample

In Gabon, total observation time was 27 090 minutes during the 1971–72 field study. The dots along the time-axis of Fig. 4 indicate the days during which continuous observations were made.

3. COMPARATIVE ASPECTS OF FEEDING BEHAVIOUR

3.1. Daily Variation in Food Intake

As in other areas where they have been studied (Goodall, 1963, 1965; Reynolds and Reynolds, 1965; Suzuki, 1969; Jones and Sabater Pi, 1971) the chimpanzees at Ipassa were primarily frugivorous. During the observation sample of 1971–72, 141 plant food types (plus 33 animal foods and five mineral foods) were identified and a further 144 (accounting for small amounts ingested) could not be identified. This suggests that the chimpanzees ate a higher number of food types than in Gombe, where Wrangham (this volume) recorded that they ate 140 food types during an observation sample twice as long as ours. This is supported by comparison of the average number of food types eaten per day: more than 20 at Ipassa versus 14·6 at Gombe. In contrast, the numbers of feeding bouts per day were similar in the two areas. Teleki (pers. comm.) suggested that the differences in the number of foods selected between the two areas could be related to the differences in the age classes observed.

Although this may be a contributory factor, the greater number of edible species available in Gabon, must also be involved.

Different foods tend to be eaten at different times of day (Fig. 2) and this pattern varies seasonally. During the minor dry season, fruits are eaten at the beginning and at the end of the day, while leaves tend to be eaten most during the middle of the day, following the main period of fruit-eating. In the rainy season, fruits are eaten throughout the day (generally because they are found in small amounts dispersed across the range) and leaf-eating shows a marked peak in the late afternoon. The species from which leaves and stems are eaten, are generally abundant and can be found easily in the different parts of the range, and the diurnal rhythm in food choice is not a product of the occasional finding of different plant species. Wrangham (this volume, Fig. 8) found a

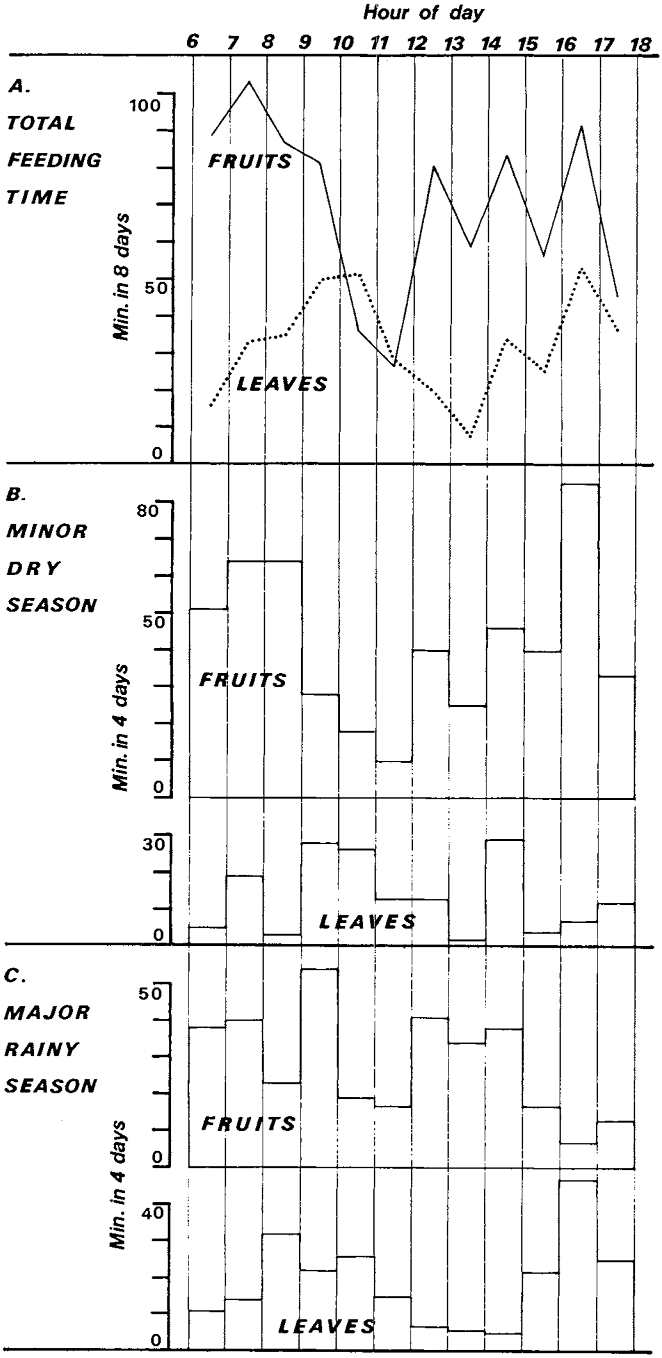

FIG. 2. Diurnal variation in time spent feeding on fruits and leaves by *Pan troglodytes troglodytes*, in Gabon.

similar difference between the times when leaves and fruits were eaten at Gombe.

3.2. Feeding Techniques and Traditions

Some differences in feeding behaviour between the chimpanzees in Gabon and at Gombe are noticeable (Hladik, 1973) and the main points of comparison are related to tool-using.

Feeding on ants and termites is important to maintain the protein balance of the diet of the chimpanzee (see Section 5.2). Several ant species including *Macromiscoïdes aculeatus*, *Oecophylla longinoda*, *Polyrhachis militaris*, *Paltothyreus tarsatus* and *Camponotus* sp. are eaten, many of them after "fishing", a technique similar to that described for termite-eating at Gombe (Goodall, 1968), using a stem from which leaves have been stripped off with the mouth. At Gombe, *Macrotermes bellicosus* are caught with a grass stem (McGrew, 1974) while *Macrotermes muellerii*, although obviously edible, are not eaten by the chimpanzees in Gabon.

In contrast, feeding on scorpions was only observed in Gabon. At least one species, *Opisthacanthus lecomtei*, was killed by a rapid hand-slap before being chewed with some pieces of bark.

The bark from different trees and lianas is utilized by the chimpanzees in Gabon and chewed with any kind of animal food such as eggs and fledglings. At Gombe, some leaves are utilized for the same purpose. In addition, leaves that are never taken as food are also chewed to make "sponges" to extract the brain of prey (Teleki, 1973a) or to clean out the inside of hard-shelled fruits (Wrangham, this volume). The fibre wad although made by the chimpanzees in Gabon, was never actually made intentionally, as it was at Gombe. It was generally made from the stems of *Hypselodelphis violacea*, which was frequently eaten throughout the year (Fig. 3): the fibre, generally spat out, can be used as a sponge to drink water in a hole of a tree trunk.

Nut breaking with a tool was observed neither in Gabon nor at Gombe. In places where *Panda oleosa* and *Coula edulis* are eaten by the chimpanzees after breaking the hard shell of the nut (Struhsaker and Hunkeler, 1971; Rahm, 1971), there are obvious traces which have never been observed in Gabon, in spite of the abundance of *Panda* and *Coula.*

4. VARIATION IN FEEDING AND RANGING BEHAVIOUR

4.1. Seasonal Variation

Changes of the relative proportions of the fresh weight of fruits and leaves ingested (Fig. 4) can be related to the seasonal changes below.

FIG. 3. A subadult female chimpanzee peeling, before chewing, the stem of a Marantaceae: *Hypselodelphis violacea*.

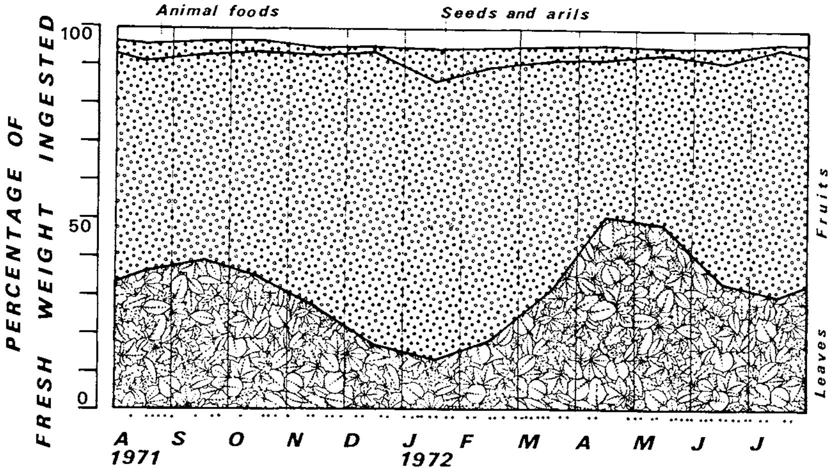

FIG. 4. Percentages of fresh weight of different food categories ingested by the chimpanzee in Gabon and their variation throughout the year. Young and mature leaves and stems are all included in the same category (bottom of the graph).

(a) During the major dry season (approx. July–Sept.) in Gabon, few fruit species are available. Consequently, the leaves and stems of some common species are eaten in large proportions (up to 40% of the diet).

(b) During the major rainy season that follows (Oct.–Dec.), many species start fruiting and the proportion of leaves included in the diet decreases as soon as the fruits are eaten in large amounts.

(c) A maximum of fruits is available during the minor dry season (Jan.–March). Very few leaves and stems (15% of the diet) are eaten in January but the proportion increases rapidly and the diet includes many young leaves and shoots available at this time.

(d) During the minor rainy season (April–June), when fruits are less abundant, the proportion of leaves and shoots in the diet reaches the maximum of 50%.

Animal foods are eaten in small amounts (4%) throughout the year. The mature or immature seeds of a few species are also eaten (more than 5%) when they are available.

The progressive variation in the gross food categories included in the diet of the chimpanzee in Gabon is the result of the addition of a large number of food species (see Hladik, 1973, fig. 13). No one species accounts for a large proportion of the annual diet.

At Gombe, according to Wrangham (Fig. 7, this volume), a similar pattern of annual variation of the diet results from the utilization of a smaller number of food species but one of these species, *Elaeis guineensis*, accounts for the bulk of feeding time (and, according to the high lipid content of *Elaeis* fruits, this must also be the bulk of the diet in terms of calories). In the rainy season, the leaves of two species (*Pterocarpus tinctorius* and *Baphia capparidifolia*) account for about 25% of the feeding time, while in Gabon at the same time, the leaves and stems of four species (*Baphia leptobotrys*, *Hypselodelphis violacea*, *Pterygota bequaertii* and *Newbouldia laevis*) account for 30% of the food intake with about 20 other species being eaten in small amount.

Many trees in the rain forest present an irregular phenological pattern (A. Hladik, 1977) and there are important differences of production between successive years (for example, the average production of fruits during the 1972 minor dry season was half that of the 1975 minor dry season). The resulting differences in the diet of the chimpanzees seem as important at Gombe as in Gabon. For instance, the fruits of *Parinari curatellifolia* were an important food resource in 1973, at Gombe (41% of the feeding time during the fruiting period) but were not available in 1972. Similarly, in Gabon, the fruits of *Irvingia gabonensis* were extremely abundant in 1975 (more than 50% of the food ingested in the records of February) but no fruiting occurred in 1972. Nevertheless, the general pattern of the diet was very similar in 1972 and 1975.

4.2. Annual Food Intake

Figure 5 shows the average proportions of the different foods eaten by the chimpanzees in Gabon during one year, in terms of fresh weight: 68% of fruits; 28% of leaves and stems; 4% of animal food (insects and small prey) plus a very small amount of earth ingested.

Variations in the proportions of the different foods eaten each day is illustrated by the hatched columns indicating the maximum and the minimum observed. Fruits may form up to 90% of the daily intake and never less than 40%, but most of the daily records include between 55 and 80% of fruits. The daily intake of animal food (essentially the ants, some termites, bird eggs and fledglings) varies between 2·5 and 6%.

A comparison with Gombe is difficult in terms of food intake. The similar seasonal variation in feeding times cannot be applied to food intake, as shown in Section 2.2. The feeding time on leaves is shorter at Gombe than in Gabon and the proportion eaten may be smaller. On the other hand, the chimpanzees at Gombe eat small-sized game (Teleki, 1973a, 1975) and adult males spend a long time interacting and sharing the meat. The average consumption is around 10 g of meat per

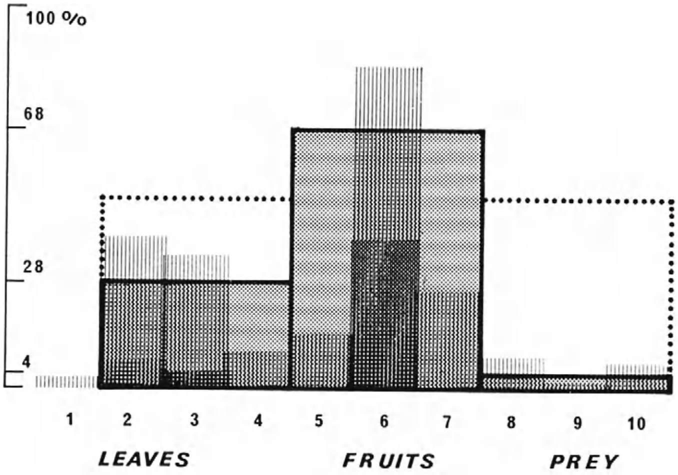

Fig. 5. Relative proportions of different food categories in the annual food intake of the chimpanzee in Gabon. The three shaded areas represent leaves (28%), fruits (68%) and animal foods (4%).

Maxima and minima of daily food intake are shown by the hatched columns for earth (1); bark and stems (2); leaves, shoots and pith (3); flower buds and gums (4); immature fruits (5); ripe fruits (6); seeds and arils (7); small arthropods (8); large arthropods (9) and eggs and fledglings (10).

day per chimpanzee (Wrangham, pers. comm.) and, as a dietary protein complement, is of little importance (less than 0·5% of the diet) compared with the other types of animal foods, especially ants and termites.

4.3. Ranging Patterns

The distance travelled each day by the subadult female chimpanzees observed in Gabon was smaller than in Gombe, but on the small island where they have been observed, the physical limits may have restricted ranging patterns. The subgroupings and some other sociological factors of the history of the group (see C. M. Hladik, 1974) were partly related to the direction of travel, but movements were also influenced by the distribution of food.

Foraging was more frequent in the mid-canopy than on the ground. They had some preferred nesting places in tall trees (40–50 m) but none of these sites were ever occupied on two consecutive nights.

TABLE II

Composition of some important food samples eaten by the chimpanzee in Gabon

		Per cent of dry weight								
	Water (%)	Protein	Lipids	Sugars after hydrol.	Cellulose	Minerals	Phosphorus	Calcium	Chlorides in NaCl	Potassium
FRUITS										
Nauclea diderrichii (Rubiaceae) seeds not extracted	76·7	4·5	5·3	47·2	17·3	3·0	0·11	0·27	0·10	0·97
Duboscia macrocarpa (Tiliaceae)	68·0	4·2	1·8	44·8	35·0	3·1	0·09	0·32	0·06	0·97
Aframomum giganteum (Zingiberaceae) seeds not extracted	55·9	8·2	11·1	48·8	11·6	5·2	0·18	0·10	0·13	1·68
Musanga cecropioides (Moraceae) seeds not extracted	72·8	8·8	6·3	31·5	25·9	4·5	0·17	0·67	0·19	1·19
Sarcophrynium schweinfurthianum (Marantaceae) seeds not extracted	61·8	11·3	0·9	61·8	14·6	4·7	0·19	0·66	0·13	0·85
Mammea africana (Guttiferae)	81·1	5·1	—	—	10·6	2·7	0·09	0·17	—	0·69
Pseudospondias longifolia (Anacardiaceae)	73·7	7·5	0·6	17·4	28·8	14·0	0·07	0·23	0·19	1·83
Rytigynia sp. 2032 (Rubiaceae)	84·9	8·1	5·9	8·6	27·6	3·5	0·07	0·13	0·10	1·18
Musa sapientnm										
(Musaceae) banana pulp	69·1	4·5	1·2	84·7	1·7	3·8	0·11	0·14	0·32	1·28
with skin	78·4	5·6	6·6	42·0	8·6	7·8	0·16	0·61	0·44	2·73
SEEDS AND ARILS										
Dichostemma glaucescens (Euphorbiaceae) unripe seeds	88·9	10·1	0·8	37·7	15·0	2·4	0·14	0·17	0·19	0·83
Cryptosepalum congolanum (Caesalpiniaceae)	67·1	10·6	3·0	7·0	2·4	2·3	0·20	0·15	0·13	0·73

Oubanguia africana (Scytopetalaceae) unripe seeds	68·8	7·0	0·4	—	4·5	2·8	0·14	0·22	0·35	0·97
Treculia africana (Moraceae) seeds	18·2	13·3	11·9	74·0	1·9	11·9	0·25	0·11	0·26	1·17
Trichilia prieureana (Meliaceae) arils	46·2	11·5	73·2	5·6	5·3	1·6	0·12	0·13	0·06	0·46
FLOWERS										
Neuropeltis acuminata (Convolvulaceae)	68·8	25·4	1·8	16·7	19·2	6·8	0·28	0·45	0·28	2·47
Cryptosepalum congolanum (Caesalpiniaceae)	65·0	18·5	1·7	—	12·5	4·9	0·30	0·24	0·10	1·39
LEAVES AND STEMS										
Baphia leptobotrys										
(Papilionaceae) leaf buds	80·7	55·0	—	—	12·3	6·4	0·69	0·49	—	1·28
young leaves	74·3	36·3	2·3	20·1	14·9	3·7	0·20	0·27	0·06	1·18
large leaves	59·0	31·9	1·9	11·4	28·0	11·1	0·12	1·75	0·13	1·77
old leaves	56·7	26·1	1·3	—	36·6	8·9	0·19	1·14	—	1·26
Newbouldia laevis (Bignoniaceae) young leaves	76·6	21·7	4·1	—	13·8	5·4	0·28	0·22	—	1·91
Dinophora spenneroides (Melastomaceae) young leaves	83·6	16·7	10·7	31·2	11·0	3·6	0·20	0·46	0·15	1·72
Ongokea gore (Olacaceae) young leaves	66·3	19·3	1·2	25·0	8·9	3·9	0·22	0·22	—	1·21
Baphia sp. 1383 (Papilionaceae) young leaves	67·5	24·5	1·3	14·5	37·0	4·1	0·22	0·19	0·16	1·42
Hypselodelphis violacea (Marantaceae) stems	74·1	5·7	1·1	11·4	51·3	4·9	0·10	0·22	0·50	1·38
Musanga cecropioides (Moraceae) petioles	91·7	11·6	0·6	17·0	19·3	17·1	0·26	2·40	1·34	5·44
INVERTEBRATES										
Macromiscoides aculeatus total ant nests	±50	29·0	4·2	20·0	—	5·0	0·36	0·61	—	—
Œcophilla loginada ant grubs	—	71·5	—	—	—	—	—	—	—	—
Mixture of insects from the litter	—	70·2	3·5	0·5	—	6·1	0·76	0·70	—	—
Caterpillars, sample An 15	72·9	62·3	21·2	6·4	7·3	3·2	0·39	0·21	0·19	1·11

5. FOOD COMPOSITION

5.1. Variability Among Food Categories

The results of the analysis of food samples collected in Gabon (Table II) show the necessity of combining different food categories to obtain a balanced diet. Protein content of fruits is generally low: the sample average (6·8%) is biased by the presence of fruits with small seeds (seeds are broken during the process of homogenization preceding analysis but usually found intact in the animals' faeces). Thus, in the pulp of most of the fruits, there is no more than 5% protein, which is insufficient to compensate for the loss of nitrogen of an adult chimpanzee. Seeds and arils are not rich enough (average 10·5% protein) to complement the fruits and not available in sufficient amount. By contrast, leaves and stems are common and have a high protein content (average of 24·9% for the ten samples). These, especially young leaves and shoots, may be eaten to complement fruit when invertebrates or the other animal prey cannot be obtained in sufficient quantity. A further ecological analysis of the relation of the food types with body mass and food availability is presented in C. M. Hladik (1977).

A rapid review of the other components listed in Table II indicates that only a mixture of the different food categories can give a balanced diet. Energy is found in the lipids of seeds and arils and in the glucids of the fruits (a technique of weak hydrolysis shows in terms of sugars what would be available as nutrients).

The proportion of different minerals varies between the different samples and only the combination of many plant species can result in a constant and balanced average. Phosphorus must be partly taken from animal foods while calcium is abundant in most leaf specimens. Some vegetable food, especially *Hypselodelphis violacea* stems and the petioles of *Musanga cecropioides* are extremely poor in nutrients: their selection by the chimpanzee is presumably related to their exceptionally high mineral content.

5.2. Protein Intake

Why are invertebrates eaten by chimpanzees? Leaves, which can be collected and eaten in a relatively short time, yield more protein than the small amounts of insects for which the chimpanzees foraged for 30–50% of the feeding time. One explanation may be the lower digestibility of plant protein when the proportion of fibre is high in the

TABLE III

Comparison of the relative proportions of the essential amino acids in the vegetal and animal food samples accounting for most of the dietary protein ingested by the chimpanzee, Pan troglodytes troglodytes *in the forest of Gabon*

Amino acid	Stems of *Hypselodelphis violacea*	Leaves of *Baphia leptobotrys*	Ants nest of *Macromiscoides aculeatus*	Ants and grubs of *Œcophylla longinoda*	Total average	Protein of egg as reference
Cystine	4·6	7·7	2·7	1·75	5·9	4·8
Histidine	4·8	2·9	9·0	6·6	4·3	4·6
Isoleucine	11·0	11·5	11·3	12·4	11·6	10·4
Leucine	20·3	13·5	19·2	22·1	16·2	16·7
Lysine	10·5	8·7	12·9	15·0	10·4	13·9
Methionine	4·6	2·7	3·4	3·5	3·1	6·1
Phenylalanine	11·5	8·7	8·1	7·6	8·7	11·6
Threonine	11·8	7·9	11·3	10·2	9·0	9·3
Tyrosine	6·1	9·0	8·7	8·4	8·6	9·3
Valine	15·2	27·6	13·4	12·4	22·3	13·5

The percentages of essential amino acids are related to their sum. The "total average" is calculated according to the importance of each sample in the diet of the chimpanzee. From Hladik and Viroben, 1974.

sample. In addition, insects may be eaten to supply essential amino acids, not present in sufficient amounts in plants. In Gabon, the chimpanzee utilizes relatively few plant species in large quantities: during the rainy season, most of the leaves and stems are taken from four species (see Section 4.1) and two of them are eaten throughout the year (*Hypselodelphis* and *Baphia* leaves). It is noticeable that the amino acids of these two plants are partly complementary: the leaves of *Baphia* contain little leucine and threonine, while the shoots and stems of *Hypselodelphis* have a larger proportion of these amino acids in their protein (Table III). Nevertheless, the average proportions of histidine, leucine, lysine and threonine are low, due to an excess of valine. The ants eaten throughout the year (*Macromiscoïdes* and *Oecophylla*) compensate this lack of some essential amino acids. Conversely, feeding solely on insects would result in a lack of cystine (Hladik and Viroben, 1974).

The termites eaten at Gombe by the chimpanzees probably play the same role as the ants in Gabon and complement the proteins obtained from leaves. The composition of the protein fraction of *Macrotermes bellicosus* (Table IV) is fairly similar to that of the ants, with a percentage of phenylalanine and, to a lesser extent, of methionine, closer to the ideal proportions of egg protein used for comparison.

Among the termites of the above species, reproductives and soldiers

TABLE IV

Results of the analysis of the protein fraction of a sample of reproductive Macrotermes bellicosus *collected at Gombe by R. W. Wrangham*

Protein	% of total protein	% of essential amino acids
Aspartic acid	7·6	
Threonine	3·7	9·1
Serine	3·4	
Glutamic acid	10·0	
Proline	4·8	
Glycine	4·8	
Alanine	5·9	
Valine	5·1	12·6
Isoleucine	3·8	9·5
Leucine	6·8	16·9
Tyrosine	6·3	15·7
Phenylalanine	4·1	10·1
Lysine	5·6	13·9
Histidine	2·7	6·6
Arginine	5·1	
Methionine	1·6	4·0
Cystine	0·7	1·6

TABLE V

Comparison of protein content of different samples of Macrotermes bellicosus *collected at Gombe by R. W. Wrangham*

	Per cent of dry weight		
	Protein (N × 6·25)	Lipids	Glucids after hydrolysis
Reproductives (eaten)	40·6	52·8	—
Soldiers (eaten)	58·7	<35	—
Workers (not eaten)	68·4	<25	2·1

but not workers are eaten by the chimpanzees. Curiously, analysis of the samples collected in Gombe by Wrangham, indicates that workers yield the maximum amount of protein (Table V). Selection of termites as food may be related mainly to the lipid content (detected by taste). Reproductives yield 52·8% lipids, while in the workers lipids account for less than 25%. The unsaturated fatty acids found in animal lipids may be as important in the diet as the amino acids.

In Gabon, scorpions, of which the hepatopancreas and haemolymph are the main edible parts, are often eaten. Haemolymph is poor in fat but rich in free amino acids (M. Goyffon, pers. comm.) while glycogen and phospholipids are important components of the hepatopancreas. It is likely that the grouping of several of those components are responsible for the attractiveness of these arachnids.

5.3. Mineral Intake

Geophagy is common in chimpanzees, both in Gabon and at Gombe. Up to twice a day, animals ate pieces of earth of about 10 to 20 g. The different earth samples are described in Hladik (1973). All of them are made of clay or other phyllitous materials with particules smaller than 2 μm and most of them from earth that has been moulded by insects (very soft and with fine structure). The cylindric constructions ("chimneys") built by the larvae of *Muansa clypealis* (Homoptera) were often eaten by all the chimpanzees of the group.

The mineral content of these specimens of earth (Table VI) does not reveal any element in sufficient concentration to interact with mineral nutrition (Hladik and Gueguen, 1974). This was also the case of the earth samples eaten by the *Presbytis* species in Sri Lanka (see Hladik, this volume) and by other primates, mostly leaf-eaters, for which analytical data are available. The elements which might have some nutritive value for the chimpanzees occur at lower levels in the earth

TABLE VI

Mineral content of different earth samples eaten by the chimpanzee, Pan troglodytes troglodytes, *in Gabon*

	P	Ca	Mg	K	Na	Fe	Zn	Mn	Cu
Earth from cylindric construction of *Muansa clypealis* larvae	94	114	100	440	104	8600	21	18	8
Earth from mounds of *Macrotermes muellerii*	10	94	—	182	4	—	—	—	—
Earth sample collected near the above mounds	10	8	—	100	5	—	—	—	—
Earth from dripping part of the nest of *Procubitermes* sp.	490	448	70	540	95	33 000	35	54	14

The proportions of the different elements are in 10^{-6} (millionth of the dry weight). After Hladik and Gueguen, 1974.

samples than in many common food plants (Table VII). The low levels of some minerals in the diet are compensated by feeding on a few species with a high mineral content, such as the stems of *Hypselodelphis violacea* and particularly the petioles of *Musanga cecropioides* which contain 13 380 × 10^{-6} of chlorides. A similar example of adaptation to mineral nutrition is presented by Oates (1974 and this volume): a *Colobus* monkey obtained most of its sodium from *Hydrocotyle ranunculoides*, a plant occurring only in a swamp. The situation at Gombe seems quite similar. The composition of the earth samples ingested by the chimpanzees (Table VIII) differs only in the larger amounts of calcium and potassium.

The most likely function of eating clay and other phyllitous material is that it acts as an adsorbant of certain components of the stomach content such as tannins (C. M. Hladik, 1977 and this volume).

TABLE VII

Mineral content of some food samples eaten by the chimpanzee, Pan troglodytes troglodytes, *in Gabon*

	P	Ca	K
Baphia leptobotrys, young leaves	1990	2660	11 790
mature leaves	2510	3690	16 140
Hypselodelphis violacea, stems	990	2180	13 790
Nauclea diderrichii, fruits	1090	2680	9650
Musanga cecropioides, petioles of leaves	2620	23 970	54 440

The proportions of the different elements are in 10^{-6} (millionth of the dry weight).

TABLE VIII

Mineral content of samples of the earth eaten by the chimpanzee, Pan troglodytes schweinfurthii, *at Gombe (Tanzania), collected by R. W. Wrangham*

	Ca	Mg	K	Na	Zn	Mn	Cu
Termite mound of *Macrotermes bellicosus*							
sample RW 1	600	600	5490	210	23	137	24
sample RW 2	580	4200	4580	130	20	96	19

The proportions of the different elements are in 10^{-6} (millionth of the dry weight).

5.4. Secondary Compounds

Tannins, alkaloids, saponines, terpenes and other secondary compounds are found in small quantities in many plant species and in large amounts in a few species. Where they are very abundant, some parts of the plant may be toxic and inedible.

