Factors limiting the abundance and distribution of hirola (*Beatragus hunteri*) in Kenya.

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Abstract

This study investigates the factors limiting the abundance and distribution of hirola, or Hunter's antelope, (*Beatragus hunteri*), in Kenya's Tsavo East National Park (*ex-situ* population) and Garissa (*in-situ* population). The hirola is widely recognized as the most severely threatened monotypic species of antelope in sub-Saharan Africa. Data were collected between 1996 and 2000 on the *ex-situ* population, with occasional comparative sampling of the *in-situ* population. The study was carried out almost entirely in the field. Hirola were located by ground searching, by radio tracking and occasionally using aircraft; animals were observed from a landrover.

In Tsavo NP the population was found to be static (71.1±9.3 in 844 km^2 range), while the Garissa population was declining with about 672 animals remaining in a 5,171 km^2 range. Calving in Tsavo took place between August and March, with the peak occurring in late October and early November. About 69.8% of calves died or disappeared within the first 6 months of life and about 18.0% survived to the age of 2 years. Mortality in Tsavo was predominantly associated with predation, while in Garissa, mortality was associated with disease and poaching.

Hirola occurred in 8 distinct family groups in Tsavo, each with an adult male and a number of females and their offspring; temporary separations involving the adult male, or females with young, were also recorded. Remarkably, offspring left their natal groups at about 6-15 months of age and spent a period isolated or with other young animals; females eventually rejoined a family group or joined a lone male to form a new group. Young males generally formed bachelor groups and eventually separated as adults to become solitary. Hirola were most active in the early morning hours and late evening when it was cool; hot times of the day were spent resting in the shade of trees and bushes.

Densities of other ungulate species within the hirola range varied seasonally, being more abundant in the wet season. Controlling for the relative abundance of other herbivore species, hirola in Tsavo were found to associate predominantly with Grant's gazelle (*Gazella grantii*), while in Garissa they associated mainly with topi (*Damaliscus korrigum*). The presence of fewer associates and fewer alternative prey in the dry season appears to have increased the risk of predation to hirola, perhaps due to reduced detection and dilution effects.

Home ranges occurred on generally elevated areas associated with red soils (in Tsavo) or sandy soils (in Garissa), and scattered seasonal waterholes. Vegetation in these areas was composed of tall, fairly open bushes interspersed with short green grass patches, that offered preferred food, shade and cover. In Tsavo, hirola fed on a total of 56 plant species (grasses, 74.9%; forbs, 24.2; and sedges, 0.9%) while in Garissa, 27 plant species were eaten (grasses 85.2% and forbs 14.8%). Hirola selected short green grasses and forbs, eating an entire plant (leaf, stem and inflorescence) at a mean bite height of 7.4±3.93SD cm. The nutrient content of the preferred plant species were measured on a seasonal basis.

The Garissa population has declined as a result of range reduction, caused by human encroachment. In addition, it has been further affected by poaching and spread of diseases from cattle. The factors limiting the Tsavo population were investigated by multivariate analysis of the relationship between the main candidate factors (estimates of predation pressure, food abundance, shade tree densities, competitors, etc) and variation in the size, reproduction and mortality rates across the hirola family groups studied. The main limiting factors in the Tsavo population appeared to be predation pressure and the amount of specific microhabitats available for shade, cover against predators, and food.

Finally, I discuss how these results may shape the development of conservation management strategies for hirola in the future. Recommendations include the restoration of protected areas in Garissa and the establishment of further *ex-situ* populations, preferably in predator free environments, to allow a rapid increase in numbers and to spread the risk of species extinction.

Declaration

I, Samuel Ambindi Andanje, declare that the work reported in this thesis is original, and has not been published or submitted as part or whole requirements for any other degrees or qualifications.

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Dedication

To my late beloved family members, brothers Newton and Seth, and my father Javan and mum Juliana Andanje.

Chapter I:

Introduction and Study Animal

1.1 The conservation of threatened species

The primary objective of threatened species conservation is to reduce the risk of population extinction. A first step in achieving this objective this is to identify those factors that can potentially cause extinction in the population (Ballou et al., 1989). If a population is declining in numbers, and no action is taken to reverse the trend, then extinction is imminent (Ballou et al., 1989). The foremost problem facing the conservation of small populations is that these populations may still be highly vulnerable to extinction even when they are maintaining their size or even increasing in numbers. Small populations are challenged by a number of factors that increase the likelihood of the population going extinct simply because the population is small (Ballou et al., 1989).