Chimpanzees, like many other primates, are unable to detoxify substances by a fermentation preceding absorption and might be poisoned if the toxic substance is ingested. Thirty-eight foods eaten by the chimpanzees in Gabon were tested for alkaloids with Mayer and Dragendorff reagents. Testing was restricted to the foods (leaves and seeds) in which alkaloids were likely to occur. Similar tests were also carried out on a sample of 382 plant species collected at random in the rain forest of Ipassa where the chimpanzees have been observed (A. Hladik, 1977). In both samples, around 15% of species gave positive results indicating that the chimpanzees showed little selection against plants containing alkaloids. The main conclusion is that the alkaloids, in most of the plants in which they occur, are not toxic or not concentrated enough to be toxic. By contrast, a few species with a high alkaloid content such as the fruit of *Picralima nitida* (Apocynaceae) are not eaten by the chimpanzees.

Saponines, steroids and terpenes were found by Bouquet (1972, 1975) in a few species of the Congo rain forest, which also occur in Gabon and are eaten by the chimpanzees; but only tannins occur frequently in the leaves and bark of many species and are likely to interact with feeding behaviour (see discussion about leaf-monkeys, Hladik, this volume). In the bananas eaten by the chimpanzees at Gombe (and also frequently eaten in the old plantations in Gabon) some 3,4 dihydroxyphenylalanine (Waalkes *et al.*, 1958) may be concentrated in the skin (700×10^{-6}) which is chewed with the pulp without any apparent effect.

6. CONCLUSION

The study suggested that food choice in the chimpanzees was affected by variation in the levels of specific nutrients in different foods rather than by variation in secondary compounds. Several points supported this view. When the chimpanzees did not appear to be maximizing their energy return they compensated for deficiencies in the qualitative composition of their diet by ingesting species yielding specific nutrients. For example, they ate the tiny leaf buds of *Baphia leptobotrys*, weighing 0·05 g each and the rate of ingestion when feeding on these parts was evidently slow. This item is of great importance for it provides certain amino acids. Similarly, when the chimpanzees ate the petioles of *Musanga cecropioides*, which yield mostly fibre as a primary component, this helped to balance the mineral content of the diet.

The feeding strategy of the chimpanzee appears to be based on food resources that yield the maximum amount of nutrients. Such resources are generally widely dispersed and may also vary in temporal distribution from year to year. This explains the exceptional size of the range of the chimpanzee and its large "supplying area", compared to that of the other frugivorous primate species (Wrangham, this volume; Hladik, 1975). The feeding strategy of *Presbytis senex* (Hladik, this volume) is exactly the contrary of that of *Pan troglodytes*, with the utilization of common food sources associated with low costs in ranging and feeding movements and with low return in energy.

Feeding behaviour is conditioned by the long term response to the nutrients (see Hladik *et al.*, 1971a; Casimir, 1975; Hladik, this volume); but the chimpanzees selection of food must necessarily be based on the immediate effects of the soluble substances detected by taste. This is the only way to increase the efficiency of foraging and gathering in an animal looking for food species dispersed over a wide range. There is no evidence that all the important nutrients can be detected by taste but the secondary compounds can be associated with the long term response and provoke an immediate effect; this might be the reason why some substances (see Section 5.4) which have no obvious effect on nutrition are selected.

7. SUMMARY

1, 2. A field study of one year (1971–72) and three months (1975) was carried out on a population of chimpanzees reintroduced to the rain forest of Ipassa, near Makokou, Gabon. Quantitative data on the food ingested were collected. Results of this study are compared with data collected by R. W. Wrangham in the Gombe National Park, Tanzania. The number of plant species is greater in Gabon than at Gombe and the variety of food plants eaten is also greater.

3. In Gabon, as at Gombe, chimpanzees fed more on fruits in the first-half of the day and more on leaves in the second-half. During the rainy season, a marked peak in leaf eating occurred in the last two hours of activity.

Small differences in the feeding techniques and food choice appear between the chimpanzees in Gabon and at Gombe. "Fishing" concerns mainly termites at Gombe and ants in Gabon. *Macrotermes* are eaten at Gombe, not in Gabon. Bark is utilized as a fibre complement with animal food in Gabon, while at Gombe, leaves play this role.

4. Seasonal changes in diet were related to plant phenology and, as at Gombe, there are important differences between years. Ranging patterns are partly related to plant distributions (data from Gabon not sufficient for comparison).

The average annual food intake (fresh weight) was 68% fruits, 28% leaves and barks and stems, 4% animal food.

5. The composition of the food specimens collected in Gabon, show that the feeding strategy of the chimpanzee is based on the utilization of the dispersed resources yielding the maximum amount of nutrients. The low protein content of fruits is compensated for by the high content of young leaves. Insects are selected for specific amino acids.

Minerals are mostly supplied by different food plants and geophagy is not an adaptation to dietetic balancing. The earth ingested may serve to adsorb tannins or other secondary compounds.

Some rare plants showing high levels of toxic compounds are avoided by chimpanzees. Although "secondary compounds" are found in small amounts in many food plants, there is no evidence that chimpanzees select plant species where these are absent.

ACKNOWLEDGEMENTS

The project related to the chimpanzees in Gabon, was initiated by Professor P. P. Grassé, in 1963. Many other scientists of the CNRS co-operated for its continuation, at the Ipassa field station. Annette Hladik developed the botanical researches and the tests for alkaloids presented in this paper. R. W. Wrangham collected the food samples from Gombe, for which analytical data are presented.

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Feeding Behaviour of Chimpanzees in Gombe National Park, Tanzania

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1. INTRODUCTION

Most studies of the feeding behaviour of chimpanzees (*Pan troglodytes* Blumenbach) have been in Tanzania, along the shore and inland from Lake Tanganyika, often as part of more widely based behavioural observations (Goodall, 1963, 1965, 1968 in Gombe National Park; Azuma and Toyoshima, 1962; Izawa and Itani, 1966; Suzuki, 1969; Izawa, 1970 and Kano, 1971 around the Kasakati Basin; Nishida, 1968, 1974 in the Mahali mountains). General descriptions from the Budongo forest, Uganda were given by Reynolds and Reynolds (1965) and Sugiyama (1968). The most detailed study in West Africa was of chimpanzees reintroduced to the wild in Gabon (Hladik, 1973, this volume): some data were also given by Nissen (1931) and de Bournonville (1967) from Guinea, and by Jones and Sabater Pi (1971) from Rio Muni.

Despite the number of reports little is understood of the role of chimpanzee feeding behaviour in mediating the relationship between the environment and social structure: the difficulty of obtaining properly sampled observations, the complexity of the environment and the continuing debate over the nature of chimpanzee social structure have been considerable obstacles. In this paper data on feeding behaviour are given in detail. These are subsequently related to observations of ranging and grouping behaviour, summarized from Wrangham (1975).

2. METHODS

2.1. Study Area and Study Population

The study area was approximately 20 km^2 of Gombe National Park, Tanzania, on the shore of Lake Tanganyika. Its eastern boundary, the running crest of hills bordering the lake, lies at around 1500 m above mean sea level (a.m.s.l.). From there, a series of parallel dendritic streams flow 3 to 4 km to the lake, 683 m a.m.s.l. Figure 1 shows the study area and the distribution of habitats in the central part and Fig. 2 illustrates riverine forest: vegetation types correspond to those described by Clutton-Brock (1975a) for a typical part (*c.* 1·4 km^2) of the park. There were no geographical boundaries except the lake shore to the west.

The subjects were 36 independent and 19 dependent chimpanzees,

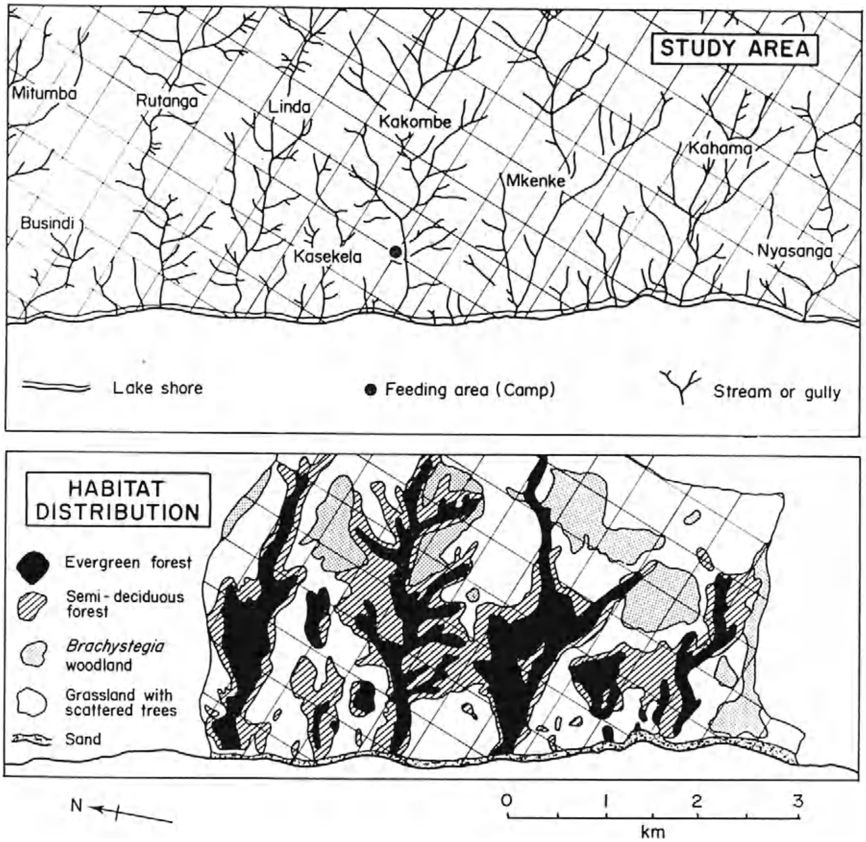

FIG. 1. Study area. The scale is approximate since the ground was uneven: the eastern boundary of the study area was about 1500 m a.m.s.l., the western boundary 683 m a.m.s.l.

most of whom were fully habituated to human observers. (Dependents were those who spent more than 50% of their time with their mothers, and are not included in analyses except where specifically stated.) Recent data on the social structure of the population (Goodall, 1973) demand a revision of the view (Goodall, 1968) that the only permanent social bonds are between mothers and their young. On the basis of ranging and association data adult males were found by Bygott (1974, in press) to belong to one of two "communities", northern and southern. Individuals within a community had more overlapping ranges and spent more time together than those of different communities, and interactions between males of different communities were normally aggressive. Wrangham (1975, in press) proposed that the community concept be limited to males until the relationship of the ranges of females to male communities is clarified. However, since female ranges are smaller than those of males the distinction is not crucial when male community ranges are stable. In this paper individuals of both sexes are regarded as being part of particular communities, whose composition is shown in Table I.

FIG. 2. Riverine forest in the lower part of Mkenke valley.

An artificial feeding area (camp) was maintained in the centre of the northern community range (Goodall, 1968; Wrangham, 1974). Individuals obtained bananas less than once a week (for nine males and 11 females in the northern community, mean = 9·9 days between feeds, range 6·1–19·3). A ration of bananas (up to 15) presumably supplied less than 20% of an adult's daily food requirements, and since less than 10% of the northern community were fed per day (mean 2·2 individuals) the feeding area contributed less than 2% of the total food intake. During this study individuals under observation were not given bananas except by mistake, which happened twice.

TABLE I

Age/sex class composition of study communities

	Northern community	Southern community
Independent males		
past prime	2	2
prime	6	4
adolescent	1	1
Independent females		
past prime	1* + 1*	0
prime	11 + 13	4 + 6
adolescent	2	2
Total	23 + 14	13 + 6

Data from 1972 and 1973 (abridged from Wrangham, 1975).

Figures after plus signs show dependents.

* Died during study period.

Note that assignation of females to male communities is a convenience and not necessarily a biological reality.

2.2. Observation Samples

Observations were made from May 1972 to January 1973, and July to September 1973. An observation period was a continuous period of recording or trying to record the behaviour of a target individual and those in his "party" (i.e. those within 100 m). Activities of the target were recorded every minute on the minute, those of the party every five minutes, and calls by the target were recorded as they occurred. In analysis, activities were scored every 30 minutes to reduce dependence (Tables III, IV, V).

Only the 14 prime or past-prime males were selected as targets, in order to focus attention on behavioural responses to environmental change. The feeding behaviour of females and young is presumably affected relatively more by changes in reproductive state, parental responsibilities and age and remains to be described in detail.

Individuals could not always be found when wanted, so strictly even sampling was impossible. Table II shows the distribution of observation hours on different target individuals. Some of the variation was intentional, such as the many hours spent on HG, EV and GI as part of a ranging study. In selecting targets and deciding when to leave them the problem of bias was always present. Most observation periods began at dawn, selection of the target being made the previous night from

TABLE II

Observation time as target individuals

Northern community			Southern community		
Target	Periods	Hours	Target	Periods	Hours
Hugo	18	159	Goliath	5	25
Mike	10	64	Hugh	5	35
Humphrey	10	56	Charlie	6	50
Faben	9	68	Willy-Wally	4	20
Evered	24	195	De	3	28
Figan	14	92	Godi	10	88
Jomeo	14	64			
Satan	11	82			
Total	110	780	Total	33	246

those individuals whose sleeping site was known. The decision to end an observation period was taken at least an hour in advance, to prevent the temptation to proceed merely to include a rare event in the sample. However many periods had to end when the target was lost. Observation hours were evenly distributed across the day but for many analyses only all-day observations were used (i.e. continuous observation between morning- and night-nest): at least one was collected for each male.

In some analyses, especially of ranging behaviour, data collected by more than 30 observers were combined with observations made during this study. These data were recorded on standardized "group travel" charts whose reliability is discussed elsewhere (Wrangham, 1975).

2.3. Food Eaten and Food Availability

The diet was recorded only by direct observation of feeding, defined as having food in the mouth or being in the process of transferring it to the mouth. Food was anything known to be ingested. This definition made recording simple, but "feeding time" consequently varied in its biological meaning. For instance chimpanzees sometimes carried already chewed fruit of *Parinari curatellifolia* Benth. on the lower lip while walking; though recorded as feeding they were getting less nourishment than when actively chewing. Inclusion of chewing as a separate category would have reduced greatly the proportion of minutes of good observation.

A number of other terms need to be defined: "food type": particular part (e.g. fruit, leaf, resin) of particular species; "feeding site": position from which a chimpanzee could collect food without moving his feet;

"food source": volume containing feeding sites sufficiently close together for a chimpanzee to move from one to another without ceasing to feed; "feeding bout": a continuous number of minutes at the beginning of which the chimpanzee was eating the same food type as on the previous minute.

No strictly independent measures of food availability were attempted: practical and theoretical difficulties were considered prohibitive (Wrangham, 1975). Without independent measures of some environmental variables, however, it is normally impossible to isolate the significance of particular variables. Between seasons, for instance, there may be changes in food availability, habitat structure, predation or parasite pressure and climate, any of which could contribute to observed behavioural changes.

The solution adopted here was to control for as many environmental changes as possible by comparing observations during the same months in successive years. The only expected ecological change was therefore in the nature of food sources: in Gombe most plants have regular rhythms of productivity but crop failures are known to occur (Goodall, 1968).

Three seasons, each of three months, were selected for comparison: these were July to September 1972 (D_1), November 1972 to January 1973 (W), and July to September 1973 (D_2). D_1 and D_2 fell in the middle of the five-month dry season, and the only recorded climatic difference between them was a single rainfall (0·2 cm) in September 1972. The rains normally begin in October. In W there were 49 cm of rain, and visibility was considerably less than in D_1 and D_2, when the grass was low and most deciduous species had lost their leaves.

Owing to the difficulty of interpreting the significance of changes in behaviour between wet and dry seasons the major comparison here is between D_1 and D_2, when the only expected change is in the nature of food sources. However observations from W are included as a partial test of the proposed relationship between environmental and behavioural changes. Seasonal comparisons are made by matching all-day observations of the same target individuals in a Wilcoxon test whenever possible: sample sizes are consequently small.

3. FEEDING BEHAVIOUR

3.1. Feeding Techniques

Most of a chimpanzee's feeding time occurred in a few uninterrupted bouts. For ten males in D_1, for instance, the mean number of bouts per day was 37·8; 13·9 of these (37%) lasted at least five minutes, and accounted for 88·3% of feeding minutes. Different feeding bouts normally occurred at different food sources, so we may picture chimpanzee feeding behaviour as the composite of visits to about 14 major sources during a day.

A feeding bout was often preceded by conspicuous inspection of the food source. Under some of the tallest trees, for instance, those of up to 30 m, a lone chimpanzee might spend up to four minutes examining the canopy above him from different angles or sniffing fallen fruit. If another adult was already feeding, the newcomer would climb straight up and join him: but if a baboon, *Papio anubis* J. P. Fischer, or sometimes a young chimpanzee, was feeding he would examine the food as usual. Occasionally when individuals inspected a source they did not feed at the time, but climbed straight up to feed on their return up to two days later. Inspections seemed more thorough if the tree was tall and the climb vertical: possibly the chimps were judging not only the quality of food items but also whether the quantity justified the climb.

Having occupied a feeding site the chimpanzee often inspected individual food items by sight, touch or smell. The frequency of inspection during a bout appeared to depend on variation in item quality. Every item of some foods such as large fruit was individually examined, and many were rejected. Seed-bearing trees on the other hand were tested by opening two or three pods: after finding a "good" tree, the chimpanzee might take almost every pod, and feed for up to four hours without a break. Leaves were normally stuffed into the mouth after only a casual glance.

Food-bearing branches were occasionally broken off and carried to a convenient (e.g. shaded) spot, and some fruits were collected together before being eaten one by one. However chimpanzees normally ate the food where they found it (e.g. Fig. 3). Leaves were stripped off the stem and immediately chewed, though exceptions were *Aspilia* sp. (Section 4) and *Ficus urceolaris* Hiern: the latter were sometimes piled together and rolled into a crude cigar shape before being chewed.

Only fruits, seeds and pith needed to be prepared before being eaten. Variation in the techniques used appeared largely attributable to the particular problems imposed by the food item. When eating the fruit of *Garcinia huillensis* Oliv. for instance, males placed only one in the mouth, squeezed it, took out the compressed skin and held it between the lips or thumb and forefinger while crushing the extruded flesh within the mouth. A few seconds later the skin would be returned to the mouth, squeezed and removed again. A captive infant chimpanzee from Zaïre adopted this technique in eating the second fruit given to him: baboons, on the other hand, invariably peeled the skin with their fingers before

FIG. 3. An adult male eating the flowers of *Pterocarpus angolensis* DC. The use of all his limbs allowed even an adult male to feed from the slender outer branches, but individuals sometimes broke thin branches and carried them to a more convenient feeding site.

eating. The pods of *Diplorhyncus condylocarpon* (Muell. Arg.) Pichon were placed upside down between the incisors after being cracked with the molars, and then pulled open with one or two hands, using the thumb and forefinger. Techniques such as these varied little: but individuals differed consistently in hand preference, when smashing or pulling at hard-shelled fruit, and whether lips or hands were most often used for holding items about to be eaten. (Of 11 individuals, six were right-handed, four left-handed and one ambidextrous.)

Special techniques have been described for eating meat (Teleki, 1973b) and insects (Goodall, 1968; McGrew, in press). It is of interest that one potential food, the kernel of palm nuts *Elaeis guineensis* Jacq., is not eaten. In Gombe both chimpanzees and baboons eat the outer flesh, but only baboons have sufficiently strong jaws to crack the nut. Beatty (1951) saw chimpanzees in Liberia using rocks to smash open palm nuts, but no similar tool use has been seen in Gombe. The only tool seen in eating vegetable food was a wad of leaves, used to sponge out the inside of *Strychnos* sp. fruit, and this occurred only once out of many observations.

3.2. Feeding Heights

Individuals were recorded as being either "on the ground" or "in a tree": when in trees their feet were within 2 m of the ground on 7% of observation points. In all seasons most of their feeding time was spent in trees, up to 88% in W (Table III). The lower proportion in the dry season (down to 57%) probably reflects a shift in the vertical distribution of food, due both to ground-level production (fruiting shrubs etc.) and the preference of chimpanzees for eating some fruit after they had fallen (e.g. *P. curatellifolia*). Another factor responsible for the seasonal difference was that chimpanzees disliked sitting on wet ground: they

TABLE III

Activity budgets in trees

	% observation points of different activities recorded in trees		
	D_1	W	D_2
All activities	44·0	66·8	35·5
When feeding	68·7	87·9	56·6
When resting or grooming	7·5	62·9	13·5
When travelling	12·1	11·9	3·6

spent more time resting or grooming in trees in W than in D_1 or D_2 ($P<0{\cdot}01$).

3.3. Activity Budgets

Activities are likely to be affected by changes in the environment, and are therefore related here to different habitats and different seasons. Variation of activity budgets with gross habitat categories is shown in Table IV. Between natural vegetation types the only differences were in the type of food eaten, and this was clearly related to availability. In the artificial feeding area, however, less time was spent eating or travelling, and more resting and grooming. The similarity of activity budgets in the different natural habitats allows data to be lumped across them. However because of the abnormal distribution of activities in camp, data collected there have been omitted from most of the analyses.

TABLE IV

Habitat variation in activity budgets

Activity	Semi-evergreen forest		Deciduous forest		Grassland		Camp	
Eat fruit	37·9	53·9	34·6	56·7	21·2	56·1	6·9	6·9
Eat leaf	13·5		10·5		10·4		0·0	
Eat other food	2·5		11·6		24·5		0·0	
Travel		13·5		13·2		15·8		6·9
Allogroom	5·8	30·7	5·6	29·7	7·2	28·8	32·8	86·2
Rest	16·6		18·1		16·9		44·8	
Lie (not night-nest)	8·3		6·0		4·7		8·6	
Not observed		2·1		1·1		0·0		0·0
n (30-min pts)	326		619		278		58	

Figures show % of 30-min point records. Eating could be combined with grooming or travelling, so some percentages total more than 100.

Table V shows seasonal variation in activity budgets. More time was spent feeding in D_1 and D_2 (57% and 60%) than in W (46%). Possibly this reflects differences in food quality, but the difference was not significant, and it should be noted that the significance of feeding time varied between foods (1·3). More time was spent travelling in D_2 than in D_1: this is discussed below (Section 4).

TABLE V

Seasonal variation in activity budgets

Activity	D_1		W		D_2		May 72–Sept. 73	
Eat fruit	33·8		32·9		35·8		33·1	
Eat leaf	12·4	60·2	8·4	46·5	11·1	56·7	11·8	55·7
Eat other food	14·0		5·2		9·8		10·8	
Travel		8·4		14·5		20·0		13·8
Allogroom	5·5		8·8		4·1		6·2	
Rest	17·4	29·8	22·9	39·0	16·5	24·9	17·8	30·3
Lie (not in night-nest)	6·9		7·3		4·3		6·3	
Not observed	1·6		0·8		0·8		1·2	
Total	100·0		100·8		102·4		101·0	
n (30-min pts)	379		249		369		1197	
Mean time to leave night-nest	6·50h		6·28h		6·47h		6·42h	
Mean time to enter night-nest	18·34h		18·36h		19·06h		18·43h	
Mean time between night-nests (min)	704		726		739		721	

Figures show % of 30 min point records. Mean times of leaving and entering night-nests are shown from all observations (*n* = 75).

During the day there were three feeding peaks, between which grooming tended to occur (Fig. 4). Goodall (1968) and Nishida (1974) found only two feeding peaks, in the morning and evening. Possibly the central peak in Fig. 4 is not real: diurnal rhythms varied considerably between days, as found by Hladik (1973). Activity budgets also varied.

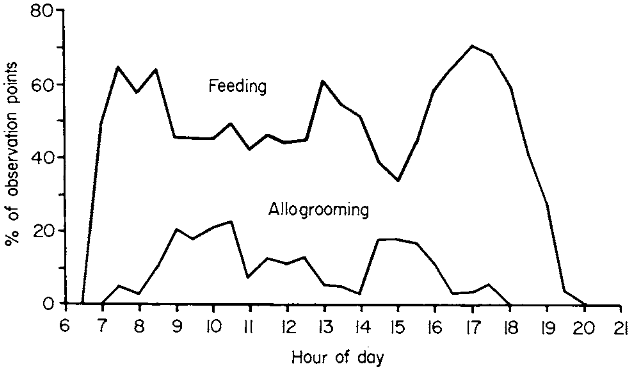

Fig. 4. Diurnal variation in activity. Data from all-day observations (*n* = 54); activity of the target was scored every 30 minutes.

For instance, the percentage of minutes between night-nests spent feeding varied, for the same male in the same month, between 55·1% and 78·9% (Hugo, June 1972), 52·8% and 79·4% (Godi, August 1972) and 50·0% and 72·3% (Evered, July 1973). Feeding was once recorded in the middle of a moonlit night in the wet season.

3.4. Diet Diversity

Diet diversity is examined between days, months and study areas. The number of food types eaten per day varied little (mean 14·6, s.d. 3·6). Table VI shows how the daily diet was composed. Fruit and leaves were the most important foods, but though the mean number of species eaten per day was similar, the number of fruit species was more consistent (s.d. 1·6) than the number of leaves (s.d. 2·4).

There was little indication of why the number of species eaten per day should be so consistent. Chimpanzees apparently sought out variety to some extent: for instance they sometimes returned on successive days to trees in which all the seeds had appeared to be ready to eat, yet which they had previously left in preference for a variety of other foods. On the other hand, the only individual difference observed for diet variety appeared due to passive acceptance of the availability of a broader diet. This occurred in D_1, when one male (Hugo) ate significantly more plant foods per day (mean 17·8) than others in the northern community (mean 11·5, data lumped for six males) (Mann-Whitney $P<0·001$).

TABLE VI

Number of food types eaten per day

Food type		Mean number per day
Plant	Fruit	5·2
	Leaf	4·9
	Seed	0·5
	Other parts*	2·2
Animal	Insects†	0·3
	Vertebrates	0·1
	Earth	0·6
	Water	0·8
Total		14·6

* Other plant parts were pith, galls, flowers, resin.

† Insects eaten incidentally with vegetable food are not included.

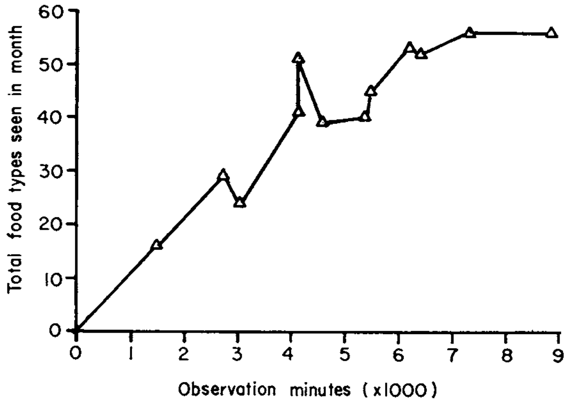

FIG. 5. Number of food types per month. All food types (plant, animal and miscellaneous) are included.

At this time males tended to occupy small areas within the community range, and Hugo spent more time than others in the lower stream bed of Kakombe valley, where there grew a wide variety of small edible leaves. In D_2 there was no difference in daily diet breadth between Hugo and other northern males: all tended to travel widely over the community range, but when Hugo or other males spent half the day in lower Kakombe, they ate as many leaves as Hugo had done regularly in D_1.

The number of food types recorded per month was related to observation time (Fig. 5). The asymptotic form of the curve suggests that about 60 types were eaten in typical months, and the smoothness of the curve suggests a similar variety in all months.

During this study 140 plant food types were observed, 77 of which were new feeding records for Gombe chimpanzees. Sixty-one further plant foods have been recorded in Gombe by other observers (Goodall, 1968 and unpublished files in the Gombe Stream Research Centre) (Table VII). Diet breadth appears similar elsewhere. Hladik (1973)

TABLE VII

Total number of food types recorded in Gombe

	Plants									Animals		Miscellaneous	All
Source	F	S	B	L	P	R	C	G	Total	I	V		
This study	60	8	13	37	13	3	4	2	140	11	7	9	167
Gombe files	26	6	6	17	2	1	3	0	61	2	8	4	75
Total	86	14	19	54	15	4	7	2	201	13	15	13	232

Different parts of the same plant species are scored as different food types: F: fruit; S: seed; B: flowers; L: leaves; P: pith; R: resin; C: cambium; G: galls; I: insects; V: vertebrates.

observed 141 foods in a 12-month study of chimpanzees reintroduced to a forest in Gabon, and Nishida (1974) recorded 205 food types over a seven-year period in the Mahali mountains, Tanzania.

3.5. Time Spent Eating Different Foods

Even over periods as long as two months most of the feeding time was spent on few foods. Figure 6 shows that in July and August 1972 and 1973, 50% of feeding time was spent on the first two to five food types, and 50% of food types accounted for 93–95% of feeding time. The inclusion in the diet of numerous food types appeared due both to the rare availability of some preferred foods and to the occasional selection of common types. The latter is illustrated by the fact that 15 of the 27 foods recorded only once were commonly available: intermittent experimentation could be an important strategy in an unpredictable environment. However, there are no feeding records yet for more than 300 plant species found in the study area.

Changes in feeding time on the major foods appeared largely related to availability. Figure 7 summarizes the monthly variation, which was comparable to that found in similar habitats (Suzuki, 1969; Nishida, 1974), and was thus largely predictable. However, there was one important difference between D_1 and D_2. In D_1 the fruit of *Parinari curatellifolia* were hardly eaten, whereas in D_2 they were eaten for up to 41% of feeding time. The difference was clearly due to the almost complete absence of *P. curatellifolia* fruit in D_1. This species appears to have a fairly regular two-year cycle of fruiting in Gombe.

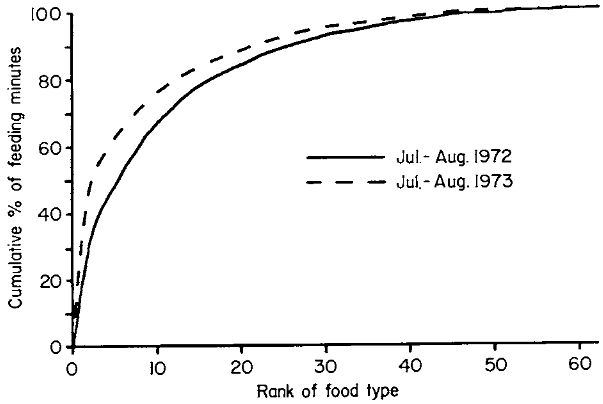

FIG. 6. Number of food types in relation to total feeding time. Data are from 14 all-day observations in each two-month period.

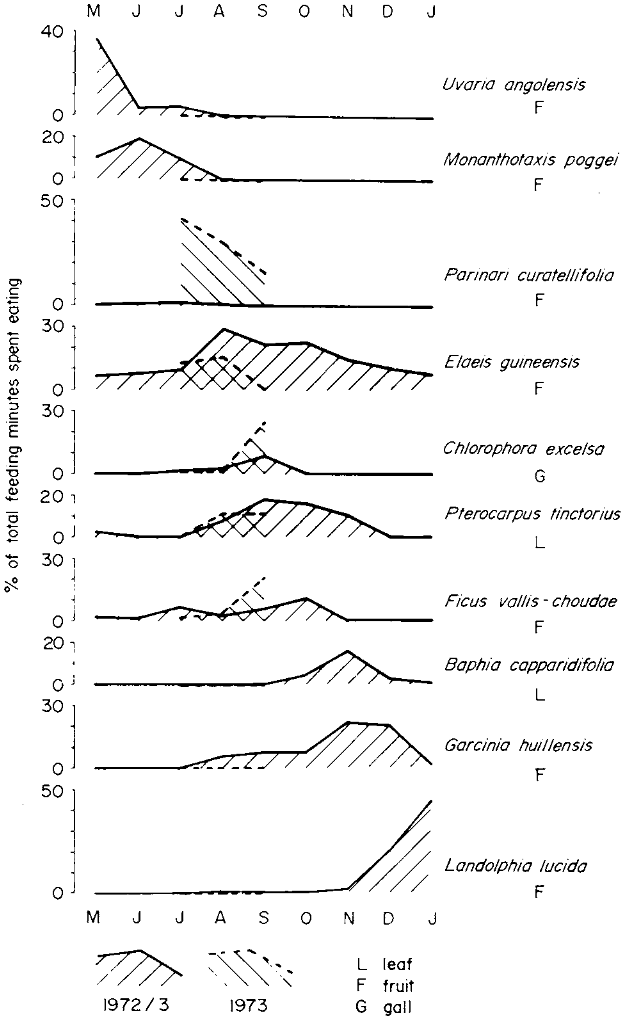

FIG. 7. Seasonal change in diet. The ten food types shown were all those eaten on more than 15% of observation minutes (by target individuals) in any month.

Animal foods formed a small part of the total intake. Insects were eaten incidentally in all months in figs and galls. Winged termites (*Macrotermes bellicosus* and *Pseudacanthotermes militaris*) were eaten when found flying, and tools were used to "fish" for *M. bellicosus* soldiers at mounds where passages had been made for the reproducing caste (Goodall, 1968; Teleki, 1974; McGrew, in press).

No fish, amphibians or reptiles have been seen to be eaten, though drying fish (*Stolothrissa* sp.) were frequently encountered on the lake shore, and these were eaten by baboons. Skinks (*Mabuya* sp.) and monitor lizards (*Varanus* sp.) were common, and young chimpanzees sometimes played with them, twice killing skinks, but no attempt was made to eat them. Similarly chimpanzees have handled a fruit bat (*Eidolon helvum*?) (Thorndahl, pers. comm.) and cane rat (*Thryonomys* sp.) without eating, though the bat was killed and the same species is eaten by baboons.

Other vertebrates which could be seized were eaten. Birds or their eggs were taken occasionally, by both sexes, but of 14 records (nine species) in three years, seven were due to a juvenile female (Pom). The mammalian prey species, in approximate order of frequency of capture, were colobus monkeys *Colobus badius* (Kerr), bushpig *Potamochoerus porcus* (L.), bushbuck *Tragelaphus scriptus* (Pallas), redtail monkeys *Cercopithecus ascanius* (Audebert), blue monkeys *Cercopithecus mitis* Wolff and baboons. The main factor influencing whether predations occurred appeared to be the vulnerability of the prey species at the time of the encounter, and adult males were found to eat meat about once every two weeks (Wrangham, 1975). The main prey species, colobus monkeys, contributed about 50% of the total animals killed.

The only inorganic food eaten regularly was earth from termite mounds (not of *M. bellicosus*), of which a walnut-sized piece was eaten on average once a day. Other miscellaneous food types included ash, rotten wood and soil, each eaten rarely but for up to 20 minutes at a time. Individuals were seen to eat their faeces five times. There were no obvious dietary deficiencies associated with the sporadic use of these foods.

Chimpanzees also occasionally licked a concrete slab which had once been covered in common salt. The frequency of this salt-licking varied considerably between seasons, but was not correlated with variations in rainfall or temperature. However, a correlation was apparent with changes in the weights of adult males. By luring individuals up a rope hung on a spring balance weights were measured sufficiently often to rank 12 three-month periods according to male weights: for eight males the mean minimum weight was 36·2 kg, and the mean maximum was 42·6 kg. Periods in which males weighed the most were those in which least salt-licking occurred (Spearman $P<0{\cdot}01$). Weight losses and increased salt requirements may both be caused by a variety of metabolic stresses, including low glucose levels (Forbes, 1962: laboratory rats). The observed relationship suggests that seasonal variation in food availability could have been responsible for changes in the frequency of licking salt.

3.6. Variation with Location

Differences between communities in time spent eating particular foods were clearly related to availability. Southern males, for instance, did not eat *P. curatellifolia* fruit any more frequently in D_2 than in D_1: there were no fruiting stands of this species in the southern community range. *Uapaca nitida* Muell. Arg., on the other hand, was common in the southern but not in the northern community range, and eating time varied similarly. Local variations in food availability were probably also responsible for individual variations in diet of females and sometimes of males within communities: an example was given above (Section 3.4).

It is generally also likely that recorded differences in diet between populations in different study areas are explicable in terms of food availability. However, there is some evidence of "cultural" differences in food selection in relation to tool use and animal foods (e.g. Section 3.1; Goodall, 1973; Hladik, 1973; Nishida, 1973). This subject needs further investigation of the availability of food types: for instance, the fact that termites are not eaten in some areas may be because the particular species which are susceptible to being "fished" are not present. Again, variation in the frequency of predation on monkeys may be due more to regional differences in ease of capture than to "culture" (Wrangham, 1975). For plant foods there is also some evidence of geographical variation in food selection: in Nishida's list (1974) of food types from the Mahali mountains, Tanzania, 35 types appear which are known to occur in Gombe but have not been seen in the diet.

4. DIURNAL RHYTHMS IN FOOD CHOICE

Fruit tended to be eaten earlier in the day than leaves: in 14 days the median time of fruit-eating was 11.33 compared to 14.22h for leaf-eating ($P<0{\cdot}01$) (Fig. 8). This was possibly related to digestive rhythms: if leaves take longer to digest than fruit, night could be the best time to eat them. However two other factors may be responsible for diurnal variation in eating particular foods.

Diurnal variation in item quality might explain the tendency of chimpanzees to eat *Aspilia pluriseta* Schweinf. and *A. rudis* Oliv. and Hiern. only in the early morning. The midpoints of all bouts (on 20 days) were before 8.00h, though the plants were commonly encountered throughout the day. These were the only leaves which broke the general

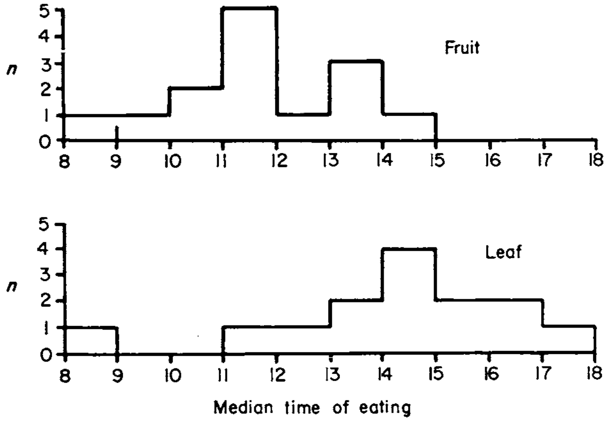

FIG. 8. Median time of eating fruit and leaves. Data from 14 all-day observations.

fruit-leaf rule: a bout of eating *A. pluriseta* was responsible for the early leaf-eating shown in Fig. 8.

Aspilia leaves were eaten only when young. Typically the distal half of a leaf was clipped off and taken into the mouth on the tongue: instead of chewing the chimpanzee would leave his lower jaw slack while apparently rubbing the leaf against his upper palate. Only one leaf, between 2 and 10 cm long, was eaten at a time, and much more slowly than those of other species: in one bout the mean time to eat each leaf was 24·9 sec ($n = 40$), compared with, for instance, 1·5 sec for *Mellera lobulata* S. Moore leaves, which are twice the size. Individual leaves were carefully inspected: a chimpanzee would sometimes close his lips over a leaf up to six times before tearing it off. A further feature when eating *Aspilia* leaves was that chimps sometimes wrinkled their faces above the nose when swallowing.

These curious behaviour patterns suggest that young *Aspilia* leaves contained a special component which was responsible for their selection as food. Robinson (1974) gave three examples of plants in which alkaloid levels fluctuate markedly during the day. Alkaloids are known to affect food selection (Freeland and Janzen, 1974), and it seems possible that diurnal variation in these or other compounds were responsible for *Aspilia* leaves being a dawn delicacy. I could distinguish no changes in taste, however, between different times of day.

The second case of diurnal variation was in the frequency of eating palm nuts: here there was no suggestion of diurnal variation in food quality. Palm nuts were eaten throughout the day in W and D_2 [54% of feeding bouts in all-day observations were before 12.30h, $n = 16$ (W), 42 (D_2)]. In D_1 however the fruit were eaten significantly more often in the morning, 81% of bouts occurring before 12.30h (χ^2, $P<0{\cdot}02$). The tendency to eat palm nuts in the morning in D_1 may have been related to other differences between D_1 and D_2.

(a) Instances of overt competition at palm trees between chimpanzees and baboons were more frequent in D_1 (mean 0·30 per target-palm-nut-hour) than D_2 (mean 0·00/t-p-n-h). Adult male baboons supplanted female and juvenile chimpanzees ($n=3$) but lost to adult male chimpanzees ($n=14$), though the process was sometimes protracted: one baboon was punched on the jaw and in the belly before he climbed away.

(b) The mean length of all bouts of eating palm nuts was longer in D_1 (25·4 min, $n=87$) than in D_2 (17·4 min, $n=54$) (Mann-Whitney $P<0{\cdot}01$). This suggests that more palm nuts were available in D_1 or that they were relatively more important in the diet then. The latter seems more likely since competition with baboons was greater in D_1.

The data suggest that competition for palm nuts may have been greater in D_1 than D_2. Since most of the animals eating palm nuts were diurnal, the time when fruit were most likely to be on the tree was the beginning of the day: competitors should therefore arrive early at palm trees. Thus the tendency to eat palm nuts in the morning in D_1 may have been caused by increased feeding competition. The argument is speculative but suggests that the factors affecting diurnal variation in food selection may be complex. Thorington (1967) found that squirrel monkeys (*Saimiri* spp.) ate more fruit in the morning and insects in the afternoon, and Chivers (this volume) showed that siamang (*Symphalangus syndactylus* Gloger), like chimpanzees, eat fruit more in the morning and leaves in the afternoon. No explanations of these tendencies have yet been proposed.

Teleki (1973b) found that chimpanzees tended to eat mammals in the morning. This now appears to have been an artificial consequence of observations being made near camp, where baboons spent most time with chimpanzees in the morning (Wrangham, 1974). Predations occurred throughout the day from 1970 to 1973.

5. FEEDING BEHAVIOUR AND PARTY SIZE

Individuals feeding together spaced themselves evenly, generally maintaining a distance of more than one arm's reach away from each other. However, the structure of the food source affected spacing. Palm trees were the only ones with a single dense clump of fruit, and at this

FIG. 9. Reassurance as a result of competition for feeding sites. Hugo (adult male) sits in the crutch of a *Sterculia quinqueloba* at the only feeding site. Gilka (adolescent female) squats beneath him grunting softly, and Hugo reaches down to touch her extended hand. Gilka then climbed past him to share the feeding site. Sharing of feeding sites (sitting within arm's reach) was rare at most foods. Hugo and Gilka had been travelling together for two days, and Hugo may have become more tolerant than usual.

species chimpanzees commonly sat within arm's reach. The quality of individual relationships was also important in affecting tolerance of proximity during feeding.

A consequence of respect for personal space was that at sources with unevenly distributed food items some individuals could feed for longer than others. Such differences, of up to 90 minutes of feeding time, were attributed to competition for feeding sites in four types of observation. There were:

(i) where one individual supplanted another (seen 17 times);

(ii) where one individual sat without feeding and moved into another's feeding site as soon as the latter left (seven times);

(iii) where one individual "protected" his food site, e.g. by pulling a food-branch away from another who was reaching for it (14 times);

(iv) where one individual occupied a preferred site, preference being inferred from other observations (11 times).

These instances occurred about once every 20 observation hours. Females and young did not "win" any interactions against males ($n = 30$). Between adult males the "winner" was more high-ranking in 69% (χ^2 n.s.) and older in 90% (χ^2, $P < 0{\cdot}001$, $n = 19$) of events. Figure 9 shows chimpanzees interacting in a tree of *Sterculia quinqueloba* Garck. (K. Schum), in which competitive interactions of type iii were seen five times. Feeding competition occurred frequently at mammal predations and is discussed elsewhere (Teleki, 1973b; Wrangham, 1975).

It was obvious that social interactions unrelated to feeding interfered with feeding time and therefore that increasing party size might be a disadvantage to an individual wanting to eat without being distracted. The occurrence of overt competition for feeding sites further suggests that the mere occupation of feeding sites by others was a potential interference. The following observations support this suggestion.

First, party size appeared to vary with food type. This was difficult to test because the large number of foods meant that sample size on any pair was small. My observations suggested that parties in which the target was eating palm nuts were smaller than those in which he was eating *Harungana madagascariensis* Poir. fruit. The data from other observers confirmed this (χ^2, $P < 0{\cdot}01$) (Table VIII). This relationship appeared due to the number of feeding sites: sources of *H. madagascariensis* occupied a greater volume than *E. guineensis*. Similarly parties were larger in the artificial feeding area when more bananas were available (Wrangham, 1974).

Second, in parties of the same size, there was evidence that the number of individuals feeding varied with the number of feeding sites.

TABLE VIII

Party size at different foods

		Food of target	
		H. madagascariensis	*E. guineensis*
Party size	1–2	3	15
	3–8	6	3

Data from files of Gombe Stream Research Centre. Cells show number of bouts for different party sizes (recorded at the mid-point of the bout).

This was tested by comparing parties of six or more individuals at different food sources. *G. huillensis* trees had many feeding sites and tended to fruit abundantly or not at all. In November 1972 the median percentage of party members feeding when the target ate *G. huillensis* fruit was 74·7%, against 33·3% for other foods (median test, $n=23$, $P<0{\cdot}05$).

Third, the probability of feeding decreased with increasing party size. Bygott (1974) found that individuals spent more time feeding when alone than when they had companions. To explore this relationship the effect of party size was tested by comparing the percentage of individuals feeding in parties up to size i with those of size $i+1$ and larger ($i=1$ to 16). In 22 out of 35 possible comparisons the percentage of individuals feeding in smaller parties was significantly higher than in larger parties (χ^2, $P<0{\cdot}05$–$0{\cdot}001$). The results are shown in Fig. 10, which also shows that in D_1 the rate of decline of feeding probability with party size was greater than in W or D_2. To an individual wanting to feed, therefore, it was relatively more important to be in a small party in D_1.

Problems in describing the nature of the food source impose difficulties in analysing the relationship between feeding competition and party size: a feeding site is not an absolute unit. Nevertheless the data indicate that feeding time varied with the availability of feeding sites and hence with party size. Therefore, even though diverse social relationships must influence party formation, we may expect the tendency to leave or join parties to be a consequence of feeding success. This possibility is now examined.

Parties sometimes divided at food sources with limited feeding sites. The clearest kind of example was when one member of a party found a single bunch of fruit and his companions left him to eat it alone. However it was difficult to test the importance of food availability in affecting the break-up of parties.

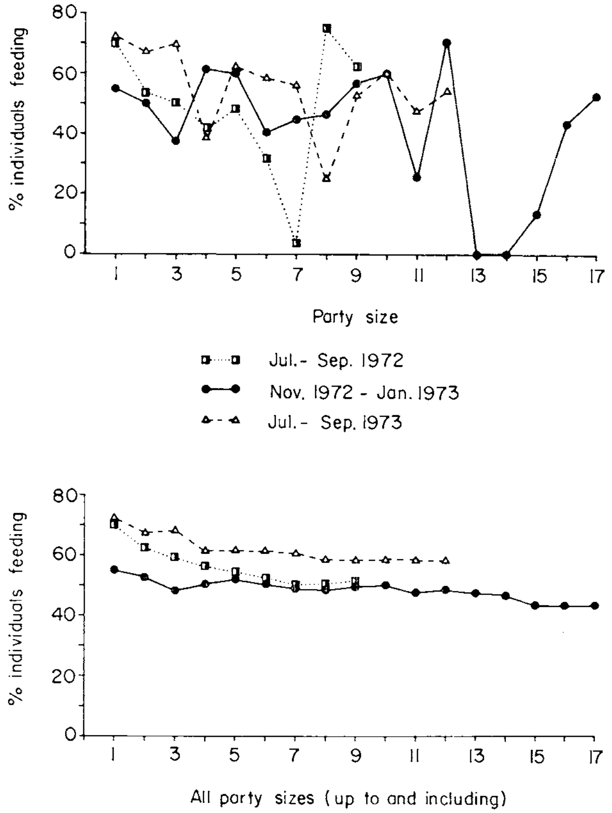

FIG. 10. Party size and probability of feeding. The number of individuals present, and the number feeding, were scored on 30-min points in all-day observations. Sample sizes as in Table V.

The tendency to aggregate could be examined more easily. To find out if individuals tended to travel together after feeding records of arrival and departure at the artificial feeding area were analysed. The results are shown in Table IX. Previously separate individuals were more likely to form a party if they fed together (χ^2, $P<0{\cdot}05$).

Aggregation also occurred as a consequence of long-distance food-calls. Food-calls are defined as pant-hoots (Goodall, 1968) given within two minutes of starting to eat: though variable in quality extreme forms could be classified as "food-pant-hoots", which were given only on arrival at a food source (Plooij, in prep.). Between food types the probability of food-calls increased with mean length of feeding bout (Spearman $n=20$, $P<0{\cdot}05$); and for particular food types mean bout lengths were longer following a food-call (Sign test, $P<0{\cdot}05$).

TABLE IX

Effect of feeding together on tendency to travel together

	Both individuals given bananas	Neither individual given bananas
Individuals leave together	13	29
Individuals leave separately	2	25

Only individuals arriving separately (from different directions and in different 15-min periods) were scored: subjects were sampled at random and the behaviour of companions recorded. Data are from camp attendance files for January to September 1971. The figures show the number of times each combination occurred in the sample.

Thus a chimpanzee appeared more likely to call if he saw that food was abundant at the source. The consequence of his food-call is shown in Fig. 11. Though only adult males gave calls, both sexes tended to respond by joining the caller (and feeding with him). These results confirm the suggestion that individuals tended to aggregate at good food sources and as a consequence of feeding together. Their significance is examined in Section 8.

6. SEASONAL VARIATION

6.1. Food Availability and Feeding Behaviour

Interpretation of the significance of seasonal changes in feeding behaviour is dependent on some estimate of the extent of changes in the

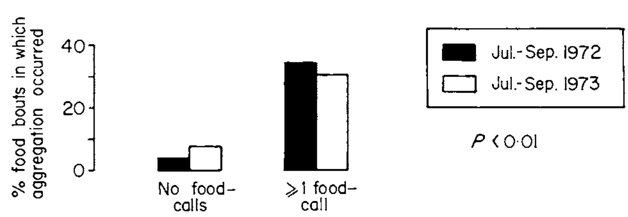

FIG. 11. Aggregation probability in relation to food-calling. Only food-calls given by the target were scored. Within seasons feeding bouts were matched for food type and as closely as possible for bout length, and all bouts begun with a food-call in D_I were used. The figure shows that individuals were more likely to arrive at a target who had started his feeding bout with a food-call than at one who had not (χ^2, $P<0{\cdot}01$). For each sample $n = 26$ food-bouts, matched within seasons for length and food type.

environment. As argued earlier (Section 2.3), the most meaningful comparison is likely to come from the successive dry seasons, D_1 and D_2. Some data from the wet season, W, are also given, but change in a number of environmental variables between wet and dry seasons makes their interpretation hazardous.

The only independent indication of a change in food availability between dry seasons was that the major food (*P. curatellifolia* fruit) in D_2 failed almost completely in D_1, while there were no comparable failures in D_2. A number of dependent measures also indicate that more food was available in D_2. First, when 12 three-month periods were ranked according to the weights of adult males, D_2 was six ranks (and W three ranks) higher than D_1. The most obvious explanation of the higher weights in D_2 is that the males ate more: note that their energy costs were apparently higher, travelling twice as far per day in D_2 as in D_1. Second, changes in feeding behaviour indicated that competition was greater in D_1 than in D_2 (or W). These changes were (a) in behaviour when eating palm nuts (Section 4), and (b) in the rate of decrease of feeding probability with party size (Fig. 10). Third, it is possibly relevant that in D_2 fewer food species made up the bulk of feeding time than in D_1 (Fig. 6): this result accords with models of feeding strategy (e.g. Schoener, 1971) which predict that diet breadth should increase as overall food availability decreases. The available evidence, therefore, suggests that in D_1 chimpanzees found it harder to eat well than in D_2, the fruiting failure of *P. curatellifolia* being an important cause.

6.2. Party Size

It was earlier found (Section 5) that parties became larger as a consequence of high food availability at a source. This suggests that parties could become larger as a consequence of increased food availability between seasons. Seasonal changes in the frequency of food-calling and in overall party size are accordingly examined.

The median frequency of food-calling per feeding bout was 0·00 in D_1, 0·08 in W and 0·13 in D_2. Frequencies were compared in relation to the total number of calls in order to discount calls occurring at the beginning of a bout by chance: fewer food-calls were given in D_1 than in W ($P<0{\cdot}05$) or D_2 ($P<0{\cdot}05$), and the difference between W and D_2 was not significant. However, although food-calls were less frequent in D_1 than D_2, the tendency to join the caller was the same in both seasons (Fig. 11).

Party sizes were analysed using data from all observers. Targets were matched between seasons, and party size recorded at 12.30h provided that the target had left the artificial feeding area at least two hours previously. All available individuals were used ($n \geqslant 17$). In D_1 parties were found to be significantly smaller than in D_2 or W ($P < 0{\cdot}01$), while the difference between D_2 and W was not significant. It is difficult to give meaningful averages of party size, because of the sampling problems, aggravated by considerable individual variations in sociability. For instance Halperin (in press) found that mothers spent between 50 and 80% of their time alone (apart from dependent young), and adult males between 2 and 54%. As an indication of the seasonal differences for adult males, however, party sizes scored on 30-minute points during all-day observations gave medians of 1·4 independents in D_1, 1·9 in W and 2·4 in D_2. The change in sociability between D_1 and D_2 is exemplified in Fig. 12, showing how five males increased the amount of time they spent with each other and with females between D_1 and D_2.

Thus the postulated increase in food availability from D_1 to D_2 was accompanied by increases in the frequency of food-calling and party size, as expected from the results in Section 5.

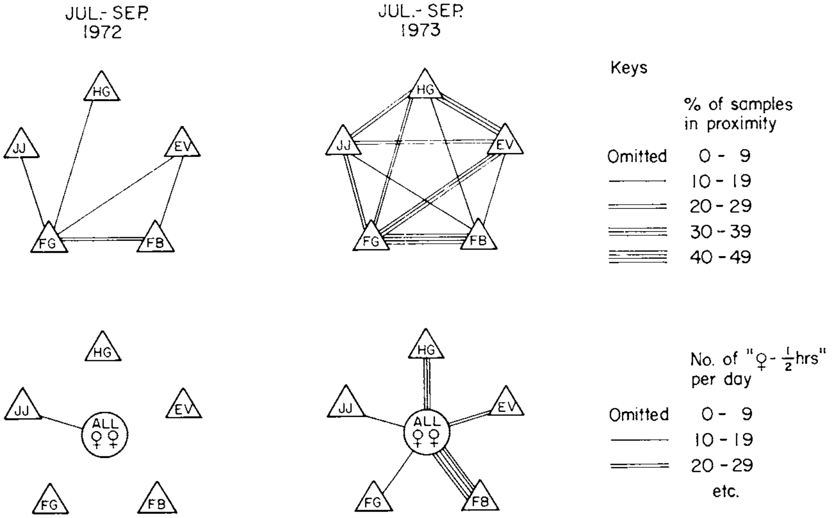

FIG. 12. Seasonal change in association patterns. Data for five northern males during all-day observations. Records of association (two individuals within 100 m) were scored on 30-min points, and each individual contributed 20% of total observation time as target (20% × 5 = 100%). Top: dyadic association patterns among the five males sampled. Per cent time together increased for all pairs between D_1 and D_2 (EV–FB increased from 10·8 to 15·6%). Bottom: time spent by each male with all females. Total half-hours with each female present were scored and summed across females. All males spent more time with females in D_2 than D_1 (JJ increased from 15 to 18 "female-half-hours" per day).

$n = 10$ days (D_1), 20 days (D_2).

7. RANGING BEHAVIOUR

7.1. Individual Ranging Patterns

All the target males in this study were seen regularly between 1968 and 1973, and were thus largely resident in the study area. Within it, however, their ranging patterns were protean. Fig. 13 shows an example of the travel path of a male over four days. The shape of a day's path varied from straight to convoluted or even circular, when the target slept in the same nest on consecutive nights, but individuals of both sexes tended to avoid crossing their own path more than once, doing so twice or more on 15% of days. Analysis of ranges over four days and one year showed that individuals tended to occupy "core areas" within the community range, "core area" referring merely to frequency of use of the area. Both core areas and full year ranges of anoestrous females were smaller than those of males, for which the maximum observed year range was 12·5 km^2. The location of individual core areas was stable over at least one year, but there was evidence that the size of male core areas varied seasonally. Females in oestrous had variable ranging

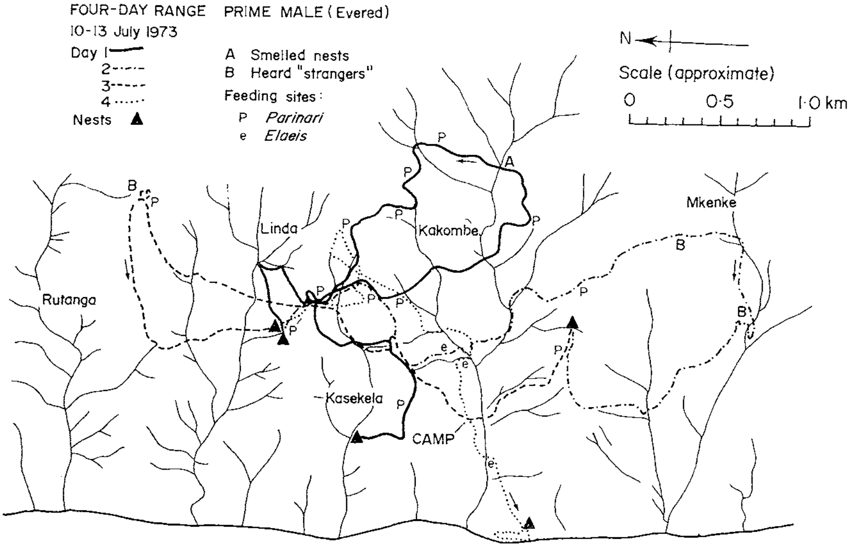

FIG. 13. Four-day travel path of adult male. The example is for Evered, 10–13 July 1973. "P" (*P. curatellifolia*) and "e" (*E. guineensis*) mark food sources accounting for about 60% of feeding time. Interactions involving members of other communities occurred at points A and B: these were on the boundaries of the four-day range, which approximately covered the community range. No other individual was with Evered for the complete four days.