There are two sets of processes that drive wildlife species to extinction (Caughley, 1994). Initially, certain factors act on a population to reduce numbers considerably, and then other processes act on the low numbers (Caughley, 1994). The factors causing species to decline are overkill, habitat destruction and fragmentation, the impact of introduced species, and chains of extinction (Diamond, 1984; Caughley, 1994). The factors affecting small populations are environmental stochasticity, epidemics and catastrophes (for example floods, fires, hurricanes), demographic stochasticity (normal variation in the population's birth and death rates and sex ratios) and genetic deterioration, especially inbreeding depression (Frankel & Soule, 1981; Shaffer, 1981; Lande, 1988a; Lande, 1993). However, these agents may often act on a species concurrently, though with less severity, on larger populations (Hedrick et al., 1996).

Overkill results from hunting at a rate above sustainable yield (Hedrick et al., 1996). Harvesting strategies based on models that neglect the possibility of extinction have been found to provide lower mean annual yields, and to subject populations to a greater risk of extinction, than do optimal harvesting strategies that take into consideration the possibility that demographic and environmental stochasticity can lead to extinction (Lande et al., 1995). These effects can be more pronounced if the affected animals are long-lived, as for example in the cases of elephants and rhinos (Caughley, 1994) and whales (May, 1976). Die-offs themselves may not often drive natural populations to extinction, but such demographic bottlenecks may put large populations at risk from factors that affect small populations (Simberloff, 1988; Berger, 1990; Hedrick et al., 1996). Species on 'islands' are also at risk from overkill because they cannot be replenished by immigration (Olson, 1989). Stochastic processes by themselves, or in interaction with deterministic factors, may contribute to the eventual collapse of a species (Hedrick et al., 1996). Many managed fisheries have collapsed in this fashion (Ludwig et al., 1993). Other examples include the loss to disease of the last wild population of black-footed ferrets (*Mustela nigripes)* (Clark, 1989; Seal et al., 1989) and the decimation and subsequent extirpation of the last non-migratory population of whooping cranes (*Grus americana*) as a result of a hurricane (Doughty, 1989).

Habitat destruction by agents such as change in a fire management regime, grazing by sheep or goats, drainage of a wetland, or cutting down of a forest patch may cause a dependent species to decline (Caughley, 1994). Habitats may become fragmented when large tracts are converted to another land-use (Graetz et al., 1992). Loss of habitat does not necessarily increase the vulnerability of a species nor decrease the number of its members by a given proportion, except in the special case of habitat being cleared from the edge inwards (Caughley, 1994). More commonly, the modification acts to produce a patchwork pattern as it erodes the tract of habitat from the inside and changes microhabitats (Saunders et al., 1991). At this stage, there may even be an increase in the number of species using the total area, because of additional microhabitats and the increase in number of those that benefit from the increased length of edge (Caughley, 1994). However, this phase is short-lived as the desert islands multiply and enlarge, thus reversing the trend (Hobbs et al., 1992). Once deterministic factors have led to fragmented and isolated populations, stochastic factors may further reduce numbers, and the interaction of the forces may contribute to further endangerment (Gilpin & Soule, 1986). Research has shown that endangered remnants of a once widespread species tend to settle not in the most favorable habitat, but in habitats least favorable for the agent causing their decline (e.g., the New Zealand takahe rail, *Notornis mantelli* (Caughley, 1989), the Hawaiian goose, *Branta sanvicensis* (Kear & Berger, 1980b) and the Lord Howe wood hen, *Tricholimnas sylvestris* (Miller & Mullette, 1985).

Introduced species may cause the decline of native species by competing with them, preying upon them, or destroying a habitat (Atkinson, 1989). A good example is the Lord Howe wood hen (*Tricholimas sylvestris*) whose incubating birds were being decimated by the feral pig (Miller & Mullette, 1985); other examples of the impact of introduced species include the extinction or near extinction of 31 bird species and 14 reptile and amphibian species in New Zealand (Atkinson, 1989). In other cases, species declines may be caused by extinction or local extermination of another species upon which it depends (Diamond, 1989). Domesticated species may act as aliens that result in the decline of native species and the increase in numbers of livestock in the hirola's native range is a notable example.

In small populations, demographic stochasticities reflect the uncertainty of individual fortunes (Caughley, 1994). The interaction of demographic and environmental factors also affects small populations. For example, the last five Dusky Seaside Sparrows (*Ammodrumus maritimus nigrescens*) were males (Hedrick et al., 1996) and the last Illinois population of lakeside daisy (*Hymenoxys acaulis* var. glabra) was of the same self-incompatible mating type (DeMauro, 1993). Rare plants (Karron, 1987) and those in small populations (Widen, 1993) can suffer reduced seed set due to lack of pollinators. In general, small, local populations of animals have been found to be more likely to go extinct (Soule et al., 1988; Berger, 1990; Rosenzweig & Clark, 1994; Hanski et al., 1995; Newmark, 1995).