FIG. 14. A group of chimpanzees moving between feeding sites.

patterns which included travelling more widely than usual in the community range, consorting with a male on the edge of the community range, or travelling in a different community range (Wrangham, 1975; Tutin, in prep.).

7.2. Food Searching

Observations of lone males demonstrated clearly their intimate knowledge of the environment. They were excellent botanists, discriminating finely between subtle visual cues of species type or plant condition; and the frequency and direction of visual inspection appeared to vary according to the food types the habitat could be expected to contain. There was evidence also of a capacity for and continual use of a detailed spatial memory. Chimpanzees were capable of returning to known food sources precisely and by economical routes, apparently from any direction. This was an important skill. Table X shows that when a male crossed his own path he was more likely to do so at a food source if he returned within three days than after a month (χ^2, $P<0{\cdot}001$). Botanical and spatial memories seemed to be used together in cases where individuals travelled directly to habitat types in which the exact location of resources could not be known, but where some "ripe" sources were likely to occur. Examples included gullies where patches of *M. lobulata* could be expected to be in fresh leaf; deciduous forest dominated by *Combretum molle* G. Don, with some trees exuding edible resin; and grassland containing sporadic plants of *Aspilia* spp., hunted only at dawn. No experimental analysis of spatial memory skills was attempted, but Menzel (1973) showed that captive chimpanzees could

TABLE X

Activities where a male crossed his own path

	% of occasions when crossing path after elapsed time	
Activity	4 hr–3 days	More than 30 days
Feed	57	14
Sit in camp	24	24
Travel along ridge	5	5
Return to nest site	5	0
No apparent reason for return	9	57

$n=42$ path-crossings for each time period.

remember accurately the locations of objects hidden in a 122 m × 30 m enclosure.

Convincing examples of individuals locating major food sources without some prior knowledge of them were difficult to obtain. Doubtless they sometimes occurred: but far more often the chimpanzees would have seen, as I did, that particular trees were slowly coming into fruit, for example, and returned to them accordingly. My subjective impression was that a chimpanzee noticed and remembered enough about the environment on his daily travels for his best feeding strategy to be reliance on the knowledge so gained.

The problem with this idea is the difficulty of testing it. However its value lies in raising doubt about assumptions underlying previous discussions of the food searching methods of frugivorous primates. Reynolds and Reynolds (1965) and Eisenberg *et al.* (1972) considered that repeated dispersion and recombination of parties was a necessary adaptation for increasing the searching power of a social group. These views are discussed in Section 8.

7.3. Seasonal Changes

Males spent more time travelling per day in D_2 than in D_1 ($P<0{\cdot}01$) or W ($P<0{\cdot}05$) (Table V). The sample was based mostly on northern males, for whom the median length of day range increased from 3·8 km (D_1) to 6·4 km (D_2). Table XI gives further data on distances travelled, and indicates that the day ranges of southern males were similar in different seasons. A possible explanation is that the abundant fruiting of *P. curatellifolia* in D_2 was virtually confined to the northern community range. Few data are available for anoestrous females, but certainly they travelled less widely than males in D_2. Sparse data on four-day ranges also indicated an increase in size for northern males from D_1 to D_2. The median number of squares (0·5 × 0·5 km) occupied was 15·0 in D_1 ($n=4$) and 19·0 in D_2 ($n=7$).

TABLE XI

Seasonal variation in day ranges

	D_1			W			D_2		
	Distance	*ni*	*nr*	Distance	*ni*	*nr*	Distance	*ni*	*nr*
Northern males	3·8 km	8	28	4·2 km	8	21	6·4 km	6	26
Southern males	3·8 km	4	11	4·8 km	1	1	3·3 km	3	6
Northern females	3·0 km	5	17	2·0 km	4	7	3·9 km	2	17

ni = no. of individuals sampled, *nr* = no. of observations.

Thus in D_2 northern males apparently travelled farther per day, and individuals used the community range more evenly, than in D_1. This result is supported by analysis of the directions used by northern individuals when entering the artificial feeding area, which was sited near the middle of the community range. The strength of the tendency to use a particular direction varied between the sexes: females were more highly "directed" than males (Mann-Whitney $P<0{\cdot}05$). However this was not true in D_1, when the similarity between the sexes appeared due to males being more highly "directed" than in other seasons, rather than females less so. This indicates that individual males were more confined to particular parts of the community range in D_1 than D_2. Wrangham (1975) found that the wider travel in D_2 was associated with an increase in the frequency of interactions with individuals of other communities: such interactions occurred on 35% of days in D_1, 37% of days in W and 67% of days in D_2 (see Fig. 13).

In summary there were no striking seasonal changes in the ranging behaviour of females or southern males. In D_2, however, when food availability appeared higher than in other seasons, northern males travelled farther per day, shared the community range more fully with each other, and interacted more frequently with neighbouring communities.

8. DISCUSSION

Both within and between seasons smaller parties appeared to be a consequence of increased feeding competition. Previous studies have also indicated that party size varied seasonally, possibly in relation to food availability (Azuma and Toyoshima, 1962; Reynolds and Reynolds, 1965; Sugiyama, 1973; Nishida, 1974). If chimpanzees prefer to feed in small parties sometimes, the problem arises as to why they should be more sociable at other times. There are two possibilities. First, under certain conditions chimpanzees might feed more efficiently by being in large parties. Second, when food is abundant the disadvantage of increased feeding competition in large parties might be outweighed by advantages unrelated to feeding.

Greater feeding success as a function of grouping has been attributed to a variety of mechanisms in different species. Solitary birds, for instance, spend more time being vigilant and therefore less feeding than those in parties (Murton, 1971; Lazarus, 1972): but this does not apply to chimpanzees. Nor does co-operation in hunting appear adequate to explain sociability: (a) it is infrequent, (b) there is no evidence that larger parties cause greater hunting success, (c) after the kill competition for meat is severe and (d) the outcome is unrelated to participation in the hunt (Wrangham, 1975). The facts are not available to test for certain the suggestion that the important consequences of aggregation are to regulate the time of return to food sources so as best to crop the new growth (Cody, 1974a); or that an individual lowers his risk of finding too little food by joining others (Thompson, *et al.*, 1974). However if larger parties generally increased feeding success they would be expected to occur in D_1, when food availability appeared lowest: the reverse occurred. The observed relationship between party size and food availability could only be explained by postulating for instance that only in W and D_2 was "return time regulation" important. Conceivably this is true. However there is no supporting evidence and a simpler hypothesis emerges from considering the significance of food-calls.

Reynolds and Reynolds (1965) and Eisenberg *et al.* (1972) considered that the function of food-calling was to spread information about the location of food sources. Food-calling is thereby seen as altruistic, since calling involves time and energy expenditure as well as incurring the costs of feeding competition from those who respond by sharing the source. Benefit to the caller could come from reciprocity (Trivers, 1971) or from advantages conferred on kin (Hamilton, 1964). Neither seems important since individuals appeared to know their environment so well. Furthermore food-calling was least frequent in D_1, when food availability appeared lowest: this was presumably the time when benefits from "learning" the location of new food sources would be greatest. But if food-calling does not have the function of helping others find food, how is it to be explained?

First consider the listener. The food-call tells him (or her) that a male has just arrived at a nearby food source which is now being depleted. If he (or she) already knew of its existence, as I believe would normally be true, the important information is that it is being used: to capitalize on his (or her) knowledge, the listener must go to the source before others have finished the food. Occasionally there may be the additional benefit of learning about a new food source, but there is no need to invoke this as an explanation of the tendency to aggregate.

Now consider the caller. He (but not she) arrives at a food source which he judges to contain sufficient food for himself to feed well, even in the presence of others. He knows that the consequence of his calling is that others may join him; but we have seen that their response may be functional in reducing the effects of an announced competitor rather than in benefiting from the caller's "altruism". It thus appears that the benefit of calling lies not in informing others but rather in the advantage he confers on himself (or his kin) in creating or enlarging a social group. If such an advantage exists, neither food-calling nor the formation of large parties need be regarded as having the function of improving feeding success.

For a species in which co-operation between the sexes appears largely unnecessary except for mating, we expect the sexes to respond differently to an increase in food availability, with extra resources being used by females for increasing the rate of the reproductive cycle, and by males for increasing the number of potential mates. This suggests that the larger parties and more extensive travel of males in D_2 represented increased reproductive effort. Two possible benefits of such behaviour are proposed. First, the enlargement of a social group may increase the opportunities for a male to display characteristics which improve his chances of being selected for mating. Possibly the very fact that a male is prepared to withstand the costs of increased feeding competition may be a sexually selective character. Most females at any moment are likely to be anoestrous but reproductive competition may be expected to continue between males, since any female will be oestrous in the future and will presumably choose a male on the basis of her full knowledge of him.

Second, from recent observations of aggressive relations between males of different communities (Bygott, 1974; Wrangham, 1975) it is clear that an important factor determining the outcome of the interaction is the relative size of parties. If it is normally true that the larger party wins the encounter then the community which can most frequently form large parties will achieve territorial gain at the expense of its neighbours. Wrangham (1975) argued that the functional consequence of territorial expansion was the acquisition of females, since there is some evidence that they do not always follow a retreating male community. If so, we may view the formation of large parties as improving the reproductive success of a male community through its increased probability of winning territorial encounters, and hence females. Furthermore the evolution of communities may be explained as due to successful competition for females by groups of males, group territoriality being possible when locomotion costs are low.

This hypothesis was given in greater detail by Wrangham (1975). As it stands, it may underestimate the functional importance of the complex social relationships of chimpanzees (but note that competition between and within male communities must lead to a complex system of relationships between males). While giving a unifying framework for the present observations, it needs to be tested by further data, especially on sexual behaviour (Tutin, in prep.) and intercommunity relations.

9. SUMMARY

1, 2. Most of the data come from all-day observations of 14 adult males who were members of two neighbouring communities. Three seasons are compared: D_1 and D_2 were dry seasons from 1972 and 1973, and W the intervening wet season.

3. Variations in feeding techniques were a function of the type of food. Feeding occurred mostly in trees and occupied from 46–60% of the active day in natural habitats. Chimpanzees ate an average of 15 food types per day and 60 per month: but over a two-month period 50% of food types accounted for 95% of feeding time. The time spent eating the major foods was related to their availability.

4. Diurnal rhythms in food choice included the tendencies to eat fruit earlier than leaves, to eat *Aspilia* leaves at dawn and to eat palm nuts in the morning in D_1 but not in D_2. The factors responsible may include diurnal changes in item quality and in the intensity of competition for food.

5. Feeding time and party size were related to the nature of the food source, apparently as a consequence of competition for feeding sites, although instances of overt competition at plant foods were seen only once every 20 hours. The probability of an individual feeding declined overall with increasing party size. Males arriving at large food sources gave long-distance "food-calls", which tended to attract individuals of both sexes.

6. Between successive dry seasons, D_1 and D_2, food availability appeared to increase in the northern community range as a consequence of the successful fruiting of *Parinari curatellifolia*. In D_2 feeding competition was less severe, food-calling was more frequent and parties were larger than in D_1.

7. Individuals travelled by irregular routes within year ranges of about 12·5 km^2. Within community ranges individuals occupied different "core areas" which were larger for males than for anoestrous females. In D_2 northern males travelled farther and interacted more frequently with neighbouring communities than in D_1.

8. There is no evidence that the frequent dispersal and recombination of chimpanzee parties is a mechanism for increasing food-searching efficiency. An alternative explanation of variable party size is given, in which large parties, which appear possible only when food is abundant, are viewed as the consequence of reproductive competition by males.

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Some Aspects of Intraspecific Variation in Feeding and Ranging Behaviour in Primates

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1. INTRODUCTION

It is evident that we are, at present, only beginning to appreciate the extent to which feeding behaviour varies both between primate species, and within them. Two trends are evident from recent studies of feeding behaviour. There is an increasing awareness of the complexity of factors

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affecting food choice: it is now clear that calorific value is only one of many factors affecting food selection and that several kinds of qualitative differences between foods are important. Second, the kinds of variation which we can expect to find both between species and within them are becoming better known. It has, for example, only recently been realized that dietetic diversity varies markedly between many sympatric primate species (Hladik and Hladik, 1972; Clutton-Brock, 1974a; Struhsaker and Oates, 1975); that, in some species, food choice differs systematically between the sexes (e.g. Pollock, Ch. 2; Waser, Ch. 7); and that diurnal variation in food choice may be widespread (e.g. Chivers, Ch. 12; Wrangham, Ch. 17). Appreciation of the extent of intraspecific variation is important both because of the many insights it can provide into evolutionary and ecological influences on feeding behaviour and because it affects the ways in which data samples must be distributed to provide realistic estimates for the population.

The first section of this chapter examines some of the factors affecting food choice while the latter part reviews different aspects of intraspecific variation.

2. FOOD CHOICE

Several generalizations emerge from comparison of the diets of different primate species.

All primate species studied so far are highly selective in their choice of foods, often consistently selecting specific parts of particular species. Both red colobus and howling monkeys, for example, will carefully eat the basal portion of the leaves of some tree species and the apex of the leaves of other species (Clutton-Brock, 1975a; Struhsaker, 1975; K. Milton, pers. comm.).

In general, shoots, flowers and fruit are more commonly eaten than mature leaves. Differences at this level are easily explicable in terms of the higher protein contents and the lower cellulose levels found in these parts (Hladik, Chs 11, 16; Goodall, Ch. 15). The extent to which particular parts of leaves are selected (see above) is probably related to variation in protein or sugar concentrations within the leaf. Differences between food species in the extent to which the various parts are eaten are also, probably, related to qualitative differences. In some cases these too may be the product of simple differences in energetic value or digestibility: primates which feed extensively on mature leaves, such as *Colobus guereza*, tend to select the leaves of deciduous, colonizing tree species (see Oates, Ch. 10), which often contain lower levels of cellulose and are more easily digested than those of evergreen species.

Three other types of qualitative differences are likely to affect the extent to which different species are selected.

(i) The leaves and, to a lesser extent, the fruit of different species vary in the specific nutrients they contain. In order to achieve a balanced diet, it may be necessary for both folivores and frugivores to select particular food species for their chemical content (Westoby, 1974). For example, Oates (Ch. 10) found that at two- to four-week intervals, *Colobus guereza* groups descended from the trees and travelled to pools of open water in swampy valley bottoms, feeding there on water plants. Subsequent analysis revealed that the leaves of these species contained high levels of sodium which may have been relatively scarce in the rest of the animals' diet. It may even prove to be the case that the extent to which plant species are selected depends on the particular amino acids which they contain: chimpanzees in Gabon selected both plant and insect species whose amino acids were complementary (Hladik, Ch. 16). There is little doubt that caged mammals are able to adjust their food choice (see Hinde, 1970; Emlen, 1973), in some cases immediately selecting foods which complement deficiencies (Richter *et al.*, 1938; Barnett, 1963), in others, increasing the variability of food choice until a food is found which satisfies the deficiency (Rodgers and Rozin, 1966). It would be surprising if wild populations were not equally adept at avoiding dietetic imbalance.

(ii) The seeds and leaves of many tropical tree species contain a variety of secondary compounds, including tannins, alkaloids and terpenes (Bate-Smith, 1972). Not only may animals avoid the parts of those tree species which contain especially high levels of toxins, but they may select a varied diet within days, thus acquiring doses of different toxins which are small enough to be neutralized (Freeland and Janzen, 1974). However, there is little firm evidence of the importance of toxin avoidance in determining food choice in primates. While a wide variety of secondary compounds are present in most leaves, their levels are frequently low (A. Hladik, 1976) and small amounts can usually be eaten without danger. Moreover, some species (including chimpanzees, which possess a simple digestive system and cannot de-toxify foods by fermentation preceding absorption) show little selection against plant species in which alkaloids occur though they may avoid those carrying high concentrations (Hladik, Ch. 16).

(iii) Animals may select particular foods to facilitate digestion. A variety of primate species eat small amounts of earth (Ripley, 1970; Hladik and Hladik, 1972; Goodall, 1968; Oates, 1974; Hladik, 1973; Clutton-Brock, 1975a; Pollock, 1975b). Though this may sometimes serve to correct mineral deficiencies, the mineral concentrations available in the soil frequently do not exceed those present in many common foods (Hladik, Ch. 16; Pollock, 1975b) and an alternative explanation is that phyllitous soil may aid digestion by absorbing secondary compounds (Hladik, Chs 11, 16). Similarly, Goodall (Ch. 15) suggests that gorillas may eat a particular vine (*Schefflera* spp.), despite its low energetic value, because its woody fibres facilitate digestive action. And it is even possible (Oates, Ch. 10) that some of the primates which digest by fermentation may selectively eat foods containing a proportion of tannins to help reduce the chance of "bloat".

Either dietetic balancing or toxin absorption will probably help to explain why some foods, whose availability shows little apparent seasonal variation, are only selected at certain times of year (see Clutton-Brock, 1975a; Struhsaker, 1975); why others are eaten regularly but always in small amounts (e.g. Oates, Ch. 10; Wrangham, Ch. 17); and why many primates select a diverse diet within days, quitting food sources when food is still abundant and moving on to feed on different foods (see Clutton-Brock, 1975a; Hladik, Chs 11, 17; Smith, Ch. 4; Wrangham, Ch. 17; Rodman, Ch. 13).

3. ECOLOGICAL SEGREGATION AND SPECIES DIFFERENCES IN FOOD CHOICE

In many cases, sympatric primates overlap extensively in the species composition of their diets (e.g. Sussman, 1974; Struhsaker and Oates, 1975; Hunt Curtin, 1976). While such differences may become more obvious when food availability is low (e.g. Newton, 1967), ecological segregation between sympatric primates probably depends primarily on other differences.

Within sympatric primate faunas, differences in feeding level are common (Gartlan and Struhsaker, 1972; Eisenberg *et al.*, 1972; Hladik, 1975; Dunbar and Dunbar, 1974a; Hunt Curtin, 1976) and species tend to concentrate their time in particular levels of the canopy. For example, Waser (Ch. 7) found that mangabeys in Kibale forest tended to remain lower in tall trees and higher in low ones.

The proportion of the diet made up of different parts (leaf, shoot, flower, fruit, gum) also varies widely between species and is associated with variation in the chemical constituents of the diet (Hladik, Chs 11, 16; Hladik *et al.*, 1971a). Many folivorous species show adaptations to their diet either in the structure of the stomach (e.g. *Colobus* and *Presbytis* spp.) or in the length of the caecum (e.g. *Lepilemur*, *Alouatta*: Hladik, 1967). Other differences in diet are associated with more subtle physiological differences: those between *Presbytis entellus* and *P. senex* (see below) are not correlated with any major variation in intestinal morphology, but with detailed differences in the form of the intestinal mucosa (Hladik *et al.*, 1971a). Interrelationships between digestive physiology and diet constitute an important research area but one which, as yet, has been little explored.

The ability to feed on particular growth stages also differs between species: frugivores tend to select ripe fruit while folivores may feed both on ripe and unripe fruit. Interspecific comparisons are complicated by the fact that differences of this kind may only be apparent at certain times of year. For example, though black and white colobus spend a smaller *average* proportion of their feeding time eating mature leaves than red colobus, in some months their diet consists largely of mature foliage (Clutton-Brock, 1974a; Struhsaker and Oates, 1975; Oates, Ch. 10). This may permit them to colonize environments where the production of shoots, flowers and fruit is highly seasonal (Clutton-Brock, 1974b).

Dietetic diversity also differs between species (see Sussman, Ch. 1; Clutton-Brock, 1974b; Struhsaker and Oates, 1975; Hladik and Hladik, 1972). Folivores, particularly those which feed extensively on mature leaves, tend to select a less diverse diet than frugivores (see p. 564).

Finally, among primates which feed extensively on invertebrates, differences occur in the kinds of prey selected. In Kibale forest, redtails (*Cercopithecus ascanius*) tend to feed on more mobile invertebrate species than blue monkeys (*Cercopithecus mitis*) while mangabeys (*Cercocebus albigena*) feed extensively on insects located under bark or in dead wood (Struhsaker, 1975 and pers. comm.).

4. INTERPOPULATION DIFFERENCES IN FOOD CHOICE

Where the availability of different food species is similar, both individuals belonging to the same group and members of different groups tend to select similar diets (see Chapters 1, 2, 8, 11 and 12). Some differences emerge which cannot be explained as the product of variation in availability. For example, Richard (Ch. 3) found that the southern populations of *Propithecus verreauxi* fed extensively on the fruit of *Rothmannia decaryi* whereas the northern population ate only the flowers of this species. Interpopulation differences of this kind have also been recorded for mangabeys (Waser, Ch. 7) and chimpanzees (Hladik, Ch. 16) while studies of several species have demonstrated differences between neighbouring troops (Japanese macaques: Kawamura, 1959;

Azuma, 1973; red colobus: Struhsaker, 1975). However, where natural food sources are concerned, such differences are usually slight and the evidence supports the view that food choice among primates is usually closely constrained by qualitative and quantitative differences between foods (see above).

The species composition of the diets of most primates differs widely between populations as a product of variation in the availability of particular foods (see Chapters 1, 2, 11, 12, 16 and 17). There is no evidence that any primate species shows a high degree of food species specificity, as is the case in many invertebrates as well as in some vertebrates (Freeland and Janzen, 1974) though some primates (e.g. *Lepilemur*, *Lemur mongoz*) usually feed on few plant species (Hladik and Charles-Dominique, 1974; Tattersall and Sussman, 1975).

5. AGE AND SEX DIFFERENCES IN FEEDING BEHAVIOUR

It is evident that in many primate species, feeding behaviour varies between age and sex categories. Moreover, similar differences exist in different species.

5.1. Feeding Levels and Feeding Sites

In both arboreal and terrestrial species, younger, lighter individuals spend more time feeding in the terminal twigs than adults e.g. *Indri indri* (Pollock, Ch. 2); *Papio hamadryas* (Kummer, 1971); *Cercocebus albigena* (Waser, Ch. 7); *Colobus badius* (Clutton-Brock, 1973). In *Symphalangus*, juveniles spend more time feeding from suspended positions while *Gorilla* adults spend less time feeding in trees than juveniles (Chivers, Ch. 12; Fossey and Harcourt, Ch. 14). Similar sex differences occur in several species where the male is appreciably heavier than the female e.g. *Colobus badius* (Clutton-Brock, 1973); *Papio hamadryas* (Kummer, 1971). Other sex differences in feeding sites are probably the product of displacement of one sex by the other: in *Indri* (where the female is dominant to the male) the male spends more time feeding in the terminal twigs than the female (Pollock, Ch. 2).

In at least three species (*Indri*, *Colobus badius* and *Pongo*), males spend more time feeding at lower levels in the canopy than females or immature animals, though in others (e.g. *Cercocebus albigena*) this is not the case (Pollock, Ch. 2; Clutton-Brock, 1973; Gatinot, 1975; Waser, Ch. 7; Rodman, Ch. 13). In *Indri*, this occurs because the male is displaced from preferred feeding areas by the female (see above) but this is an unlikely explanation of the difference in the other two species. In these, increased male body size may reduce the risk of predation and males may feed more safely at lower levels than females.

5.2. Activity Budgets

As in many ungulates (e.g. Spinage, 1968; Clough and Hassam, 1970; Owen-Smith, pers. comm.), adult males commonly spend proportionally less time feeding and more resting or inactive than females or young animals e.g. *Indri* (Pollock, Ch. 2); *Alouatta villosa* (Smith, Ch. 4); *Cercopithecus aethiops* (Kavanagh, pers. comm.); *Cercocebus albigena* (Waser, Ch. 7); *Theropithecus gelada* (Dunbar, Ch. 9); *Colobus badius* (Clutton-Brock, 1974c); *Symphalangus* (Chivers, 1974, Ch. 12). In contrast, in *Pongo*, adult males spend more time feeding than females (though the number of feeding bouts per day is similar) (Rodman, Ch. 13) and in *Gorilla*, silverbacked males (but not blackbacked) spend more time feeding than females or immatures. Males might be expected to feed for less time per unit body weight than females because (a) they do not incur the costs of pregnancy and lactation. This is supported by differences in feeding time between females with dependent offspring and those without (e.g. Smith, Ch. 4); (b) in most species males are dominant to females and maintain priority of access to the areas of maximal food availability; (c) they tend to feed faster than females e.g. *Indri* (Pollock, Ch. 2); *Colobus badius* (Clutton-Brock, 1972); *Gorilla* (Fossey and Harcourt, Ch. 14), though the reverse is true in *Symphalangus* (Chivers, 1974, Ch. 12).

The most likely explanation of the reversal of this trend in *Pongo* and *Gorilla* is that the extreme sexual dimorphism in body weight found in these two species (Clutton-Brock and Harvey, in press) requires the male to feed for longer periods than the female despite her increased energetic expenditure on pregnancy and lactation.

5.3. Food Choice

Sex differences in diet composition occur in several species. In *Indri* (Pollock, 1975b, Ch. 2) and in *Colobus badius* (Clutton-Brock, unpublished data) males may eat more fruit and less foliage than females; and in *Cercocebus albigena*, Waser (Ch. 7) found that males spent proportionately (though not absolutely) more time feeding on fruit and less time foraging for insects than females and immature animals, while immatures spent more time feeding on flowers and the stems of leaves.

Conversely, male orang-utans may eat less fruit and more bark than females, particularly when food is scarce (Rodman, Ch. 13).

Sex differences in the proportion of time spent on particular plant species also exist. In *Cercocebus albigena* in Kibale forest, Waser (Ch. 7) found that males spent more time eating the fruits of *Diospyros absyssinica* than females or immatures. In *Gorilla*, silverbacked males fed more on thistles than other individuals, while immatures spent more time on *Vernonia* and *Pleopeltis* than adults (Fossey and Harcourt, Ch. 14). Finally, male chimpanzees kill more vertebrates than females (Wrangham, 1975) and eat different amounts of particular invertebrate species (McGrew, in press).

Many of these differences, like those in feeding level and height, are probably the product of sex differences in body size or strength. Increased foraging for insects in *Cercocebus albigena* males may be connected with superior dentition since many invertebrates are collected by pulling or biting sections of bark from tree trunks (Waser, Ch. 7) and the same factors may also help to explain why the fruits of *Diospyros abyssinica* were eaten to a greater extent by males. Similarly, male chimps may kill more vertebrate prey (Wrangham, 1975) because they are better equipped to do so. In contrast, the trend towards increased fruit intake in males is more likely to be related to sex differences in nutritional requirements. Females and young animals may need higher levels of protein in their diet than fully grown males and may consequently feed more on foliage and insects (see Hladik, Ch. 16, pers. comm.): there is extensive evidence from other vertebrate groups that young animals tend to take a higher proportion of animal matter than adults (Clark and Gibbons, 1969; Collias and Collias, 1963; Schoener and Gorman, 1968; Schoener, 1968; Ward, 1965; Newton, 1967; Royama, 1970a). The fact that male *Indri* take more fruit than females despite being subordinate to them, suggests that this trend is not a product of increased access to preferred resources in males.

Three evolutionary explanations of sex differences in feeding behaviour exist.

(a) In polygamous species, sex differences in the intensity of competition for mates may have selected for sexual dimorphism in body size and musculature (Trivers, 1972; Clutton-Brock and Harvey, 1976), and these differences may produce coincidental variations in feeding behaviour. In this case, differences in feeding behaviour should be most evident in strongly dimorphic species and least in monomorphic ones.

(b) The costs of pregnancy and lactation may have led to selection for sex differences in diet. In particular (see above) this may help to explain why females may require more protein in their diet than males.

(c) Selection may favour individuals who avoid competing for limiting resources with their mates or offspring (Selander, 1966, 1972). One might expect this to be most advantageous where:

(i) the animals are territorial and feed outwards from a fixed base, such as a nest or sleeping hole: here, divergence in food selection would have a considerable effect both on the distance covered in search of food and on territory size (see Smith, 1968);

(ii) feeding rate is limited by search time (see Schoener, 1971) rather than by handling time; for this reason, one might expect maximal divergence to occur in food specialists rather than generalists;

(iii) the adult sex ratio is close to parity (since, as the relative number of adult males in the troop declines, the advantage of feeding divergence to females and young will decrease) and where males maintain exclusive mating access to group females and are thus closely related to a considerable number of immature animals in the troop.

As yet, there is no need to invoke the third explanation to account for sex differences in feeding behaviour in primates, though observations of orang-utans (Rodman, Ch. 13) are puzzling. Males may feed more on "less preferred" foods than females, emigrating when food availability is low (Rodman, Ch. 13). Although one explanation is that males avoid competition with females and offspring, it seems more likely that they are optimizing food choice in some way which is not immediately obvious.

6. DIURNAL VARIATION IN FEEDING BEHAVIOUR

6.1. Feeding Levels

At least two studies have demonstrated the existence of diurnal variation in the feeding levels used. Siamang tend to use the upper levels of the canopy most in the morning and late afternoon, spending relatively more time in the middle canopy in the middle part of the day (Chivers, 1974). This pattern was related to their choice of emergent tree species to sleep in. In red colobus at Gombe in October (dry season), animals spent more time feeding at lower levels during the middle part of the day (10.00–15.00h) than during the morning or evening (Clutton-Brock, 1973). In the wet season, the proportion of time spent in the upper levels of the canopy tended to increase with time of day. The most likely explanation of this variation was that in October, when temperatures of over 32° C occurred regularly during the midday hours, the animals selectively fed and rested in the shade (which was more abundant in the lower levels of the forest) during the midday period, whereas this response was absent in the cooler wet season.

6.2. Activity Patterns

The earliest primate field studies (e.g. Carpenter, 1934, 1935) noted the presence of consistent diurnal variation in activity and subsequent research both on wild populations and on enclosed or caged animals (Kavanau, 1971; Bernstein, 1970a, b, 1972, 1975) confirms that regular patterns often exist.

In many primates, feeding activity peaks in the first half of the morning and the second half of the afternoon e.g. *Lemur fulvus*, *L. catta* (Sussman, Ch. 1); *Propithecus verreauxi* (Richard, Ch. 3); *Alouatta villosa* (Carpenter, 1934; Richard, 1970; Chivers, 1969; Smith, Ch. 4); *Callicebus torquatus* (Kinzey, Ch. 5); *Ateles geoffroyi* (Carpenter, 1935; Richard, 1970); *Cercopithecus aethiops* (Kavanagh, pers. comm.); *Cercocebus albigena* (Chalmers, 1968a); *Macaca mulatta* (Lindburg, Ch. 8); *Macaca radiata* (Nolte, 1955); *Erythrocebus patas* (Hall, 1965); *Papio hamadryas* (Kummer, 1968); *Colobus badius* (Clutton-Brock, 1974b; Struhsaker, 1975); *Colobus guereza* (Oates, Ch. 10); *Presbytis entellus* (Yoshiba, 1967, 1968); *P. geei* (Mukherjee and Saha, 1974); *P. cristatus* (Bernstein, 1968); *P. melalophos*, *P. obscura* (Hunt Curtin, 1976); *Hylobates lar* (Carpenter, 1940); *Pongo pygmaeus* (Rodman, Ch. 13); *Gorilla gorilla beringei* (Fossey and Harcourt, Ch. 14) and *Pan troglodytes* (Goodall, 1968; Wrangham, Ch. 17).

In several of these studies, feeding also increased in the middle of the day: *Alouatta villosa* (Chivers, 1969); *Callicebus torquatus* (Kinzey, Ch. 5); *Cercocebus albigena* (Chalmers, 1968a); *Papio anubis* (Dunbar and Dunbar, 1974a); *Colobus badius* (Clutton-Brock, 1974b; Struhsaker, 1975); *Pan troglodytes* (Wrangham, 1975, Ch. 17). Midday feeding may, in fact, be more common than was originally supposed (see Chalmers, 1968a), and its presence may often have been masked by combining data: the occurrence of regular feeding bouts during the midday period will not necessarily produce a peak when data from different days are lumped if the timing of bouts is irregular. For example, in red colobus in the Gombe National Park at least one bout of feeding activity usually occurred during the middle-day period in both wet and dry seasons (Clutton-Brock, 1974b). However, in the wet season, the timing of the bout was irregular and, when data from different days were lumped, no feeding peak was evident.

Some species apparently show activity variation which contrasts with the usual pattern. In *Indri* [as in one of the *Propithecus* populations observed by Richard (Ch. 3)] feeding activity peaks at midday, declining after 14.00h (Pollock, Ch. 2). In *Theropithecus gelada* and *Cercopithecus aethiops*, feeding activity increases from 10.00–11.00h and peaks around 15.00h (Dunbar and Dunbar, 1974a), while in siamang feeding peaks 8.00 to 10.00h, remains high through the middle day and declines after 15.00h (Chivers, 1974, Ch. 12). In *Hylobates lar* (Raemakers, pers. comm.) feeding reaches a high level by 7.00h, remains approximately constant throughout the day but ceases some three hours before sunset. Finally, some studies (e.g. *Papio cynocephalus*: Altmann and Altmann, 1970; *P. ursinus*: Hall, 1962) have found little regular variation in diurnal activity.

As yet, we do not know to what extent activity patterns are species-specific. Both differences between sympatric species (see Sussman, Ch. 1; Dunbar and Dunbar, 1974a; Chivers, 1974; Mackinnon, unpublished data) and the persistence of diurnal patterns in captive animals (e.g. Kavanau, 1971; Bernstein, 1972, 1975) suggest that some consistent species differences will be found. However, patterning evidently varies widely within species and may differ considerably both between seasons (see Sussman, Ch. 1; Richard, Ch. 3; Chivers, 1974; Clutton-Brock, 1974b) and between populations. For example, gray-cheeked mangabeys in Kibale forest showed little consistent diurnal variation in feeding activity (Waser, Ch. 7) whereas in eastern Uganda, the same species showed morning and evening peaks in feeding activity, with a lesser peak at midday (Chalmers, 1968b). Similarly, red colobus in Kibale forest apparently do not show such well-defined peaks in feeding activity as those in the Gombe National Park (Clutton-Brock, 1974b; Struhsaker, 1975).

The functional significance of diurnal variation in activity patterns is not obvious and several factors are presumably involved. Morning and evening feeding peaks and midday resting periods may represent an adaptation to temperature variation (e.g. Chivers, 1969, 1974). This suggestion is supported by some patterns of intraspecific variation: in several species, midday resting peaks are more regular in the hotter seasons of the year (*Propithecus verreauxi*: Richard, Ch. 3; *Macaca mulatta*: Lindburg, Ch. 8; *Papio hamadryas*: Kummer, 1968) while, within seasons, they may be more marked on sunny days than on cloudy ones (Chivers, 1969, 1974). However, there is often little relationship between diurnal temperature changes and feeding activity, both because feeding peaks occur in the middle day (see above) and because midday resting periods frequently occur before the hottest time of day. In addition, this argument fails to explain the occurrence of peaks of activity in several nocturnal species in the first and last parts of the night e.g. *Galago demidovii*, *G. crassicaudatus*, *G. senegalensis*, *Microcebus murinus*, *Lemur mongoz* and *Perodicticus potto* (Vincent, 1969; Charles-Dominique, 1971; Tattersall and Sussman, 1975; Doyle, 1974).

While adaptation to temperature regulation has probably played some part in the evolution of diurnal variation in feeding behaviour, other factors are presumably involved. In particular, early and late peaks in feeding activity may serve to maximize the amount of food that can be digested per day and differences in the duration and patterning of feeding peaks within the day may be related to variation in stomach size and intestinal morphology (Clutton-Brock, 1974b). As yet, the data are inadequate to demonstrate relationships of this kind.

6.3. Food Choice

In several species, there is evidence that food choice varies with time of day. In at least some of these, differences may be produced by diurnal variation in the location of the animals. For example, in the dry season, geladas eat proportionately more grass leaves (compared with rhizomes) in the morning and evening than during the midday period because the former are abundant in the bush country abutting their sleeping cliffs (Dunbar, Ch. 9). In other cases, diurnal variation in food choice occurs which is less easy to explain. In *Callicebus torquatus* there is a tendency for fruit to be eaten at the beginning and end of the day, insects during the middle-day period and leaves throughout the day (Kinzey *et al.*, in press; Kinzey, Ch. 5) while squirrel monkeys (*Saimiri sciureus*) feed more on fruit in the morning and on insects in the afternoon (Thorington, 1967). In *Colobus guereza*, fruits and leaf buds tend to be eaten more in the second half of the day than in the first half, while floral parts are eaten more in the middle day period (Oates, Ch. 10). In siamang (Chivers, Ch. 12) the proportion of feeding time spent on fruit declines from around 70% at dawn to 20% by mid-afternoon (though it shows a tendency to increase immediately before the group settles for the night) while the proportion of time spent on young leaves increases from around 30% at dawn to 70% in the afternoon. Consumption of leaves, stems, flowers and insects apparently varies little throughout the day. Similar patterns of behaviour occur in *Hylobates lar*: the proportion of feeding time spent on figs is high in the morning and evening while feeding time spent on other fruit shows similar, though less pronounced, changes. The proportion of time spent on flowers is also high in the evening while time spent on foliage increases through the day, until the late afternoon (Raemakers, pers. comm.). Orang-utans (Rodman, Ch. 13) tend to eat fruit early and late while, in chimpanzees at Gombe, bouts of fruit-eating occurred earlier than bouts of leaf-eating (Wrangham, 1975, Ch. 17). Some nocturnal species, too, show consistent variation in food selection: *Galago demidovii* eats more fruit early in the night and more insects later on (Charles-Dominique, 1971). Not all studies report consistent variation in food choice: for example, no consistent variation was found in either *Cercocebus albigena* (Waser, Ch. 7) or *Galago elegantulus* (Charles-Dominique, 1971).

As yet, we cannot tell either how general or how stable this kind of dietetic variation is. Nevertheless, there appears to be a common tendency for fruit to be eaten relatively more than foliage early in the activity period. This may occur because fruit is more swiftly digested and early fruit-eating helps to restore any energy deficit that has accumulated during the period of inactivity (Chivers, 1974; Wrangham, Ch. 17). On the same argument, it may be advantageous to feed on foliage immediately before retiring, so that the digestive system is active for as long as possible. However, this hypothesis fails to explain why, in a few species, peaks of fruit-eating occur immediately before the inactive period (see above). The tendency for insects to be eaten later than fruit (as in *Callicebus torquatus*, *Siamiri sciureus* and *Galago demidovii*) may occur because ingestion rate is usually low for primates feeding on insects (Hladik, Chs 11, 16) and it is advantageous for them to obtain the bulk of fruit necessary for the day before switching to insects.

The extent to which particular foods are eaten can also vary with time of day. In *Colobus guereza*, *Markhamia platycalyx* is used relatively little in the first part of the day while *Celtis africana*, *Spathodea nilotica* and *Olea welwitschii* are used comparatively heavily (Oates, Ch. 10). Chimpanzees in the Gombe National Park regularly ate the leaves of *Aspilia rudis* and *A. pluriseta* during the early morning: Wrangham (Ch. 17) suggests that this may be related to diurnal variation to alkaloid levels (see Robinson, 1974). An alternative explanation might be that these leaves contained components which facilitated the digestion of fruit in some way.

7. SEASONAL VARIATION IN FEEDING AND RANGING BEHAVIOUR

Even in equatorial forests, the phenology of many trees is well synchronized within, if not between, species (Richards, 1966; Struhsaker, 1975) and the diets of all primates studied so far vary extensively between months, often showing little or no dietary overlap between contrasted seasons. Few studies have described feeding behaviour over several years and there is consequently little firm evidence of seasonal cycles in feeding behaviour. Moreover, in some cases, there is little similarity between the same months of different years (Struhsaker, 1975). However, many studies have demonstrated relationships between intermonth differences in feeding and ranging behaviour and similar variation in climate or food distribution. The effects of climatic variation clearly differ between species: thus in Richard's study (Ch. 3) of *Propithecus*, food quality and quantity were lower in the dry season than in the wet, whereas for red colobus in the Gombe National Park and for siamang, quality if not density of food supplies increased in the dry season (Clutton-Brock, 1975b; Chivers, 1974, Ch. 12). Since food availability is likely to have a stronger effect on feeding behaviour than climatic variation *per se*, the rest of this discussion concentrates on comparisons between periods of low and high food availability.

When food availability declines, non-migratory animals might be expected either to increase searching time (thus accepting increased energetic costs of food-finding) or to reduce selectivity, minimizing energetic expenditure at the expense of food quality (see Schoener, 1971; Emlen, 1973). Several primate species appear to adopt the latter strategy. In *Propithecus verreauxi*, the marked dry season was associated with a decline in overall food availability; a decrease in the proportion of feeding time spent on fruit and flowers and an increase in time spent on mature foliage; a decrease in the proportion of daytime spent feeding, in day range length and rate of movement around the home range; and a tendency to spend more time in fewer quadrats (Richard, Ch. 3). The southern population studied (which inhabit relatively dry, arid forest where overall food availability may have been low) differed from the northern in the same ways that, within populations, the dry season differed from the wet. In red colobus in the Gombe National Park (Clutton-Brock, 1974b, 1975a,b) the wet season was associated with a reduction in the availability of young foliage and an increase in the proportion of feeding time spent on mature leaves, a slight decrease in the proportion of time spent feeding (which, alternatively, may be attributable to changes in observation conditions: Clutton-Brock, 1974b) and a decrease in day range length and rate of movement about the home range. Similarly, in *Alouatta villosa* (Chivers, 1969; Smith, Ch. 4) and *Symphalangus syndactylus* (Chivers, 1974, Ch. 12) reduced time spent feeding on fruits and flowers during the wetter parts of the year, is associated with reduction in the amount of time spent feeding and moving as well as (in the latter case) with reduced day range length and more concentrated use of particular parts of the home range. In *Hylobates lar* (Raemakers, pers. comm.) day range length is positively correlated with the availability of young leaves, flowers and fruit, with the combined proportion of flower and fruit eaten, and negatively with the proportion of mature foliage eaten. In *Cercocebus galeritus* on the Tana river (Homewood, pers. comm.) the proportion of time spent foraging (but not that spent actually feeding) increased at times of reduced food availability and was associated with a reduced proportion of feeding time spent on fruit, as well as with increased dietetic diversity.

In all these four studies the association between reduction in activity and movement and reduced food availability or quality is tenuous both because availability could not be measured and because comparisons between seasons confound changes in food availability with other seasonal differences. Wrangham's study of chimpanzees in the Gombe National Park (Wrangham, 1975, Ch. 17) offers the possibility of comparing similar seasons between years, reducing the number of associated variables. Several lines of evidence suggest that food was less abundant in the 1972 dry season than in 1973: the fruit crop of an important food species failed; body weight of males was lower and there was some evidence of increased frequency of competitive interactions at food sources. Comparisons between the two dry seasons tend to support the associations between lower food availability and reduced feeding activity outlined above. In the 1972 dry season, the animals fed more on foliage and less on fruit, spent (slightly) less time feeding and travelling and more grooming and resting while food-calling frequency, group size and day range length declined. However, the situation is complicated by differences between the dry and wet seasons which do not parallel those between the two dry seasons (Wrangham, Ch. 17).

Although some primate species (see above) show similar patterns of change in feeding and ranging behaviour, it is clear that no generalizations concerning seasonal variation can yet be made. In other species, *most* time is spent feeding or travelling at times when food availability is probably lowest e.g. *Papio cynocephalus* (Altmann and Altmann, 1970); *Papio hamadryas* (Kummer, 1968); *Theropithecus gelada* (Dunbar, Ch. 9). Surprisingly, bay range length is not related to the proportion of daytime spent feeding. In some no clear patterns of seasonal variation are evident e.g. *Indri* (Pollock, Ch. 2); *Cercocebus albigena* (Waser, Ch. 7); *Colobus guereza* (Oates, Ch. 10). Moreover, reactions to changes in food availability may differ between populations of the same species. In two of the female orang-utans observed by Rodman (Ch. 13) feeding time *increased* when the proportion of fruit in the diet fell whereas in the population studied by MacKinnon (1974) feeding time *decreased* and travel increased in months when the animals fed less on fruit (Rodman, Ch. 13). Such anomalies may possibly be the product of differences in the dispersion of food sources.[a]

Finally, ranging behaviour and group movements may not be closely related to food dispersion in some species: Struhsaker's detailed study of red colobus (Struhsaker, 1974, 1975) concludes that intergroup interactions may be more important than food dispersion in determining movement patterns and the distribution of time across the home range. Since this study questions the basic assumption that food distribution is likely to have an important effect on movement patterns, its results deserve close attention. In the single troop studied in detail, intermonth variation in day range length and ranging diversity ("quadrat utilization diversity") were positively related to rainfall but neither was significantly correlated with changes in dietetic diversity ("food species diversity") while the latter was not significantly related to the dispersion of the food supply ("the average index of dispersion of the top four food species in each month"), the relative abundance of the food species used (= the combined indices of cover for the top four food species in each month) or the percentage of young growth (flowers, buds and young leaves) available or in the diet. The situation thus contrasts with studies of red colobus at Gombe, a more strongly seasonal environment (Clutton-Brock, 1975a,b), where day range length, and rate of movement about the home range increased at the end of the pronounced dry season when both the amount of young growth eaten and available and dietetic diversity were relatively high [though, as Struhsaker (1975) notes, intermonthly differences in these variables were not significantly intercorrelated, perhaps because smaller, intermonth differences during the rest of the year were not related to each other].

At Kibale (but not at Gombe) ranging diversity was significantly related to the frequency of intergroup proximity and encounters, and Struhsaker (1974) concludes that this has a more important effect on ranging behaviour than food distribution. While this may be the case, an equally plausible interpretation would be that greater ranging diversity produced an increase in the probability of intergroup encounters (Clutton-Brock, 1975b). Moreover, Struhsaker's conclusion

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[a] Among ungulates (Owen-Smith, unpublished data) similar interspecies variation exists and may be related to dietetic differences. Grazing species (e.g. *Loxodonta africana*, *Ceratotherium simum*, *Damaliscus d. phillipsi* and *Cervus canadensis*) tend to show a reduction in the proportion of time spent feeding when overall food availability is low, while browsing species (e.g. *Aepyceros melampus*, *Antidorcas marsupialis* and *Tragelaphus strepsiceros*) tend to show an increase. This difference may occur because food shortage forces grazers to feed on abundant low quality food found in large clumps (e.g. grass stems) while browsers maintain dietetic quality but are forced to increase the amount of time spent finding food items.

that ranging behaviour and food distribution show little relationship to each other requires careful examination since both his results and his conclusions reveal several anomalies. Thus evidence that dietetic similarity (across months) is not significantly correlated with similarity in the extent to which different parts of the range are used leads him to conclude (1975, p. 155) that, "it is clear from this analysis that the manner in which the monkeys distribute their time in space is not strongly correlated with what they eat" while contrary evidence that utilization of different parts of the range was related to spatial variation in the abundance of different food species produces the contrasting statement (1975, p. 161) that "clearly, the abundance and distribution of food affects the manner in which red colobus distribute their time in space". Although it is possible to reconcile the situation by suggesting that spatial variation in ranging behaviour but not seasonal change is related to variation in food distribution, this seems an unlikely position. Close inspection of the Kibale data shows that relationships between monthly increases of ranging diversity and measures of dietetic diversity and availability of common food species (Struhsaker, 1975, figs 33, 34) are largely spoiled by a small proportion of aberrant points, a result which might be expected on the grounds that estimates of ranging diversity were based only on five consecutive days of observation (see Clutton-Brock, 1975b). Moreover, ranging diversity was significantly related to the mean rank (per month) of dietetic diversity and abundance of the top four food species (Clutton-Brock, 1975b). In other words, ranging behaviour was most diverse in months when the animals distributed their feeding time relatively evenly over common food species, a situation not dissimilar to the patterns of change evident in several other species (see above).

The most obvious conclusion to be drawn from comparative studies of seasonal variation in feeding and ranging behaviour is that the topic is an extremely complex one. Perhaps the most useful approach may be to examine changes in the behaviour of animals with relatively simple diets (such as *Theropithecus* or *Lepilemur*) before extending research to rain forest species.

8. SUMMARY

1, 2. The factors affecting food choice in primates are complex. They include: energetic value; protein availability and, perhaps, availability of specific amino acids; toxin content and physical characteristics affecting digestive processes.

3. Sympatric primates often overlap extensively in their use of particular food species. Ecological segregation is achieved primarily by differences in the heights and habitats used and in the parts and growth stages eaten.

4. Though different populations of the same primate species frequently utilize different plant species, their preference for particular species probably varies by very little.

5. In several species, males spend less time feeding than females and relatively more feeding on fruit. Both differences may be the product of nutritional costs resulting from pregnancy and lactation.

6. Utilization of different levels in the canopy, feeding activity and food choice vary with time of day. Several species spend relatively more time eating fruit in the first half of the day and foliage in the second.

7. In most species, seasonal variation in feeding behaviour is closely associated with variation in ranging behaviour. Some species apparently react to decreased food availability by reducing day range length and the proportion of time spent feeding, others by increasing them.

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Species Differences in Feeding and Ranging Behaviour in Primates

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1. INTRODUCTION

While it is clear that many aspects of feeding and ranging behaviour vary widely within species (see Chapter 18), the recent development of comparative studies (e.g. Hladik and Hladik, 1969, 1972; Gartlan and Struhsaker, 1972; Charles-Dominique, 1971; Clutton-Brock, 1974a; Sussman, 1974; Hunt Curtin, 1976) shows that consistent differences in feeding ecology exist between species. The same studies suggest that behavioural and ecological variables may be similarly associated in phylogenetically diverse taxa (see Eisenberg *et al.*, 1972; Hladik, 1975). For example, differences in food selection, activity patterns, ranging

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behaviour and social organization between *Lemur fulvus* and *L. catta* (Sussman, 1974, Ch. 1) are similar to those between *Presbytis senex* and *P. entellus* (Hladik and Hladik, 1972), between *P. obscurus* and *P. melalophos* (Hunt Curtin, 1976) and between *Colobus guereza* and *C. badius* (Clutton-Brock, 1974a; Struhsaker, 1975). To provide convincing evidence of associations of this kind, systematic investigation is necessary (see Lack, 1968), and comparisons of selected pairs of species are an inadequate basis for generalization.

Such an approach faces many problems. (a) Methodological differences between studies are often large enough to prevent close comparison and may introduce sufficient error to obscure important relationships. (b) It is frequently difficult to construct realistic species averages in the many cases where intraspecific variation (see Chapter 18) is marked. (c) Field research has not been evenly spread across taxonomic groups and results may be strongly biased by over-representation of particular genera or families. (d) Comparisons are effectively restricted to gross behavioural and ecological traits. (e) If relationships between variables differ radically between taxonomic groups, correlations which apply to particular taxa but not across the order as a whole may be obscured.

Though these problems weaken this method of investigating relationships between behaviour and ecology, they do not invalidate it. Both differences in methodology between studies and marked intraspecific variation may introduce error but there is usually no reason to suppose that they could be responsible for creating a relationship between two variables where none existed. For example, the common tendency for observers to select study sites in areas of high population density may lead to underestimates of average home range size. While this might affect the elevation of the plot of home range size on group weight (Fig. 5), there is no reason to suppose that it would increase the value of the regression coefficients. Secondly, where samples are strongly biased by over-representation of particular taxa, it is possible to move the level of analysis to the genus (Clutton-Brock and Harvey, in press) or even the family (Lack, 1968). And, although comparisons are restricted to gross variables, there is evidence that the distributions of many behavioural and morphological traits are related to major ecological differences, such as the kind of habitat occupied or the type of diet (see McNab, 1963; Schoener, 1968; Lack, 1968; Milton and May, 1976; Clutton-Brock and Harvey, in press). Lastly, though some relationships between variables may differ between phylogenetic groups, most of those investigated in this chapter should apply to the majority of mammals belonging to the same trophic level.

Nevertheless, the results of interspecific comparisons must be interpreted with great care. It is seldom safe to assume that a significant correlation or regression indicates a direct causal relationship since many ecological and behavioural traits are interdependent. Second, comparisons between individual studies must be regarded as unreliable because methodological differences or unrealistic averages produced by intraspecific variation (see above) can affect the values of particular estimates. Finally, one cannot accept the apparent absence of any relationship between two variables as evidence that they do not affect each other since relationships may easily be obscured either by the heterogeneity of the data or by the effects of associated variables.

2. METHODS

In this analysis, we have tried to include all primate species for which quantitative estimates of activity patterns or food selection were available. This included a total of 56 species (see Tables I and II) each of which was classified as primarily nocturnal or primarily diurnal and as primarily arboreal or primarily terrestrial.

For each species we calculated the average figure (see below) for the following variables.

1. Body weight: average of adult male and adult female weight.
2. Feeding group size: the number of individuals usually found feeding together.
3. Population group size: the number of animals which regularly associate together and share a common home range. (This is the same as the feeding group in most genera, but not in *Ateles*, *Pan* and *Theropithecus*.)
4. Socionomic sex ratio: the number of adult females per adult male in breeding groups.
5. Feeding group weight: the total weight (kg) of the typical feeding group, calculated on the assumption that 50% of the group is made up of juveniles and adolescents with an average body weight of one-half average adult body weight (1). Calculations of group weight allowed for biased sex ratios and sex differences in body weight.
6. Population group weight: the total weight (kg) of the population group, calculated in the same way as feeding group weight.
7. Home range size: the total area (ha) used by a population group. Where two figures for home range size were quoted, one including and one excluding small lacunae within the perimeter of the home

range (e.g. Struhsaker, 1975), we have taken the larger figure on the grounds that the majority of studies have included such lacunae. Though, for several analyses, it would have been preferable to correct this figure by the proportion of the home range overlapped by those of other troops (e.g. Hladik, 1975, this volume), the data were inadequate to allow this.

8. Day range length: the daily path length of the feeding group (m).
9. Population density: the number of individuals per km^2.
10. Biomass: weight per unit area (kg/km^2) calculated by dividing population group weight (5) by population group size (2) and multiplying by population density (11).
11. Percentage of day-time spent:
    (a) resting or inactive (including scratching and grooming);
    (b) feeding or foraging;
    (c) moving or travelling.

In a proportion of the studies, percentages of "active time" spent in different activities had to be changed to percentages of day-time.

12. Percentage of feeding time, food intake or stomach contents[a] devoted to:
    (a) all foliage, including leaf petioles;
    (b) fruit, seeds or gums;
    (c) flowers or flower-buds;
    (d) animal matter.
13. The proportion of feeding time, food intake or stomach contents devoted to:
    (a) the top two;
    (b) the top five;
    (c) the top ten food species;
    ranked throughout the study as a whole.

All sources from which the data were collected are shown in Table I, the estimates in Table II.

Our rules for constructing species averages were as follows.

(i) Estimates of feeding behaviour drawn from the chapters of this volume were used wherever possible. Where the same studies provided estimates of grouping and ranging behaviour these, too, were included. Where this was not the case, the relevant data were either extracted

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[a] Since estimates of feeding time spent on different foods may be poorly related to the amount ingested (Hladik, Chs 11, 16) and (presumably) to stomach contents, inclusion of both measures in the analysis may have introduced considerable error. However, we believe that dietetic differences between species are sufficient to swamp error of this kind. Restriction of the sample to species for which estimates of feeding time were available would have greatly reduced our sample size.

from other recent studies, or average figures from a previous analysis of feeding and ranging behaviour (Clutton-Brock and Harvey, in press) were used (see Table II).

(ii) Means were used to estimate body weight; for averaging estimates of ranging and feeding behaviour across months; and for averaging the results of different field studies in the few cases where estimates were based on several studies (e.g. *Cercocebus galeritus*, *Colobus badius*, *Presbytis melalophos*, *Presbytis obscurus*, *Hylobates lar*, *Pongo pygmaeus*).

(iii) Where a study provided data on several troops, mean figures were calculated for each troop and the *median* of these was included in the analysis. This was done to avoid species estimates being severely biased by figures from extreme groups.

Where species are referred to in the text, references are quoted only where they do not appear in Table II. Estimates for congeneric species were not averaged, as in a previous study (Clutton-Brock and Harvey, in press) on the grounds that relatively few genera were represented by more than two species.

When considering relationships between behaviour and ecology, it is usually necessary to regard some variables as independent and others as dependent. Within *contemporary* primate populations, more stable variables with a strong genetic component (such as body size or digestive anatomy) are likely to constrain more flexible ones, such as home range size or the proportion of day-time spent feeding. Throughout the analysis, we have assumed that the former usually represent causes and the latter effects. The rationale underlying this position is discussed in greater detail at the end of the chapter.

For statistical testing, the data were normalized and relationships linearized using logarithmic transformations where necessary. Since many of the variables considered in the analysis are interrelated, we have relied extensively on the technique of partial regression (Bailey, 1964). In this analysis, one dependent variable is regressed on two (or more) independent variables. The technique tests whether each independent variable is significantly related to the dependent variable when the effects of the other independent variable has been removed and the significance of association is tested using "t" tests. The number of independent variables that can be included in any one analysis is limited by the necessity for estimates of all to be available for each species included in the sample. In practice, as the number of variables increases, sample size falls and the analysis becomes less reliable. Results require careful interpretation since the addition or deletion of particular independent variables can change the relationship of others to the dependent variable (Bailey, 1964).

It is worth emphasizing that the degree of scatter shown in Figs 1–8 would be considerably reduced were it possible to plot the relationship in three dimensions, thus taking into account the proportion of variance accounted for by the second independent variable. These figures should be interpreted in conjunction with Table III which shows the standardized partial regression coefficients (allowing a direct comparison between the importance of each independent variable in affecting the dependent variable) and the (total) percentage of variance accounted for by each multiple regression analysis.

3. RESULTS

3.1. Time Spent Feeding on Different Foods

Primate species can be divided into three gross dietetic groups: insectivores, folivores and frugivores (Clutton-Brock and Harvey, in press). Within each group, there is a wide variation in diet: thus the frugivore category includes some species which feed extensively on invertebrates or small vertebrates (e.g. *Saimiri scuireus*, *Macaca fascicularis*, *Papio* spp.) as well as species which eat little animal matter (e.g. *Lemur catta*, *Ateles belzebuth*, *Pongo pygmaeus*). Folivores include species whose diet, across the year, is largely made up of shoots, flowers and fruit (e.g. *Colobus badius*, *Presbytis entellus*) and more "specialized" species which feed extensively on mature leaves in certain seasons (e.g. *Lemur fulvus*, *Colobus guereza*, *Presbytis senex*). The order also includes a number of species whose diets cannot be easily classified under this system: *Lemur mongoz*, which feeds mostly on flowers and nectar; *Galago* (*Euoticus*) *elegantulus*, a specialized gum-eater, and *Theropithecus gelada*, which depends primarily on grass seeds, blades and rhizomes.

Within phylogenetic groups, larger species tend to feed more on foliage. Both the largest prosimians (*Indri*, *Propithecus*) and the largest ceboids (*Alouatta* spp.) are folivorous (though this does not apply to *Lepilemur* or *Lemur fulvus*), the siamang feeds more on foliage than the gibbon and the gorilla more than the orang and chimpanzee. The same relationship occurs across taxonomic groups but is complicated by the tendency for terrestrial species to show large body size (Clutton-Brock and Harvey, in press). However (see Fig. 1), the percentage of feeding time (or diet) spent on foliage is positively related to body weight ($r_s = 0{\cdot}48$; $P < 0{\cdot}001$; d.f. $= 45$). Most small species tend to feed on energy-rich diets and several feed extensively on insects. Insectivores occur only in the Prosimii and, with the exception of *Daubentonia*, are all of small body size.

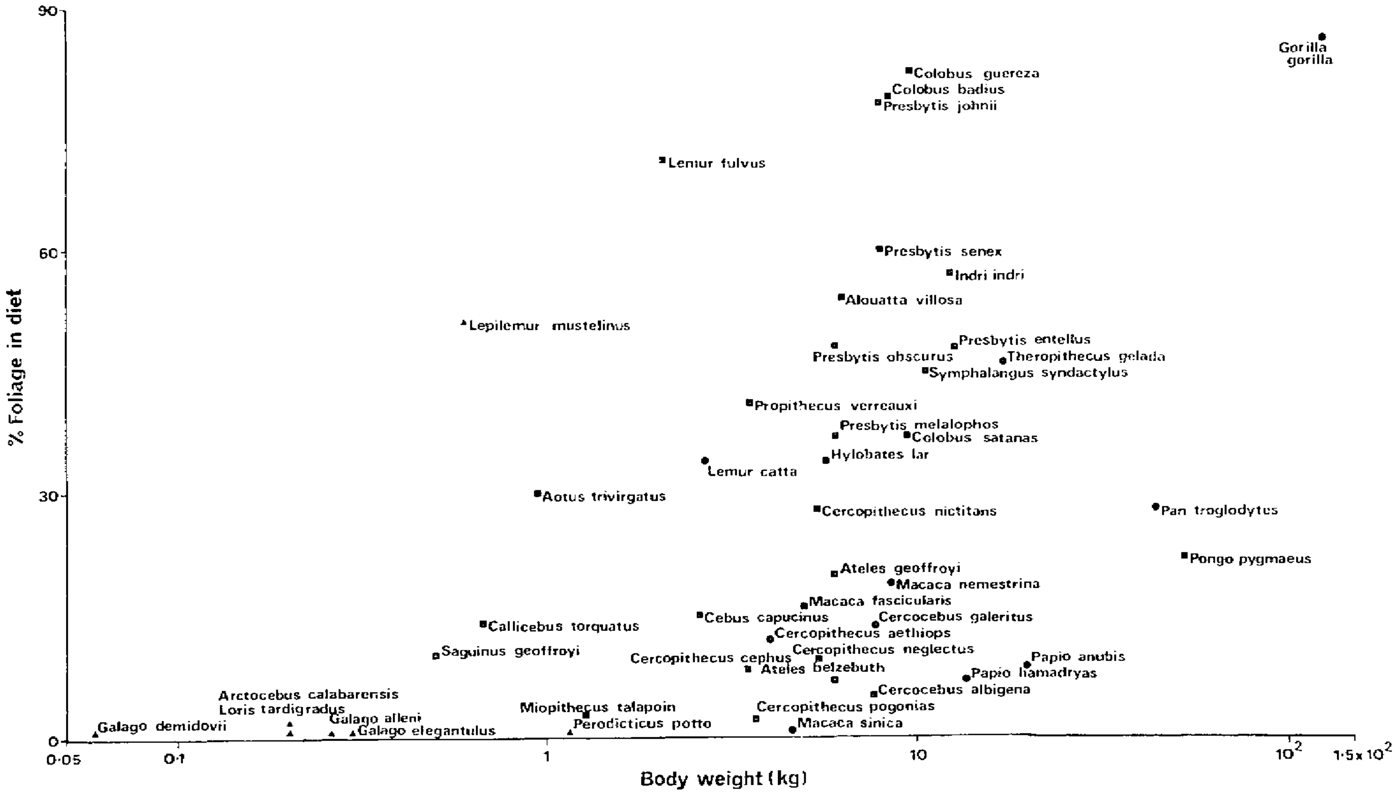

FIG. 1. Proportion of foliage eaten plotted against mean of adult male and female body weights (▲ = nocturnal, arboreal; ■ = diurnal, arboreal; ● = diurnal, terrestrial).

3.2. Dietetic Diversity

Though it is often impossible to calculate diversity indices (see Appendix II) from figures given by different studies, major differences in dietetic diversity will be reflected in the proportion of the diet or feeding time spent on the same number of food species. The percentage of feeding time spent on the two top-ranking food species varies in the sample from 9% (*Presbytis melalophos*) to 93% (*Lepilemur mustelinus*), the percentage on the top five from <30% (*Presbytis melalophos, Hylobates lar, Pongo pygmaeus*) to >95% (*Lepilemur mustelinus, Presbytis senex*). However, interspecific comparisons are complex since tree species diversity varies between continents. In particular, diversity is considerably higher in Malaysian study areas (Chivers, 1974; MacKinnon, 1974, and pers. comm.), than in African ones (Clutton-Brock, 1975a,b; Struhsaker, 1975; Waser, Ch. 7; Richard, Ch. 3) and this is reflected in generally lower proportions of feeding time or diet spent on the top two food species in Malaysian primates.

Nevertheless, some trends in dietetic diversity can be seen. Since species with large home and day ranges would be likely to have access to a greater number of food species, they might be expected to show high dietetic diversity. This is apparently the case, and the percentage of feeding time or diet spent on the top two food species is negatively related to home range size ($b = -6{\cdot}574$; $F_{1,21} = 10{\cdot}56$; $P < 0{\cdot}001$), day range length ($b = -18{\cdot}114$; $F_{1,17} = 6{\cdot}56$; $P < 0{\cdot}025$) as well as to body weight ($b = -10{\cdot}58$; $F_{1,21} = 4{\cdot}47$; $P < 0{\cdot}05$) (see Fig. 2). When the relationship between this measure and (a) home range size and (b) body weight is considered simultaneously, it is apparent that there is a close relationship with the former but not with the latter ($b_1 = -8{\cdot}313$; $t_1 = -4{\cdot}035$; $P < 0{\cdot}001$; $b_2 = 4{\cdot}234$; $t_2 = 1{\cdot}000$, n.s.). This indicates that the simple relationship between dietetic diversity and body weight is probably the product of the relationship between the latter and home range size (see Table III). However, it is clear that differences in home range size only account for a small proportion of the total variance diversity, perhaps as a result of intercontinental variation (see above).

On the grounds that fruit and flowers usually represent a smaller proportion of plant biomass than foliage, one might also predict that the proportion of feeding time spent on the top two food species would be negatively related to the proportion of fruit in their diet. However, there is no evident relationship in the data between these two measures ($b = 0{\cdot}165$; $F_{1,21} = 0{\cdot}618$; n.s.).

Though the sample of species is too small for statistical treatment,

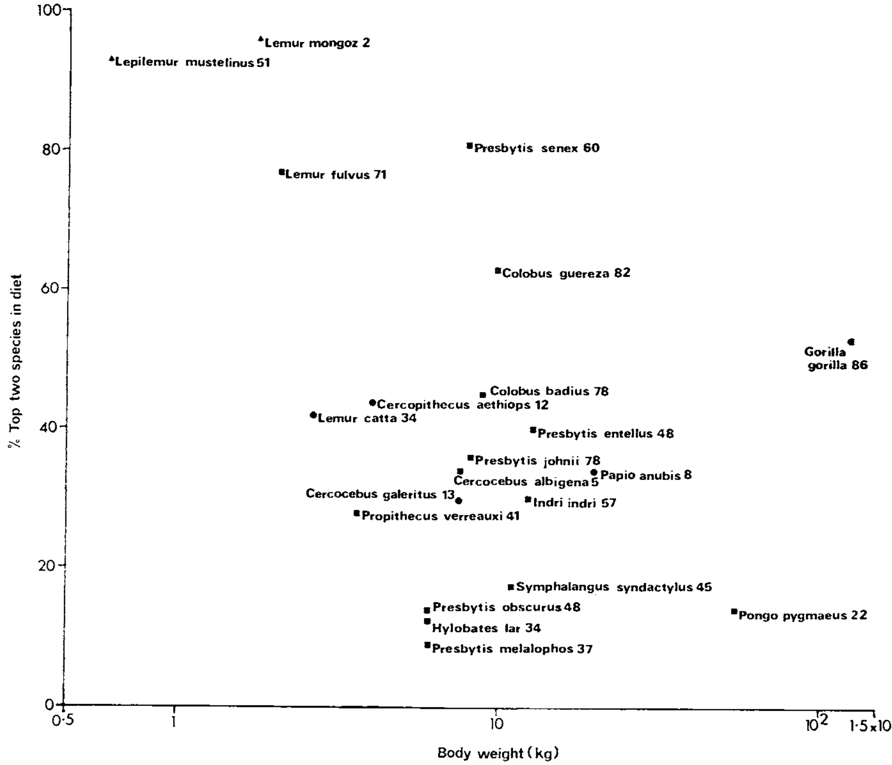

FIG. 2. Proportion of feeding time spent on the top two ranked food species plotted against the mean of adult male and female body weights. Figures following each species name show the proportion of foliage eaten (▲ = nocturnal, arboreal; ■ = diurnal, arboreal; ● = diurnal, terrestrial).

consistent differences in dietetic diversity may exist between folivores which feed extensively on mature leaves at certain times of year and those which feed largely on shoots and young leaves. For example, both *Colobus guereza* and *Presbytis senex* feed on less varied diets than *C. badius* and *P. entellus*. One possible explanation is that the ability to neutralize the toxins which mature leaves often contain (Freeland and Janzen, 1974) encourages dietary specialization.

3.3. Activity Budgets

Species also show marked variation in the amount of time spent in different activities. The proportion of day-time spent feeding varies in the sample from 11% (*Ateles geoffroyi*) to 54% (*Symphalangus syndactylus*), the proportion spent moving from 5% (*Ateles geoffroyi*) to 28% (*Papio anubis*), and the proportion spent resting from 14% (*Cercocebus galeritus*) to 80% (*Alouatta villosa*).

Since ingestion rate is likely to be limited by some aspect of body *size* (e.g. molar surface area or the cross-sectional dimensions of the oesophagus) while nutritional requirements will increase in relation to body volume (Kleiber, 1961), larger species should spend more time feeding than smaller ones. Feeding or foraging time should also be negatively related to the proportion of foliage eaten since fruit, flowers and animal matter are generally less abundant than foliage and more time should be spent in manipulation.

When the proportion of day-time spent feeding is partially regressed on body weight and the proportion of foliage in the diet (Fig. 3), it

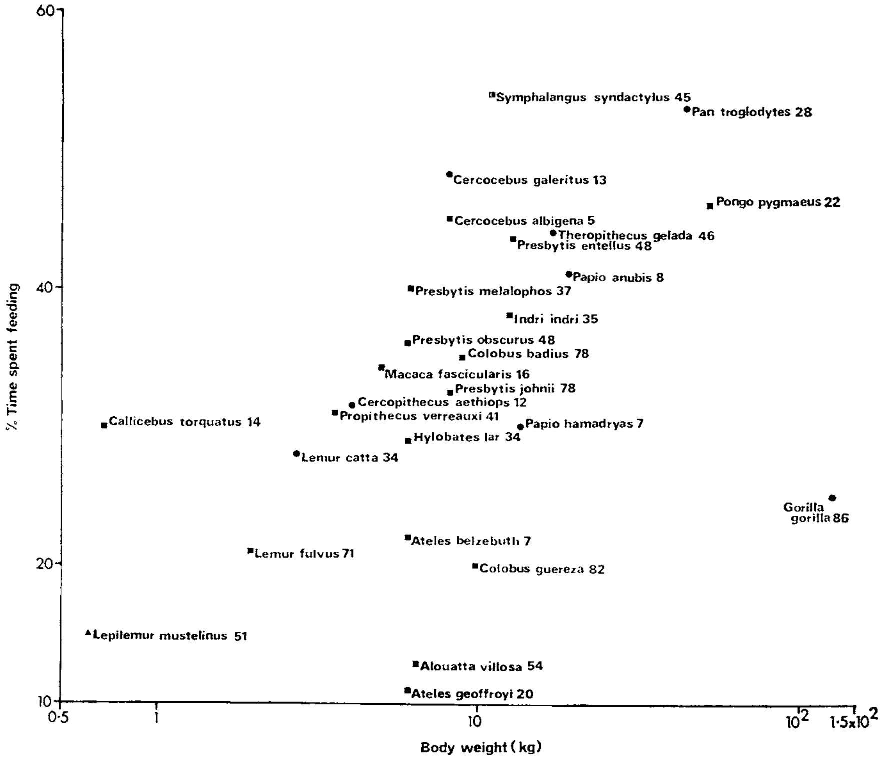

FIG. 3. Proportion of day-time spent feeding and foraging plotted against the mean of adult male and female body weight. Figures following each species name show the proportion of foliage eaten (▲ = nocturnal, arboreal; ■ = diurnal, arboreal; ● = diurnal, terrestrial). (For nocturnal species the % night-time feeding is used.)

proves to be positively related to the former ($b_1 = 4{\cdot}467$; $t = 2{\cdot}226$; $P < 0{\cdot}05$; d.f. $= 23$) and negatively to the latter ($b_2 = -1{\cdot}44$; $t = 1{\cdot}748$; $P < 0{\cdot}1$; d.f. $= 23$). As might be expected, the proportion of day-time spent moving is also negatively related to the proportion of foliage eaten (Fig. 4: $b = -0{\cdot}163$; $F = 9{\cdot}00$; $P < 0{\cdot}01$). The first relationship is somewhat closer than the second, while a large proportion of the variance is still left unexplained in both cases.

The negative association between the proportion of day-time spent feeding and the amount of foliage eaten also occurs within taxonomic groups. Thus *Lemur fulvus*, *Colobus guereza*, *Presbytis obscurus* and *Gorilla gorilla* spend less time feeding than (respectively) *Lemur catta*, *Colobus badius*, *Presbytis melalophos* and *Pan troglodytes*. Although in contravention of this trend, *Symphalangus syndactylus* spends more time feeding than *Hylobates lar*. The latter spends considerably more time moving and this apparent exception may be the product of differences in definition of activity between the two studies.

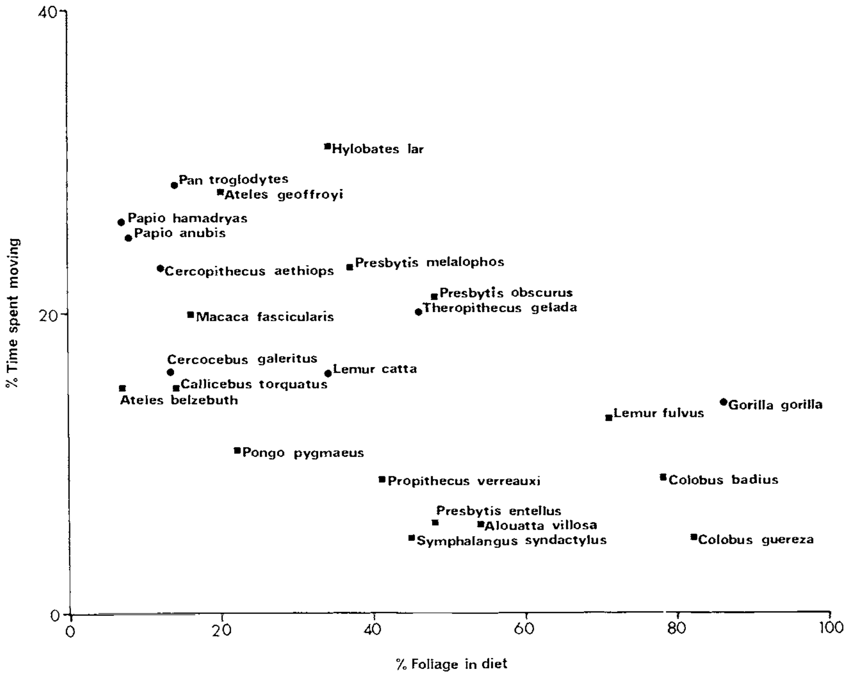

FIG. 4. Proportion of day-time spent moving plotted against proportion of foliage eaten (▲ = nocturnal, arboreal; ■ = diurnal, arboreal; ● = diurnal, terrestrial).

3.4. Day Range Length

Day range length varies in the sample from <100 m (*Callicebus moloch*) to >10 km (*Papio hamadryas*). Though factors other than energetic ones may affect the distance that groups move per day (Clutton-Brock, 1975b), food availability is likely to be an important determinant. If so, day range length should be positively related to group weight (assuming that group dispersion does not compensate for increased group or body size) and negatively to the proportion of foliage in the diet.

When day range length is partially regressed on feeding group weight (Fig. 5) and the proportion of foliage in the diet, it is positively related to the former ($b_1=3{\cdot}741$; $t=4{\cdot}97$; $P<0{\cdot}001$; d.f. $=31$) and negatively to the latter ($b_2=-0{\cdot}021$; $t=3{\cdot}62$; $P<0{\cdot}001$; d.f. $=31$). The first relationship is closer than the second and the two factors account for approximately half the total variance in day range length.

The negative association between day range length and the proportion of foliage eaten is supported by comparison with other taxonomic groups. *Lemur fulvus*, *Callicebus moloch*, *Colobus guereza*, *Presbytis senex*, *Presbytis obscurus*, *Symphalangus syndactylus* and *Gorilla gorilla* do not move so far each day as (respectively) *Lemur catta*, *Callicebus torquatus*, *Colobus badius*, *Presbytis entellus*, *Presbytis melalophos*, *Hylobates lar* and *Pan troglodytes*.

3.5. Home Range Size

Home range size varies in the sample from $<0{\cdot}2$ ha (*Lepilemur mustelinus*) to >50 km^2 (*Erythrocebus patas*). Previous studies of primates (Milton and May, 1976; Clutton-Brock and Harvey, in press) as well as of other vertebrates (McNab, 1963; Schoener, 1968) have already demonstrated that home range or feeding territory size is related both to individual or group weight and to diet type. When home range size in this sample is partially regressed on group weight and the proportion of foliage in the diet (Fig. 6) it proves to be positively related to the former ($b_1=0{\cdot}82$; $t=11{\cdot}06$; $P<0{\cdot}001$; d.f. $=36$), and negatively to the latter ($b_2=-0{\cdot}026$; $t=4{\cdot}05$; $P<0{\cdot}001$; d.f. $=36$). The first relationship is considerably closer than the second: both factors together account for approximately 75% of the total variance in home range size (Table III). The relationships presumably occur because larger groups require more food and because the availability of fruit and flowers is generally lower than that of foliage. As in the case of day range length, the trend is supported by comparisons within taxonomic groups (see references above).

FIG. 5. Day range length plotted against feeding group weight (see p. 559). Figures following each species name show the proportion of foliage eaten (▲ = nocturnal, arboreal; ■ = diurnal, arboreal; ● = diurnal, terrestrial).

FIG. 6. Home range size plotted against population group weight (see p. 559). Figures following each species show the proportion of foliage eaten (▲ = nocturnal, arboreal; ■ = diurnal, arboreal; ● = diurnal, terrestrial).

Several ecological factors other than food availability also affect home range size: terrestrial species tend to have larger ranges than arboreal ones as might be expected on the grounds that they are restricted to movement in two dimensions (though this may also be a product of relatively low food density in savannah environments) and, as in birds (Schoener, 1968) and ungulates (Jarman, 1974), species depending on clumped, unpredictable food sources tend to have larger ranges than species whose food supplies are more evenly distributed (Clutton-Brock, 1974a; Clutton-Brock and Harvey, in press).

3.6. Population Density and Biomass

Though population density varies widely within species, it also differs consistently between them. In the sample used in this analysis, density varied from <1 animal per km^2 (*Erythrocebus patas*) to >1000 (*Lemur fulvus*). Since much of this variation is likely to be a product of differences in food availability (Lack, 1954), population densities should be negatively related to body weight and positively to the proportion of foliage eaten. When density is partially regressed on these variables (Fig. 7), this proves to be the case ($b_1 = -0{\cdot}548$; $t = 4{\cdot}01$; $P < 0{\cdot}001$; d.f. $= 40$; $b_2 = 0{\cdot}032$; $t = 4{\cdot}06$; $P < 0{\cdot}001$; d.f. $= 40$). The association with diet is supported by comparisons within some taxonomic groups: *Lemur fulvus*, *Callicebus moloch* and *Presbytis senex* show higher population densities than *Lemur catta*, *Callicebus torquatus* and *Presbytis entellus*. However, in other cases the situation is reversed: *Colobus badius*, *Presbytis melalophos* and *Hylobates lar* show higher population densities than *Colobus guereza*, *Presbytis obscurus* and *Symphalangus syndactylus*. The explanation of these reversals is not obvious.

Species biomass (Fig. 8) is positively related to body weight in the sample as a whole ($b_1 = 0{\cdot}409$; $t = 3{\cdot}038$; $P < 0{\cdot}01$; d.f. $= 40$), as well as to the proportion of foliage in the diet ($b_2 = 0{\cdot}033$; $t = 4{\cdot}149$; $P < 0{\cdot}001$; d.f. $= 40$). The two factors account for similar proportions of the variance in biomass and, jointly, account for approximately half the total variance (Table III). Both the largest and the smallest species tend to show unexpectedly low biomass while there is extensive scatter among species of intermediate body size.

4. DISCUSSION

The analysis shows that, in most cases where relationships between different aspects of feeding and ranging behaviour can be predicted on

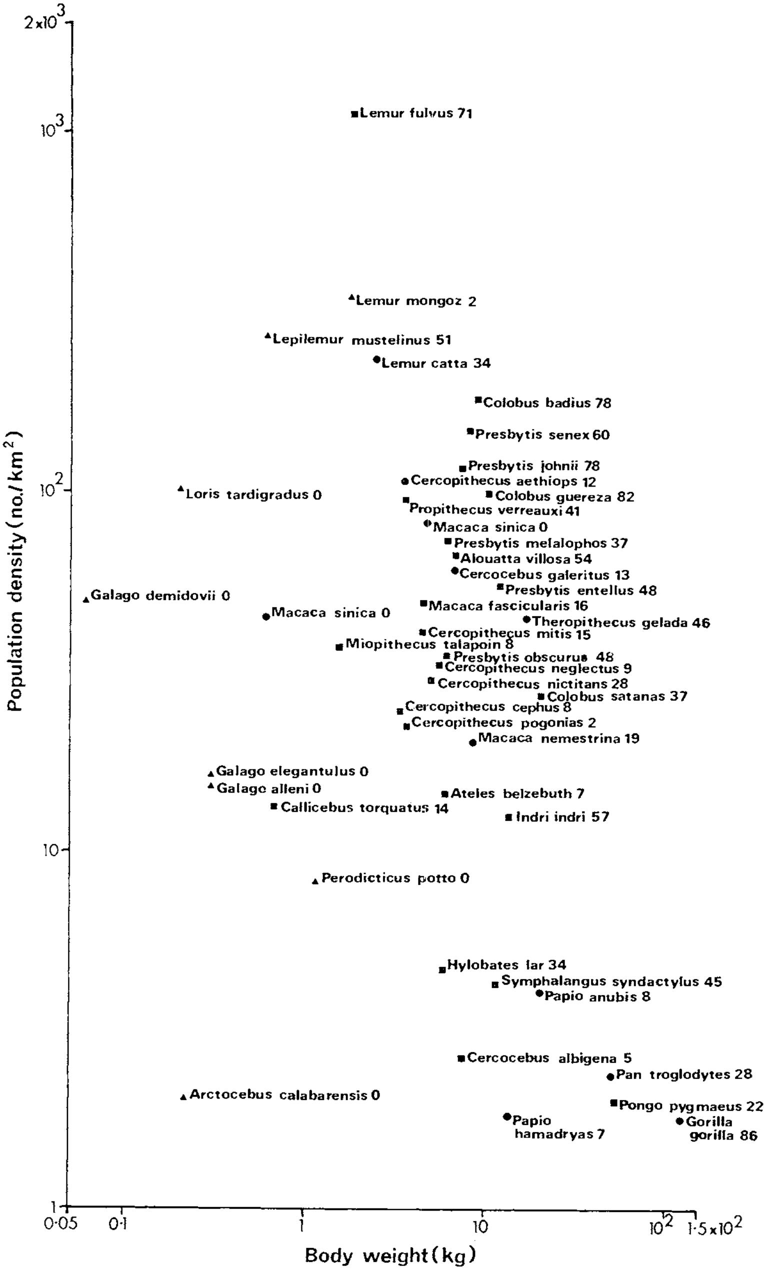

Fig. 7. Population density plotted against the mean of adult male and female body weights. Figures following each species show the proportion of foliage eaten (▲ = nocturnal, arboreal; ■ = diurnal, arboreal; ● = diurnal terrestrial).

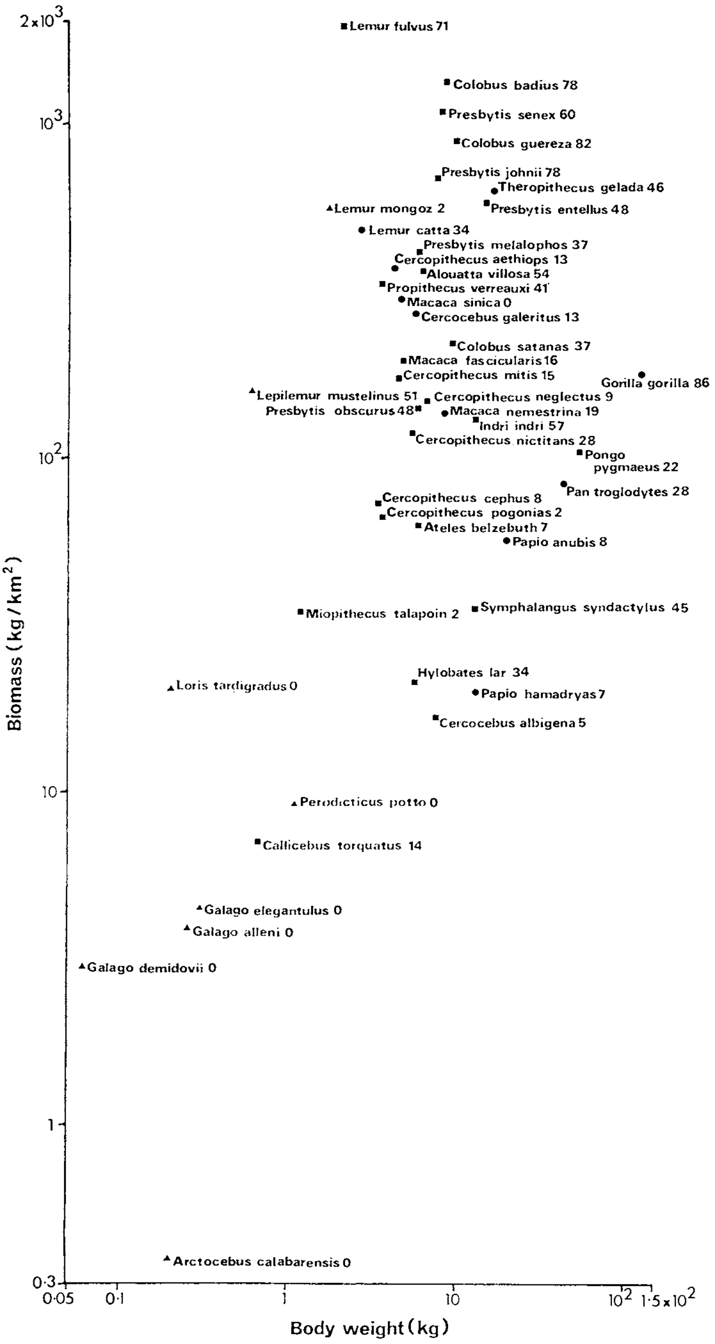

FIG. 8. Biomass plotted against the mean of adult male and female body weight. Figures following each species show the proportion of foliage eaten (▲ =nocturnal, arboreal; ■ =diurnal, arboreal; ● =diurnal, terrestrial).

energetic grounds, they can be shown to occur despite the heterogeneity of the data. Although the form of some relationships may be affected by sampling methodology (see p. 558), it is difficult to envisage bias which could produce relationships of this kind and more reasonable to suppose that they represent adaptive responses to ecological differences.

Attempts to construct realistic hypotheses concerning the biological significance of these relationships face major difficulties. The end products of natural selection are clusters of functionally interrelated traits. Although, within these, some variables are likely to constrain the values which others can take, identifying the former is often a difficult problem. For example, is high dietetic diversity a product of large home range size? Is it the cause of large home range size?[a] Or is it associated with the latter because frugivorous species tend both to feed on a large number of species and to have large home ranges? These three alternatives need to be distinguished since it is little use merely to argue that home range size and dietetic diversity are interadapted.

The problem is one of distinguishing carts from horses: to escape tautology, we must separate evolutionary effects from evolutionary causes. This distinction can seldom be based on temporal sequences since most interrelated traits may evolve simultaneously and, even where this is not the case, evidence concerning the order of evolution is usually lacking. In general we have assumed that, within contemporary populations, less plastic traits, especially those with a high genetic component, constrain more variable ones. For example, we have assumed (see p. 566) that contemporary differences in the proportion of day-time spent feeding are the product of differences in body size rather than that differences in body size are the product of differences in feeding time.

However, if we wish to ask questions about ultimate causes of behavioural and ecological differences, it is necessary to extend arguments into a timespan where we cannot assume that morphological or physiological variables are stable since they, themselves, presumably represent ecological adaptations (Lack, 1968; Wilson, 1975). Here, the problem of tautology becomes acute: it is as reasonable to suppose, for example, that the distribution of body size is the product of differences in day range length as it is to argue that the distribution of day range length is the product of variation in body size.

At this level, evolutionary arguments become highly speculative. The only way to break the circle of tautology is to assume that some aspects

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[a] In this section, we are using "causal" and "causation" in their general meanings and not in the specialized, behavioural sense.

of behaviour or ecology are particularly likely to constrain the evolution of others. The most plausible assumption is that the feeding niche occupied by the species (and the morphological, physiological and behavioural adaptations which affect food exploitation directly) is likely to constrain evolutionary changes in other variables. This is the case both because the niche is constrained by factors external to the species gene pool (including interspecific competition and geographical features: see Wilson, 1975; Lack, 1971) and because any change in feeding niche inevitably requires adjustments in a wide variety of other variables. It is worth noting that this assumption underlies many arguments concerning the evolution of social systems (e.g. Crook, 1970; Lack, 1968; Jarman, 1974) although it is rarely made explicit.

The problem of identifying causes and effects is especially important in understanding the distribution of body size. It is commonly argued that the tendency for small homeotherms to select nutritionally-rich diets is an adaptation to the higher metabolic costs associated with small size (Hladik, 1975 and pers. comm.). However, this fails to explain the functional significance of small size itself and it may be more useful to regard body size as adapted to diet type than vice versa.

The advantages of small size have recently been reviewed by Bourière (1975). His list includes the following.

(a) Relatively easy concealment from predators hunting by sight, associated with energetic advantages of predator escape through concealment versus escape.

(b) Easy and economic access to small food sources (see also Jarman, 1974).

(c) Polyestrous reproduction, large litter size, short gestation and growth periods.

(d) Short generation length, high population turnover and the possibility of rapid changes in gene frequency.

Of these four groups of advantages, the latter two should probably be disregarded: there is no obvious reason why large size should necessarily preclude polyestrous reproduction or large litter size (though it will inevitably affect gestation length and absolute growth rate). And the argument that the selective advantages of small size include reduction in generation length and increases in population turnover and the potential rate of genetic change rely on group selection (see Maynard Smith, 1976). Three additional advantages should be mentioned. Small size reduces the absolute amount of nutrients which an individual will need to collect and may thus be advantageous in "scramble" competitors (Wilson, 1975) where it does not reduce an individual's ability to contest access to food supplies. Secondly, it permits reduction of the proportion of time required for feeding (see Fig. 3) which may be an important advantage in those species whose food intake is limited by feeding time. Finally, it permits an animal to utilize food supplies distributed in small clumps.

As Bourière points out, small size has several disadvantages, including increased metabolic rate and energetic expenditure (Kleiber, 1961) requiring *relatively* higher nutrient intake, and high costs of locomotion per unit body weight (Schmidt-Nielsen, 1972a,b). In addition, it may reduce the range of potential food items (see Newton, 1967; Struhsaker, 1975), limit mobility and increase the number of potential predators.

In contrast, the advantages of large body size include:

(a) lower nutrient intake *relative to body weight* (Kleiber, 1961) permitting larger species with a given digestive rate to feed on nutritionally poorer foods than smaller species (Janis, in press);

(b) reduced costs of locomotion (Schmidt-Nielsen, 1972a,b) and the ability to travel further per unit time (thus allowing larger species to exploit more spatially heterogeneous food supplies);

(c) reduced liability to predation.

These considerations help to provide some explanation of variation in body size among primates. In the Prosimians, where small size occurs both in primarily insectivorous species (e.g. *Galago demidovii*) and in folivorous species (e.g. *Lepilemur mustelinus*), it may represent an adaptation to the vegetational substrate occupied rather than to diet quality: it is possibly significant that no large Prosimians occur in mainland Africa or Asia where the canopy niches are largely occupied by anthropoids. Increased susceptibility to predation and reduced potential for flight resulting from small size may select, in smaller species, for behaviour aiding concealment from predators, including nocturnal habits and hiding (rather than escape) when alarmed (e.g. Charles-Dominique, 1971). The tendency among Prosimians and anthropoids for the largest species to be folivorous may be related to their ability to feed on poorer quality diets than small ones:[a] the same trend occurs among the ruminating ungulates (Jarman, 1974; Janis, in press) where large species tend to have higher proportions of fibre in their diets than smaller ones. Lastly, the tendency for terrestrial species to be larger than arboreal ones (Clutton-Brock and Harvey, in press) probably occurs both because terrestriality removes constraints on body weight imposed by arboreal mobility and because terrestrial species occur in habitats

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[a] There is no obvious explanation why body size shows *no* increase in a number of specialized folivores (e.g. *Lemur fulvus*, *Presbytis senex*, *Colobus guereza*) over related species living in similar environments (e.g. *Lemur catta*, *Presbytis entellus*, *Colobus badius*).

where widely dispersed food supplies and high liability to predation select for increased body size.

Dietetic differences are also related to variation in digestive physiology (Hladik, 1967). As among ungulates, fermentation of cellulose by folivorous primates has been achieved either through the evolution of fore-stomach fermentation chambers (as in the Colobinae: Kuhn, 1964; Hladik, 1967; Bauchop and Martucci, 1968; Hollihn, 1969; Kay *et al.*, 1976) or by the development of large caeca and colons (as in *Lepilemur*, *Avahi* and *Alouatta*: Hladik, 1967). In ungulates these two methods of fermentation may represent adaptations to different diets (see Bell, 1969; Jarman, 1974; Janis, in press) rather than alternative solutions to the same problem. Fore-stomach fermentation among ungulates is apparently more efficient than caecal fermentation: horses digest cellulose with around 70% of the efficiency of ruminants (Phillipson and McAnally, 1942; Heinlein *et al.*, 1966; Vandernoot *et al.*, 1967), and consequently require greater nutrient intake per unit body weight (see Heinlein *et al.*, 1966). The ruminant system has the disadvantage that its rate of through-put is relatively slow: the digestia of cows pass through their body in 70–90 hours (Balch and Campling, 1965) whereas in horses they pass in only 48 hours (Alexander, 1946; Heinlein *et al.*, 1966; Vandernoot *et al.*, 1967). The increased rate of digestion possible in caecal fermenters may explain why caecal fermentation occurs in species which feed extensively on fibrous diets (e.g. zebra: Bell, 1969, 1971) and, consequently, require fast through-put rates to achieve adequate nutritional intake. In contrast, the advantages of rumen fermentation may be relatively high digestive efficiency and the ability to neutralize toxins by microbial action immediately after ingestion (Janis, in press; McKey, pers. comm.). However, it is not yet clear whether the constraints on digestive rate operating in true ruminants apply to primate ruminants whose stomach anatomy is less specialized.

Our analysis showed that in primates many aspects of feeding ecology, including dietetic diversity, the proportion of day-time spent feeding, day range length, home range size and population biomass are related to body weight. Several of these relationships are most easily explained as incidental effects of body size. The association with dietetic diversity may be the product of increased home range size in larger species since the latter would allow access to a greater number of plant species (see p. 564). Larger primates probably spend more time feeding than smaller ones because their total nutrient requirements are greater while feeding rate may be *relatively* slower (see p. 566). The associations with day range length and home range size probably arise either because large body size requires large range size to provide adequate food resources or because sparse and unpredictable food supplies require individuals to move over considerable distances and this selects both for large body and large range size (see above). Lastly, the low biomass shown by small primates may occur because much of their diet consists of animal matter or the reproductive parts of plants whose abundance is relatively low. This is supported by the fact that the one small folivore (*Lepilemur*) shows a biomass comparable to much larger species (see Fig. 8). The variability of biomass shown by species in the middle size range may be a product of a number of different factors including the number of interspecific competitors (see Cody, 1974b) and species differences in overall food availability and in the density of particular foods. It is not obvious why the largest species tend to show low biomass and this could be the result of human interference.

The proportion of foliage in the diet proved to be (negatively) related to the proportion of time spent feeding and moving, day range length and home range size and positively to population density and biomass. As we have argued, all six trends would be expected on the grounds that, compared to the reproductive parts of plants, foliage represents a dense and relatively predictable food supply. Contrary to expectation, the proportion of foliage eaten was not related to dietetic diversity. Though this could be a product either of continental differences in plant species diversity (see p. 564) or of our rudimentary measure of dietetic diversity, it seems likely that our initial prediction was incorrect and that species living predominantly on fruit do not necessarily show greater diversity of food choice than folivores.

Finally, it is clear that, even when methodological differences between studies are taken into account, there are many anomalies. Why do orangs show such large body size? Why is the proportion of time spent feeding by *Callicebus torquatus* so high and by *Gorilla gorilla* so low? What factors account for the wide range in biomass shown by species of similar body size and diet? The answers to such questions require detailed investigation and are outside the scope of the approach that we have adopted in this review. When answers are provided, they will almost certainly require revision of many of the explanations suggested here. However, if this analysis serves to identify such problems, it will have fulfilled its purpose.

5. SUMMARY

1, 2. Data on feeding and ranging behaviour for 56 primate species were extracted from the literature. Relationships between variables were investigated using partial regression.

3. Primate species fall into three dietetic groups: insectivores, folivores and frugivores. Among diurnal, arboreal species, the proportion of foliage in the diet is positively related to body weight.

Interspecific differences in dietetic diversity are positively related to body weight, day range length and home range area but show no overall association with the proportion of foliage in the diet.

The proportion of day-time spent feeding is positively related to body weight and negatively to the proportion of foliage in the diet.

Day range length and home range size are positively related to body weight and negatively to the proportion of foliage in the diet. Estimates of biomass were positively related to both variables.

4. The functional significance of these trends is discussed.

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TABLE I

References used for calculation of species averages

- *Lemur catta* (ringtailed lemur)
  - Jolly (1966)
  - Sussman and Richard (1974)
  - Sussman (Ch. 1)
  - Jolly (pers. comm.)
- *Lemur fulvus* (ruffed lemur)
  - Sussman and Richard (1974)
  - Sussman (1975)
  - Sussman (Ch. 1)
- *Lemur mongoz* (mongoose lemur)
  - Tattersall and Sussman (1975)
  - Richard and Sussman (1975)
- *Lepilemur mustelinus* (sportive lemur)
  - Charles-Dominique and Hladik (1971)
  - Hladik and Charles-Dominique (1974)
- *Microcebus murinus* (mouse lemur)
  - Charles-Dominique and Martin (1972)
  - Charles-Dominique and Hladik (1974)
  - Richard and Sussman (1975)
- *Indri indri* (indri)
  - Pollock (pers. comm.)
  - Pollock (Ch. 2)
- *Propithecus verreauxi* (white sifaka)
  - Jolly (1966, pers. comm.)
  - Sussman and Richard (1974)
  - Richard (Ch. 3)
- *Loris tardigradus* (slender loris)
  - Petter and Hladik (1970)
  - Hladik and Hladik (1972)
  - Jolly (1972)
- *Arctocebus calabarensis* (golden potto)
  - Jewell and Oates (1969)
  - Charles-Dominique (1974a)
  - Jolly (1972)
- *Perodictus potto* (potto)
  - Charles-Dominique (1974a, b)
- *Galago alleni* (Allen's bushbaby)
  - Charles-Dominique (1974a)

TABLE I (*continued*)

- *Galago demidovii* (dwarf bushbaby)
  - Charles-Dominique and Martin (1972)
  - Charles-Dominique (1974a)
- *Galago* (*Euoticus*) *elegantulus* (needleclawed bushbaby)
  - Jewell and Oates (1969)
  - Charles-Dominique and Martin (1972)
  - Charles-Dominique (1974a)
- *Saguinus geoffroyi* (Geoffroy's tamarin)
  - Hladik and Hladik (1969)
- *Cebus capucinus* (white-throated capucin)
  - Schultz (1956)
  - Oppenheimer (1969a, b)
  - Jolly (1972)
  - Eisenberg and Thorington (1973)
  - Hladik and Hladik (1969)
- *Saimiri oerstedi* (redbacked squirrel monkey)
  - Schultz (1956)
  - Baldwin and Baldwin (1972)
- *Alouatta caraya* (black howler)
  - Pope (1966)
  - Neville (1972)
  - Jolly (1972)
- *Alouatta seniculus* (red howler)
  - Fooden (1964)
  - Neville (1972)
- *Alouatta villosa*(*palliata*) (mantled howler)
  - Chivers (1969)
  - Eisenberg and Thorington (1973)
  - Jolly (1972)
  - Smith (Ch. 4)
- *Aotus trivirgatus* (night monkey)
  - Moynihan (1964)
  - Jolly (1972)
  - Hladik and Hladik (1969)
- *Callicebus moloch* (dusky titi)
  - Mason (1968)
  - Kinzey (pers. comm.)
- *Callicebus torquatus* (widow monkey)
  - Kinzey, Rosenberger, Heisler, Prowse and Trilling (in press).
  - Kinzey (Ch. 5) (pers. comm.)
- *Ateles belzebuth* (Colombian spider monkey)
  - Klein and Klein (1975, Ch. 6)
- *Ateles geoffroyi* (blackheaded spider monkey)
  - Eisenberg and Kuhn (1966)
  - Jolly (1972)
  - Richard (1970)
  - Hladik and Hladik (1969)
- *Cercopithecus aethiops* (vervet monkey)
  - Hall and Gartlan (1965)
  - Hill (1966)
  - Struhsaker (1967a, b)
  - Jolly (1972)
  - Kavanagh (pers. comm.)
- *Cercopithecus cephus* (moustached monkey)
  - Struhsaker (1969)
  - Gautier (1971)
  - Gautier and Gautier-Hion (pers. comm.)
- *Cercopithecus mitis* (blue monkey)
  - Hill (1966)
  - Aldrich-Blake (1970a)
  - Kingdon (1971)
  - DeVos and Omar (1971)
  - Struhsaker (1975)
  - Schlichte (1970)
- *Cercopithecus neglectus* (de Brazza monkey)
  - Gautier (1971)
  - Jolly (1972)
  - Gautier and Gautier-Hion (pers. comm.)
- *Cercopithecus nictitans* (spotnosed monkey)
  - Struhsaker (1969)
  - Gautier and Gautier-Hion (pers. comm.)
- *Cercopithecus pogonias* (crowned monkey)
  - Struhsaker (1969)
  - Gautier (1971)
  - Gautier and Gautier-Hion (pers. comm.)
- *Miopithecus talapoin* (talapoin monkey)
  - Gautier-Hion (1970, 1971, pers. comm.)
  - Rowell (1973)
- *Erythrocebus patas* (patas monkey)
  - Hall (1966)
  - Jolly (1972)
- *Cercocebus albigena* (gray-cheeked mangabey)
  - Chalmers (1968a, b)
  - Waser and Floody (1974)
  - Struhsaker (1975)
  - Waser (Ch. 7)
  - Gautier-Hion (pers. comm.)

TABLE I *(continued)*

- *Cercocebus galeritus* (agile mangabey)
  - Quiris (1968)
  - Homewood (pers. comm.)
- *Macaca fascicularis* (crab-eating macaque)
  - Rodman (1973)
  - Aldrich-Blake (pers. comm.)
- *Macaca mulatta* (rhesus macaque)
  - Southwick, Begg and Siddiqi (1965)
  - Neville (1958)
  - Lindberg (1971, Ch. 8)
- *Macaca nemestrina* (pigtailed macaque)
  - Bernstein (1967)
  - Rodman (1973a, b)
  - Jolly (pers. comm.)
  - MacKinnon (pers. comm.)
- *Macaca sinica* (Toque macaque)
  - Eisenberg *et al.* (1972)
  - Hladik and Hladik (1972)
  - Dittus (1975)
- *Papio anubis* (olive baboon)
  - DeVore and Hall (1965)
  - Rowell (1966, 1968)
  - Altmann and Altmann (1970)
  - Nagel (1973)
  - Oliver (pers. comm.)
- *Papio cynocephalus* (yellow baboon)
  - Altmann and Altmann (1970)
  - Jolly (1970)
  - Maples (1972)
- *Papio hamadryas* (hamadryas baboon)
  - Kummer (1968)
  - Altmann and Altmann (1970)
- *Papio ursinus* (chacma baboon)
  - Hall (1962)
  - Altmann and Altmann (1970)
  - Stolz and Keith (1973)
- *Theropithecus gelada* (gelada baboon)
  - Crook (1966)
  - Dunbar and Dunbar (1975)
  - Dunbar (Ch. 9)
- *Colobus badius* (red colobus)
  - Clutton-Brock (1974b, 1975)
  - Struhsaker (1975)
  - Gatinot (1975)
- *Colobus geuereza* (black and white colobus)
  - Kuhn (1964)
  - Marler (1969)
  - Clutton-Brock (1972)
  - Dunbar and Dunbar (1974)
  - Oates (Ch. 10)
- *Colobus satanas* (black colobus)
  - Sabater Pi (1973)
  - McKey (in prep.)
- *Presbytis entellus* (Hanuman langur)
  - Sugiyama (1966)
  - Yoshiba (1966, 1968)
  - Hladik and Hladik (1972)
- *Presbytis johnii* (Milgiri langur)
  - Poirier (1968, 1969)
  - Horwich (1972)
  - Jolly (1972)
  - Tanaka (1965)
  - Oates (pers. comm.)
- *Presbytis melaolphos* (banded langur)
  - Hunt Curtin (1976)
  - MacKinnon (pers. comm.)
- *Presbytis obscurus* (dusky langur)
  - Hunt Curtin (1976)
  - MacKinnon (pers. comm.)
- *Presbytis senex* (purple-faced langur)
  - Eisenberg, Muckenhirn and Rudran (1972)
  - Hladik and Hladik (1972)
  - Hladik (Ch. 11)
- *Hylobates lar* (whitehanded gibbon)
  - Tenaza and Hamilton (1971)
  - Chivers (1972, 1974, pers. comm.)
  - Ellefson (1974)
  - Raemakers (pers. comm.)
  - MacKinnon (pers. comm.)
- *Symphalangus syndactylus* (siamang)
  - Chivers (1972, 1974, Ch. 12)
  - Chivers, Raemakers and Aldrich-Blake (1975)
- *Pongo pygmaeus* (orang-utan)
  - Rodman (1973, Ch. 13)
  - MacKinnon (1974, pers. comm.)
- *Pan troglodytes* (chimpanzee)
  - Goodall (1968)
  - Wrangham (1975, Ch. 17)
  - Strhusaker (1975)
  - Hladik (Ch. 16)
- *Gorilla gorilla beringei* (mountain gorilla)
  - Schaller (1965)
  - Fossey (1974) and Harcourt
  - Goodall (Ch. 15)

Napier and Napier (1967) was also used in most cases to provide estimates of body weight (see Clutton-Brock and Harvey, in press).

TABLE II

Estimates of ecological and behavioural variables for species included in the analysis

	Body weight (kg)		Group size		Socionomic sex ratio	Home range size (ha)	Day range length (m)	Popln. density animals per km^2	% day-time spent			% of diet				% of diet		
	M	F	feedg.	popln.					restg.	feedg.	movg.	foliage	fruit, seeds, gums	flower	animal matter	top 2 sp	top 5 sp	top 10 sp
LEMURIDAE																		
Lemur catta	2·9*	2·5*	18	18	1·1	7·4	950	233	48	28	16	34	47	7	0	42	71	93
Lemur fulvus	(2·1)*	(2·1)*	9·5	9·5	1·3	0·88	138	1125	61	21	13	71	25	4	0	77	93	100
Lemur mongoz	(1·8)*	(1·8)*	2·6*	2·6*	1·0	1·2*	610*	350	—	—	—	2	18	81	0	96	100	100
Lepilemur mustelinus	(0·6)*	(0·6)*	1**	1*	—	0·2*	270	270	—	15**	—	51†	0†	49†	0†	93†	100†	100†
Microbus murinus	0.06*	0·06*	1*	1*	—	0·2	—	210	—	—	—	—	—	—	—	—	—	—
Indri indri	12·5*	12·5*	3	1·0	3·0	23	250	12·5	—	38	—	57	41	2	0	30	55	73
Propithecus verreauxi	3·7*	3·5*	6·5	6·5	1·7	7·6	850	103	60	31	9	41	40	8	0	28	48	65
LORISIDAE																		
Loris tardigradus	0·22*	0·18*	1*	1*	—	1	30	100	—	—	—	0†	15†	—	85†	—	—	—
Arctocebus calabarensis	(0·2)*	(0·2)*	1*	1*	—	—	—	2*	—	—	—	0‡	14‡	—	85‡	—	—	—
Perodicticus potto	1·2*	1·1*	1*	1*	—	10*	—	8*	—	—	—	0‡	76‡	—	10‡	—	—	—
Galago alleni	(0·26)*	(0·26)*	1*	1*	—	—	—	15*	—	—	—	0‡	73‡	—	25‡	—	—	—
Galago demidovii	0·06*	0·06*	1*	1*	—	1*	—	50	—	—	—	0‡	29‡	—	70‡	—	—	—
Galago elegantulus	(0·3)*	(0·3)*	1*	1*	—	—	—	15*	—	—	—	0‡	80‡	—	20‡	—	—	—
CALLITHRICIDAE																		
Saguinus geoffroyi	(0·5)*	(0·5)*	7·5	7·5	1·0	—	—	—	—	—	—	10†	60†	—	30†	—	—	—
CEBIDAE																		
Cebus capucinus	(2·6)*	(2·6)*	10*	10*	3·7*	86*	1600*	—	—	—	—	15†	65†	—	20†	—	—	—
Saimiri oerstedi	(0·75)*	(0·75)*	25*	25*	2·6*	18*	3400*	—	—	—	—	—	—	—	—	—	—	—
Alouatta caraya	(8·1)*	(6·4)*	7*	7*	1·0*	—	—	25*	—	—	—	—	—	—	—	—	—	—
Alouatta seniculus	8·1*	6·4*	8·5*	8·5*	1·6*	4·9	580*	108*	—	—	—	—	—	—	—	—	—	—
Alouatta villosa	7·4*	5·7*	14	14	2·4	18*	300*	67*	80	13	6	54	39	7	0	—	—	—
Aotus trivirgatus	0·92*	1·00*	1·5	3	1·0	—	—	—	—	—	—	30†	65†	—	5†	—	—	—
Callicebus moloch	(0·68)*	(0·68)*	3*	3*	1·0*	4·2	86*	24	—	—	—	—	—	—	—	—	—	—
Callicebus torquatus	(0·68)*	(0·68)*	3·5	3·5	1·0	20	684	13	55	30	15	14	71	0	15	—	—	—
Ateles belzebuth	(6·0)*	(6·0)*	3·5	20	2·9	—	—	13·5	63	22	15	7	83	0·1	0	—	—	—
Ateles geoffroyi	(6·0)*	(6·0)*	—	12	—	60	—	—	62	11	28	20†	80†	—	1†	—	—	—
CERCOPITHECINAE																		
Cercopithecus aethiops	(4·5)*	(3·6)*	15*	15*	1·4	27	1300	112	44	31	32	12	48	23	17	44	61	—
Cercopithecus cephus	4·1*	2·9*	10	10	—	35	900	25	—	—	—	8‡	79‡	0‡	10‡	—	—	—
Cercopithecus mitis	(4·5)*	(4·5)*	13·5*	13·5*	3·7*	14*	—	42*	—	—	—	15	38	20	11	48	—	—

Cercopithecus negelectus	7·0	4·0	5	5	2	15	300	34	—	—	—	9‡	74‡	3‡	5‡	—	—	—
Cercopithecus nictitans	6·6	4·2	20	20	—	67	1500	30	—	—	—	28‡	61‡	1‡	8‡	—	—	—
Cercopithecus pogonais	4·5	3·0	15	15	—	78	1750	23	—	—	—	2‡	84‡	0‡	14‡	—	—	—
Miopithecus talapoin	1·4*	1·1*	70*	70*	1·5*	120*	2300*	40	—	—	—	2§‡	52§‡	2§‡	43§‡	—	—	—
Erythrocebus patas	10*	5·6*	20*	20*	7·0*	5200*	2500*	0·3*	—	—	—	—	—	—	—	—	—	—
Cercocebus albigena	9·0	6·4	15	15	2·0	410	1200	2·7	—	45	21	5	61	3	24	34	50	69
Cercocebus galeritus	(10·2)	(5·5)	19·5	19	2·35	127·5	1290·5	60	14	48	15	13·5	77	1	2·5	30	58	79
Macaca fascicularis	5·9*	4·1*	23	23	2·0	32	700	50	34	35	20	16	52	5	23	—	—	—
Macaca mulatta	8·2*	7·5*	85	85	3·1	1500	1428	—	—	—	—	—	63	—	—	—	—	—
Macaca nemestrina	(10·0)	(7·0)	35	35	2·0	200	2000	20	—	—	—	19	72	4	2	—	—	—
Macaca sinica	5·7	3·6	12·5	12·5	—	37·5	—	100	—	—	—	0	85	12	2	—	—	—
Papio anubis	26*	13*	34*	34*	2*	2430	3600	4*	30·5	41	25·5	7·8	63	3	10	34	—	—
Papio cynocephalus	(20)*	(15)*	43*	43*	1·3*	1670*	4500*	4*	—	—	—	—	—	—	—	—	—	—
Papio hamadryas	18·3*	9·4*	5*	—	—	—	13200*	1·8*	40	30	26	7	66	22	—	—	—	—
Papio ursinus	20·4*	16·8*	41*	41*	2*	1470*	4800*	2·3*	—	—	—	—	—	—	—	—	—	—
Theropithecus gelada	20·5*	13·6*	320*	113*	3·7*	—	2500	46	35	45	20	41	26	0·2	0·03	—	—	—
COLOBINAE																		
Colobus badius	10·5*	7·0	41·3	41·3	2·4	67·3	735	186·5	50	35	9	78·3	8	8·3	0	44·7	69	87
Colobus guereza	(10·7)*	(9·0)*	11	11	2·2	15	535	104	64	20	5	82	14	2	0	63	76	88
Colobus satanas	(10·0)	(9·0)	14	14	—	60	270	30	—	—	—	37	58	5	0	—	—	—
Presbytis entellus	15·2*	10·4*	19*	19*	3·0*	340*	1000*	57	33	44	6	48	45	7	1	40	73	96
Presbytis johnii	(8·5)*	(7·8)*	13‖	13‖	5·0‖	23‖	—	107	—	31‖	—	78‖	14‖	7‖	0‖	36‖	—	—
Presbytis melalophos	6·2	6·0	9·3	9·3	2	21	1150	74	36	40	23	37	53	9	0	9	18	27
Presbytis obscurus	6·3	6·0	10	10	1·5	29	950	31	43	36	21	48	46	7	0	14	27	37
Presbytis senex	8·5*	7·8*	8*	8*	4·0*	12*	—	154*	—	—	—	60†	28†	12†	0†	81	100	100
HYLOBATIDAE																		
Hylobates lar	5·7	5·3	4	4	1·0*	54	1720	4·7	39	29	31	34	59	2·5	10	12·4	28	44·4
Symphalangus syndactylus	(10·7)*	(10·7)*	3·8*	3·8*	1·0*	23*	872	4·2*	45	54	5	45	42	4	8	17·5	26·7	35·5
PONGIDAE																		
Pongo pygmaeus	69*	37*	1·8	17¶	1·4	800	500	2	39	46	11	22	62	3	2	14	28	42
Pan troglodytes	49*	41*	4*	28	1·0†	1200†	3900†	2·5	33	53	14	28†	68†	—	4†	—	—	—
Gorilla gorilla	160*	93*	10	10	2·0†	620	400	1·8	54	25	14	86	2	2	0	53	71	—

Figures shown were calculated from references, cited in Table I, according to the rules described on p. 560. Figures for body weight shown in brackets represent approximations and were taken, in some cases, from congeneric species of similar size. Estimates of diet refer to proportions of feeding time unless marked with subscripts (see below). The authors would like to stress that individual estimates shown in this table may be unrealistic and that they should not be used for reference.

* Estimate taken from Clutton-Brock and Harvey, in press; † % of amount ingested; ‡ % of stomach contents; § figures calculated excluding casava; || preliminary data: Oates (pers. comm.); ¶ figures from MacKinnon (pers. comm.); ** % night-time.

TABLE III

Standardized partial regression coefficients and proportions of variance accounted for in analysis of six different variables (see text)

Dependent variable	Independent variables 1	 2	b_1'	b_2'	% var
% Feeding time on top 2 food species	body wt	home range size	0·18	−0·74	35·5
% Time spent feeding	body wt	% foliage eaten	0·42	−0·33	22·2
Day range length	feeding grp wt	% foliage eaten	0·65	−0·48	47·2
Home range size	pop. grp wt	% foliage eaten	0·92	−0·33	75·6
Population density	body wt	% foliage eaten	−0·53	0·53	29·6
Biomass	body wt	% foliage eaten	0·71	0·75	49·1

The first measures (b_1' and b_2') allow direct comparison of the importance of each independent variable in influencing the dependent variable. The third (% of variance) allows comparison of the total proportion of variance accounted for in the partial regressions.

Appendix I

Methodology and Measurement

T. H. CLUTTON-BROCK

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Since an extensive review of sampling methodology (Altmann, 1974) is already available, it is unnecessary to discuss the topic at length here. However, recent studies raise several detailed points concerning measures used in field work.

1. Activity Budgets

Two main methods of assessing the proportion of time spent by animals in different activities have been used. Either, an individual is selected and its activities are recorded continuously or at very short time intervals for an extended period, or the activities of all visible animals are censused at longer time intervals. The first method we shall refer to as "focal animal observation" and the second as "censusing" or "scanning".

Scanning has the obvious disadvantage that results may be biased by (a) differences in visibility between individuals engaged in different kinds of activity and (b) differential representation of the various age/sex classes (or even of different individuals) in scans. One effect of bias of the first kind can be to increase the total number of animals visible when the group is predominantly engaged in particular activities. This can be removed by expressing the number of animals engaged in each activity category *in each scan* as proportions of the total number of animals

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recorded *in each scan* and calculating overall estimates by averaging these percentages (Clutton-Brock, 1974b). However, estimates may still be affected by differential visibility between activities which will, for example, influence the probability that *any* animals are recorded in a particular activity.

So long as the observer and not the animal controls the beginning and ending of observation bouts, and selection of subjects is randomized, focal animal observation is not susceptible to the same bias as scanning. It also has that distinct advantage that it provides accurate data concerning the duration and sequencing of activities (see Chivers, 1974). Its primary disadvantages are that (i) a relatively small amount of independent data can be collected per unit time, with the effect that samples collected by this method will be more narrowly based than those collected by scanning, and (ii) it requires animals to be relatively well habituated to the presence of observers. In practice, estimates of time budgets based on the two methods tend to be similar (Clutton-Brock, 1974b; Chivers, 1974). The choice of methodology will probably continue to depend both on observation conditions and on constraints imposed by the objectives of the project.

The way in which records are taken also varies between studies. Most observers have recorded the activities of each animal "instantaneously" (i.e. at a particular point in time): for instance, Sussman (Ch. 1) scanned his lemur troops every five minutes, recording what each animal was doing as he first saw it. In contrast, others have recorded the first activity *lasting for more than five seconds* which was performed after a set time interval (e.g. Chapters 8, 11 this volume; Struhsaker, 1975). This method of recording (which we shall refer to as "duration" recording) has the advantage that it does not require the observer to identify an animal's activity at a glance, and may thus lead to more accurate measurement. However, it also has the effect of selecting against activities occurring in very short bouts. For example, where feeding is regularly interrupted by short pauses, these are less likely to be represented than where instantaneous records are taken. Struhsaker (1975, p. 177) claims this as a major advantage of the method, arguing that classification of short bouts of inactivity which occur during feeding periods with longer bouts of resting leads to serious misrepresentation of time budgets.[a] This argument is based on the assumption that inactivity-during-feeding is, in some way, different from longer periods of inactivity. In the absence of some justification of this (such as

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[a] In practice, a 5-sec "duration" criterion will select against short bouts of >5 sec duration as well as totally excluding bouts of <5 sec.

demonstration of a discontinuity in the frequency distribution of inactivity bout lengths) the method lacks obvious rationale, but the difference may be more important in theory than in practice, since it now seems likely that the two methods generally give similar results (see Oates, Ch. 10; Marsh, pers. comm.). One way of combining the advantages of instantaneous and duration sampling would be to record the behaviour of individuals a fixed number of seconds after they were first seen (e.g. Kavanagh, in prep.).

2. Diet Composition

Measurement of diet composition in wild primate populations has usually been approached in one of five ways.

(i) Analysis of stomach contents (Charles-Dominique, 1974a,b; Gautier-Hion, in prep.).

(ii) Analysis of dung samples (e.g. Goodall, 1974, this volume).

(iii) Visual measurement of amounts of different foods eaten (Hladik and Hladik, 1969, 1972).

(iv) Measurement of the proportion of feeding time spent on different foods (e.g. Richard, 1970; Chivers, 1974; Clutton-Brock, 1975a).

(v) Measurement of the frequency with which different foods are chosen (see Struhsaker, 1975; Oates, Ch. 10).

All five methods are liable to systematic errors and, as yet, there is no reliable way of estimating them. Measures of food intake based either on stomach contents or dung may be biased by differential absorption of food items. In addition, the first method is usually impracticable since most field studies rely on small numbers of habituated animals. Visual estimates of food intake may provide the best information (see Hladik, Chs 11, 16). However, even where visibility is good, it is usually difficult to measure ingestion rates for some foods (for foliage, in particular) and no check has yet been made on the accuracy of this method in the field. Measurement of time spent feeding on different items has the advantage that it is easily repeatable and that differences in recording methodology apparently have little effect on overall estimates (e.g. Clutton-Brock, 1975a; Struhsaker, 1975). However, it will not provide a reliable estimate of the amounts of different foods ingested where feeding rate varies widely between foods: for example, Hladik (see p. 329) estimated that *Presbytis entellus* at Polonnaruwa spent only 28·1% of their time feeding on the large fruits of *Ficus benghalensis* but that these constituted 77·3% of the total fresh weight of food ingested. [In contrast, estimates for both *P. entellus* and *P. senex* of time spent eating small, unripe fruits, flowers and foliage corresponded more closely to estimates of amounts ingested, though moderate discrepancies occurred in several cases (see Chapter 10)]. As Hladik points out, measures of time spent feeding on particular foods are likely to give particularly poor estimates of amount ingested in species which feed extensively on insects, where a large proportion of time is devoted to collecting and eating a small proportion of the diet.

Measurement of the frequency with which different foods are chosen is usually less satisfactory than measurement of feeding time since it is likely to produce a bias towards (i) foods that are regularly eaten but only in small amounts (see p. 542), (ii) species on which several edible parts are available at the same time, and (iii) species which are over-dispersed and do not grow in clumps. Nevertheless, this method can apparently give similar results to measures of feeding time. For example, Struhsaker's (1975) estimates of the time spent in different foods by red colobus (based on a mixture of time sampling and frequency records) were very similar to those obtained in a neighbouring troop by Clutton-Brock (1972) using 15-min censuses.

Perhaps the most obvious conclusion to be drawn from consideration of the methodology of dietetic measurement is that investigation of the relative accuracy of different methods is badly needed. In particular, it is important that attempts to quantify ingestion by observation should be checked against analysis of stomach contents or, preferably, against samples obtained from oesophageal-fistulated animals, in order to validate their claim to provide a more accurate measure of ingestion than estimates of feeding time. Until this is done, the accuracy of both measures is in question and only gross differences in feeding behaviour can be considered as reliable.

3. Dietetic Diversity

The use of measures of dietetic diversity and, in particular, of Shannon's formula (Pielou, 1966) has recently increased (see Chapters 8, 11 this volume; Struhsaker, 1975). Diversity indices and their applications are discussed in Appendix II.

4. Food Availability

The density of food species has been measured in several ways including: (a) counts of trees overlapping transect paths (Clutton-Brock, 1975a); (b) counts of trees growing within measured strips (Chivers, 1974;

Waser, Ch. 7; Struhsaker, 1975); (c) area samples distributed semi-randomly across the study site (e.g. Richard, Ch. 3).

The two latter methods represent an improvement over the first which, if it is not to bias towards species with large canopies, requires tree numbers to be corrected by estimates of their spread (e.g. Clutton-Brock, 1972).

Tree density measures presumably provide reasonably accurate estimates of spatial variation in the availability of particular foods and differences in canopy size can be taken into account (e.g. Struhsaker, 1975). No satisfactory method of measuring either temporal changes in food availability or comparative availability between food species has yet been achieved. Though it is relatively easy to estimate the proportion of trees of a given species carrying different parts (e.g. Chivers, Ch. 12, 1974; Struhsaker, 1975), some parts remain on the trees for extended periods but vary widely in density, and such estimates provide only crude measures of changes in availability.

Finally, it is (and may always be) virtually impossible to measure variation in overall food availability. An added complication in this case is that even measurement of the availability of foods selected by the animals may provide a poor estimate of overall availability if, when food is short, the animals feed less selectively (see Emlen, 1973). The most useful approach here may be to identify times (or areas) of particularly low availability by examination of dependent variables, such as body weight (Wrangham, 1975).

5. Selectivity

The extent to which animals select a particular food can be measured by dividing the amount taken by the availability of the food in the environment (Clutton-Brock, 1972). In several studies (Clutton-Brock, 1975a; Struhsaker, 1975; Oates, Ch. 10; Waser, Ch. 7) selection ratios for particular food species have been calculated by dividing the proportion of time spent feeding on the species by measures of the relative frequency of the species (or, in some cases, the relative abundance of the cover they provide). These are useful in identifying the cases where animals show strong selection for rare tree species, but clearly provide no more than approximate measure of selectivity, both because tree density (or cover abundance) provides a poor estimate of food availability and because feeding time may be poorly related to ingestion (see above). It is also important to remember that even accurate measures of selection may give no indication of the animals' preferences, though a recent study of mangabeys on the

Tana river (Homewood, pers. comm.) shows that the selection ratio of different foods is related to their maximum metabolizable energy content.[a]

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[a] Selection should be distinguished from "preference". A food is "selected" if it is chosen more often than would be predicted from its abundance on the hypothesis that the animal is choosing at random. Some foods may be selected because they are easily accessible (Landenberger, 1968), because they can be profitably exploited (Royama, 1970b) or because they are available over a long period of time (Paine and Vadas, 1969). Others may be selected because the animal prefers them to other foods (i.e. it would choose them if they were presented simultaneously, in the same amount and under the same conditions).

Appendix II

The Measurement of Dietetic Diversity

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1. Introduction

The amounts of different dietetic components can be assessed from feeding observations or gut and faecal analyses. It is the purpose of this Appendix to consider the presentation and interpretation of such data. I shall be particularly concerned with the analysis of abundance-rank diagrams (in which the components are ranked in decreasing order of abundance) and the associated concepts of dietetic diversity and evenness.

2. The Data

Ideal data would consist of the amounts (in terms of biomass, energy content or some other relevant measure) of different species (or other components of the diet) consumed per unit time by one or more individuals. In practice such data is difficult to obtain and the relative numbers of different feeding observations on various food species will be employed as a reasonable measure. For the purpose of interpretation, all observations assigned to specific food species are assumed equal, while all food species are assumed to be equally different (Peet, 1974). We thus have a sample of feeding observations on n species and can calculate p_i ($i = 1, 2, \ldots, n$), the proportion of feeding observations made on the ith species.

3. Displaying the Data

One way of displaying the various species' abundances in a sample is to plot the p_is on the y-axis of a graph with their ranks in order of decreasing value on the x-axis. Alternatively, the plot can be cumulative on the y-axis, plotting the proportion of the total observations included up to the rank given on the x-axis (e.g. Clutton-Brock, 1972). Variants include plotting either or both axes on a logarithmic scale. Finally, the distribution can be presented as a histogram of the number of species whose proportional abundances lie in specific ranges.

As May (in press) has emphasized, all such diagrams are interchangeable and equivalent ways of expressing the species abundance distribution.

4. Dietetic Diversity

The problems associated with assessing dietetic diversity from such data are similar to those of measuring community diversity. Many diversity indices exist and different authors have tried to use those most appropriate to their own studies. Hill (1973) demonstrated that the three most commonly used diversity indices are related to an arithmetic mean, a geometric mean and a harmonic mean of proportional species' abundances. If we define

$$\mathcal{N}_a = (p_1{}^a + p_2{}^a + \dots + p_n{}^a)^{1/(1-a)}$$

then the number of species in the sample is $\mathcal{N}_0$, the Shannon–Weiner function (used by Struhsaker, 1974 and Oates, Ch. 10) can be shown to be equal to $\ln(\mathcal{N}_1)$ while Simpson's (1949) diversity index is the reciprocal of $\mathcal{N}_2$. The equation gives more weight to the common species as the value of a increases. Clearly, setting $a=1$ weights the species according to their relative abundances and should be used in practice unless there are explicit reasons why a should take some other value.

5. Dietetic Evenness

When a does not equal zero, $\mathcal{N}_a$ provides a combined measure of dietetic richness and evenness. That is, the diversity measure depends on both the number of species in the sample and their relative proportions. Given that $\mathcal{N}_0$ provides a conservative estimate of the number of species in the diet, it is desirable to distinguish between the two components of diversity by attempting to quantify species evenness.

It is evident that any evenness index should be maximized when all the species are equally represented in the diet. Hill (1973) has also suggested that if the number of species is doubled so that each of the original species is matched by an additional species of equal abundance then the species evenness measure should remain constant. Pielou's $J = \ln(N_1)/\ln(N_0)$ (Pielou, 1969), the most commonly used evenness measure, does not have this latter property as it records an increased value when the number of species is doubled in the way outlined above. Hill's ratios ($E_{a,b} = N_a/N_b$ where $a > b$) are the only ones yet described which remain constant (Hill, 1973). In the final analysis, because the response behaviour of evenness indices is so little understood, examination of the underlying abundance-rank curves is always advisable (Peet, 1974).

If the abundance-rank curves indicate a specific underlying distribution, which might help in data interpretation (May, in press), then expected values of N_a or $E_{a,b}$ can be calculated to compare with the observed (May, 1974).

6. Example

Clutton-Brock (1975a) studied a troop of red colobus in Gombe National Park, Tanzania between August 1969 and June 1970. The

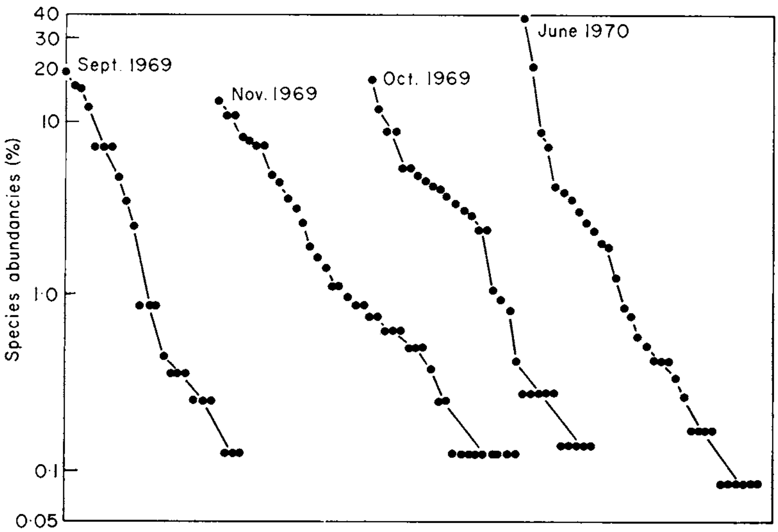

FIG. 1. Species abundance curves for feeding observations on red colobus during four months (see text).

troop was followed during the hours of daylight and, at quarter-hourly intervals, records were made of the food species of all animals seen feeding during a five-minute period. Each animal was recorded only once during that time. Clearly, the observer's position relative to the different animals in the troop and their visibility in different species of trees could have added bias to the data. However, Clutton-Brock (1972) demonstrated that such bias was small. The feeding records of four months are used below (September 1969, October 1969, November 1969 and June 1970).

Abundance rank curves for the four months are given in Fig. 1. The *y*-axis is scaled logarithmically which has tended to reduce clustering of the points and to linearize the curves, thus facilitating comparison between them. Diversity and evenness indices for the data are given in Table I. Two comparisons which can be made from the Table illustrate an important point. First, diversity measured by N_1 is higher in November 1969 than September 1969. Species evenness is similar in the two months and the differences in diversity result from the different number of species in the diet. Second, October 1969 has a higher value of N_1 than June 1970. Here the number of species in the diet is similar, but a more even distribution of feeding observations across species is apparent for October 1969 than June 1970. These comparisons illustrate the importance of examining both components of diversity in any specific study. It should be emphasized, however, that although dietetic diversity and evenness indices may act as a useful interpretation guide, they should not be used as an alternative to the examination of species abundance curves.

TABLE I

Species diversity and evenness indices for feeding observations on red colobus during four months (see text)

	N_1	N_0	$E_{1,0}$	J
September 1969	10·50	24	0·49	0·74
November 1969	18·69	40	0·47	0·79
October 1969	10·07	31	0·55	0·83
June 1970	9·72	33	0·27	0·23

Acknowledgement

I am grateful to Dr T. H. Clutton-Brock and Paul J. Greenwood for helpful comments on a manuscript of this Appendix.

Appendix III

Field Methods for Processing Food Samples

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1. Methods for Collecting Samples

Food samples and botanical specimens are generally collected simultaneously, the latter being necessary to identify different food samples. Methods for processing botanical specimens are generally well known. By contrast, food samples must be obtained in fairly large quantities (about 200 g, wet weight) to allow further analysis with standard techniques, and difficulties have been found in the collection and processing of such large samples. A few technical solutions adopted in our studies, especially on leaf monkeys and chimpanzees (Hladik, this volume), might be useful for future research about primate feeding behaviour.

Specimens located on trees were collected with the help of accessories, to avoid the risks and difficulties of climbing.

Extension poles

A tree pruner mounted at the top of a long pole was sufficient to collect all the specimens in the semi-deciduous forest of Sri Lanka where trees do not exceed 25 m in height. The pole was made of a series of five bamboos that can reach 15 m: this height is sufficient to collect specimens from the lower branches of most trees, but two persons were required to handle the pole which had a basic piece of 12-cm diameter. The bamboo pieces were held together with a wooden tenon and the end of the hollow parts reinforced with iron wire and araldite.

Tree climbing dress

In the rain forest, the lower branches of many tree species cannot be reached directly with a tree pruner. A special dress for climbing trees was designed and made of strong canvas with pieces of leather reinforcing the inside parts of knees and protecting the chest against the rough bark of the tree trunk. Direct climbing of lianas and trees is facilitated by such dress and collection of samples with the tree pruner can be done from a high position; but not without risk.

Tree climbing platform

The most useful accessory for collecting in the rain forest is the tree climbing stand sold by "Forestry Suppliers, Inc." (Jackson, Miss., USA). We used it in Gabon with the tree climbing dress (Fig. 1) to protect the chest. This platform is made of light plywood and allowed us to climb smooth vertical trunks up to 30 m without special training. From this position,[a] it was possible to collect food samples up to 40 m, with the help of the tree pruner mounted on its bamboo pole. Trees exceeding 40 cm in diameter cannot be held by the gripping bar of this stand but it is generally possible to collect samples from a nearby vertical tree trunk. Exceptionally, a 10-m collapsible aluminium ladder was used to start climbing with the platform from the point where the diameter of the trunk is small enough to mount the climbing tree stand.

2. Processing Food Samples

Drying

After collecting, the samples were carried in large polyvinyl bags to avoid desiccation before weighing. Samples of about 200 g were put in paper bags (about 50 g dry weight is enough to carry out the most important analysis with duplicates or triplicates: most of the specimens have 70 to 80% water content). Paper bags were made of non-glossy paper to allow moisture to escape (a cone of paper can be made with old newspapers).

Paper bags with food samples inside were dried in an electric oven when this was available. In the field, we used the heat of a kerosene lamp to make an "oven" with a big tin box penetrated by two tubes to allow air circulation (Fig. 2A). A cylinder of canvas maintained the

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[a] A safety rope properly tied around the trunk and around the chest of the collector *must* be utilized.

FIG. 1. The tree-climbing platform descending from 20 m height on a smooth tree trunk, in Gabon. Note the climbing marks of the gripping bar, along the trunk.

heat around the tin box and forced it to pass through the botanical samples placed above the tin box. Inside the tin box, the samples must not be pressed together and the temperature should be maintained at about 60 to 80° C. It is important not to exceed this temperature to avoid decomposition of the samples. Dryness is completed when a sample maintains a constant weight. Leaves can be dried in less than one day but some fruit samples may need several days for total drying. In the field station of Gabon, an electric dryer utilizing ten electric bulbs of 100 W each (Fig. 2B) was employed to dry large-sized food

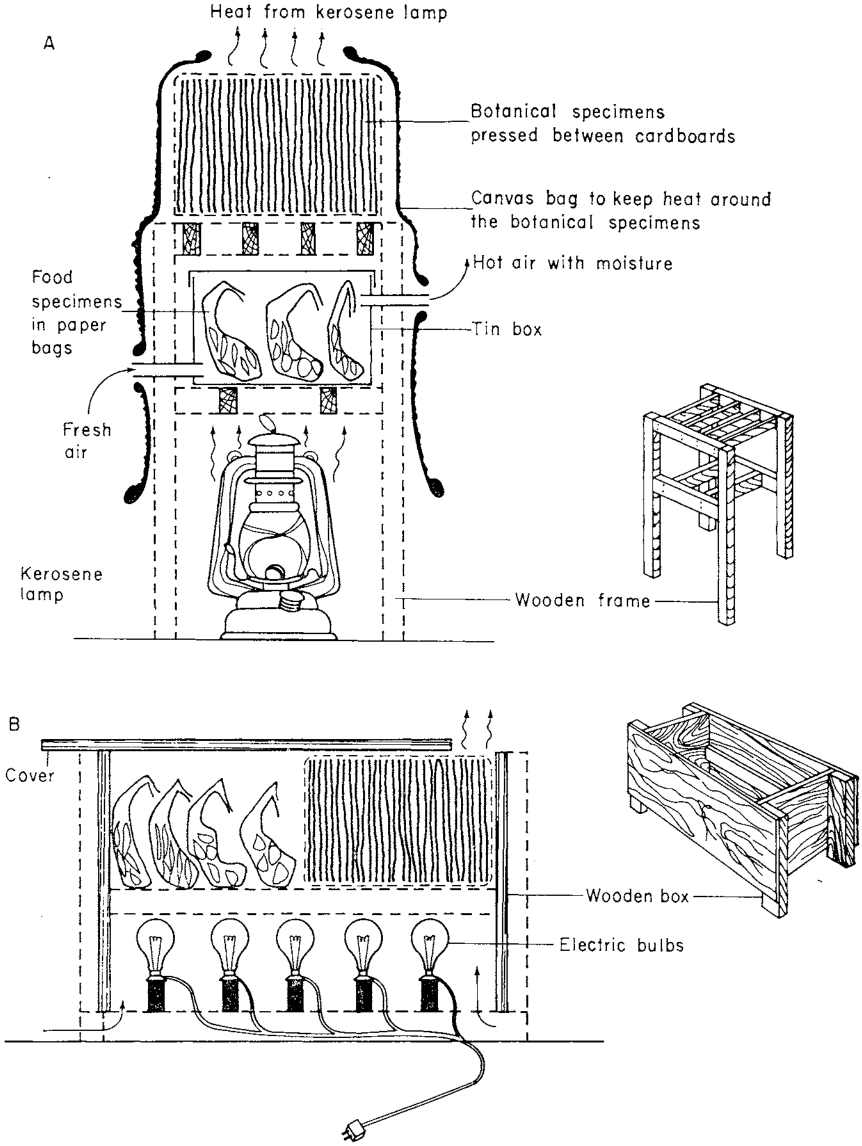

FIG. 2. Models of dryers for food samples and botanical specimens. A. To be used in the field. B. To be used at the field station.

samples. Paper bags with the dried samples can be kept in plastic bags carefully tightened or sealed.

Processing in alcohol

Fixation of the samples in boiling ethyl alcohol is one of the best methods of stopping all enzymatic reactions and preserving all components. In field conditions, samples of small size (about 20 g fresh weight) can be processed by this method. Thus, it complements the preceding method, and is necessary to allow detailed investigation on soluble sugars, amino acids and lipids (see Section 3).

Ethyl alcohol (96°) was heated to boiling in an Erlenmeyer flask and the food sample dropped into it after slicing in small pieces (less than 2 mm thickness). A condenser was adapted to a rubber cork on top of the flask. It was cooled with fresh water kept in a canvas water-carrier to prevent the alcohol from evaporating during processing. We utilized an alcohol lamp or a butane gas stove to heat the flask, with a shield to protect it as shown on Fig. 3.

The volume of alcohol in the flask must be about five times more than the volume of the food sample. It has to boil with the sample for 15 minutes. When the alcohol is no longer hot, the food sample with all the alcohol must be carefully taken out of the flask and can be stored in a plastic jar.

Freezing

Only deep freezing (below −30° C) adequately preserves food specimens. Several field stations in the tropics are now equipped with large freezers in which food samples can be kept but there are problems in long-distance transportation of such samples and the analytical operations must be started as soon as the samples are defrosted.

3. Different Types of Analysis Consistent with the Different Methods of Field Processing

Dried food samples can be used for the standard operations of analysis such as those described and referred to in Hladik *et al.*, 1971a. There was no significant difference in the titrations of minerals, nitrogen, lipids, cellulose and total glucids, between food samples boiled and preserved in alcohol and dried food samples of the same origin. By contrast, important differences between the two parts of the food sample (one processed by drying, the other one processed in alcohol) appeared when comparing the proportions of the different soluble sugars (Hladik *et al.*, in press). This was particularly obvious for samples requiring a long

FIG. 3. Students of the University of Sri Lanka processing food samples in boiling alcohol, at the Polonnaruwa Field Station. Water for cooling the condenser is in a canvas water-carrier hanging above the apparatus.

time to dry such as large flowers and leaves. In these dried samples, sucrose was missing, probably because rapid fermentations occurred at the beginning of the drying process; glucose, fructose and other glucids of small molecular size were found in larger amounts.

Food specimens boiled and preserved in ethyl alcohol can be used for analysis and titration of soluble glucids and for research on the amino acids after lyophylization and grinding (Hladik and Viroben, 1974).

Research on fatty acids can also be carried out on food samples processed in alcohol or in 10% formalin (Hladik *et al.*, 1971b). We have no comparative result with other methods for these last two analyses: although oxidation might not affect most of the lipidic components, the only reliable process for detailed analysis would be deep freezing and lyophylization.

Tests for different secondary compounds (for instance, alkaloids) can be made on dried specimens but the results may differ slightly from those obtained on fresh specimens (see discussion in A. Hladik, 1977). Nevertheless, fractioning and further chromatographic analysis necessitates dried food specimens.

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