The environment acts through its effects upon renewable resources (such as the herb layer). When this effect is translated upon the dynamics of the associated herbivores, this would cause fluctuations in numbers (Bayliss, 1987; Caughley, 1987). Environmental factors may also influence a population's rate of increase by working directly upon mortality without any intermediate action of resources (e.g., avalanche, predation and fire) (Caughley, 1994). An unusually dry year in a Costa Rican cloud forest apparently caused the extinction of the golden toad (*Bufo periglenes*) and the local extirpation of the harlequin frog (*Atelopus varius*) (Pounds & Crump, 1994). The reproductive success of the endangered Florida snail kite (*Rostrhamus sociabilis*) was directly affected by water levels, which determine prey (snail) densities: nesting success rates declined by 80% during years of low water levels (Beissinger, 1986).

The depletion of genetic variation at low population size is theoretically inevitable but has seldom been demonstrated in practice. However, good data are available to show that inbreeding depression has resulted in damaging losses of viability and fecundity in many captive stocks (Ralls & Ballou, 1983; Ralls et al., 1988; Lacy et al., 1993). Both genetic drift and inbreeding reduce heterozygosity, since for both, the rate of loss accelerates with declining numbers (Caughley, 1994). Data on ontological studies suggest that individuals with more heterozygosity are fitter than individuals of the same cohort with less heterozygosity (Allendorf & Leary, 1986; Ledig, 1986) because of the exposure of and selection against recessive semi-lethal alleles (Hedrick, 1992). Laboratory research has demonstrated that most fitness components of a species can be influenced by inbreeding (Miller & Hedrick, 1993), that inbreeding depression is greater in stressful environments (Miller, 1994), and that inbreeding may result in lowered fitness in natural environments (Jimenez et al., 1994; Keller et al., 1994). The loss of genetic diversity in small populations has apparently reduced fitness in natural populations of plants (Bijlsma et al., 1994) topminnows (*Poeciliopsis occidentalis*; (Vrijenhoek, 1994)), wolves (*Canis lupus*; (Wayne et al., 1991), African lions (*Panthera leo*; Parker et al., 1991), and Florida panthers (*Felis concolor coryi*; (Roelke et al., 1993). The important issue is to determine under what conditions genetic concerns are likely to influence population persistence (Nunney & Campbell, 1993; Mills & Smouse, 1994). Genetic factors generally do not operate in isolation but will influence a population through its effects on disease resistance, viabilility, reproductive success, behaviour, physiology, and other characteristics (Hedrick et al., 1996).

Populations are typically subdivided with varying rates of exchange between subpopulations. The dynamics of such 'metapopulations' (Hanski & Gilpin, 1991) have many implications in conservation biology (Caughley, 1994). When subpopulations become isolated or almost isolated, there are marked effects on the genetics of constituent local populations (typically a reduction in heterozygosity) and on their dynamics (including the ability of the metapopulations to 'rescue' declining local populations by dispersal from larger local populations) (Caughley, 1994). In order to offset the constraints of low effective population size active manipulations through exchange (zoos) and translocations (parks) can be effected (Caughley, 1994). Modern zoos act as a metapopulation for some species, especially those endangered in the wild (Caughley,

1994) and their stock has been used to reintroduce species back into the wild, e.g., the Arabian Oryx *Oryx leucoryx* (Price, 1989), Hawaiian goose or nene *Branda sanvicensis* (Kear & Berger, 1980a), the Indian coney *Geocarpromys brownii* (Oliver, 1985) and European otter *Lutra lutra* (Jefferies et al., 1986).

We also need to recognize when management recommendations based upon strictly demographic or genetic considerations may actually conflict with each other. For example, one management option, known as supportive breeding, consists of bringing a portion of wild parents into captivity for reproduction; their offspring are then released into the natural habitat, where they mix with wild conspecifics (Rayman & Laikre, 1991). However, under some circumstances, supportive breeding may reduce effective population size and cause a drastic reduction in genetic variation (Rayman & Laikre, 1991; Rayman et al., 1995). Supportive breeding is a conservation management option for the hirola but, for these reasons, would need to be carefully evaluated before it is implemented.

An endangered species, such as the hirola, is by definition at risk of extinction. The main objective of conservation programs for such species is to reduce the risk of extinction to the "normal" level of risk that all species face. We need to improve our estimates of risk, to better determine the risk due to different potential management options, to improve objectivity in assessing risk and to add quality control to the process (through internal consistency checks). The information acquired through these processes can then be used in Population Viability Analysis (PVA). PVA is an important analytical method that provides an estimate of how long a population will persist if nothing external to it changes. An effective PVA requires a study of the natural history of a species to gain a knowledge of, and the feel for, its ecology, and conservation status (Caughley, 1994); the general aim of this thesis is to gain such knowledge about the hirola, in preparation for a future PVA.

1.2 The study animal (hirola)

1.2.1 Taxonomy

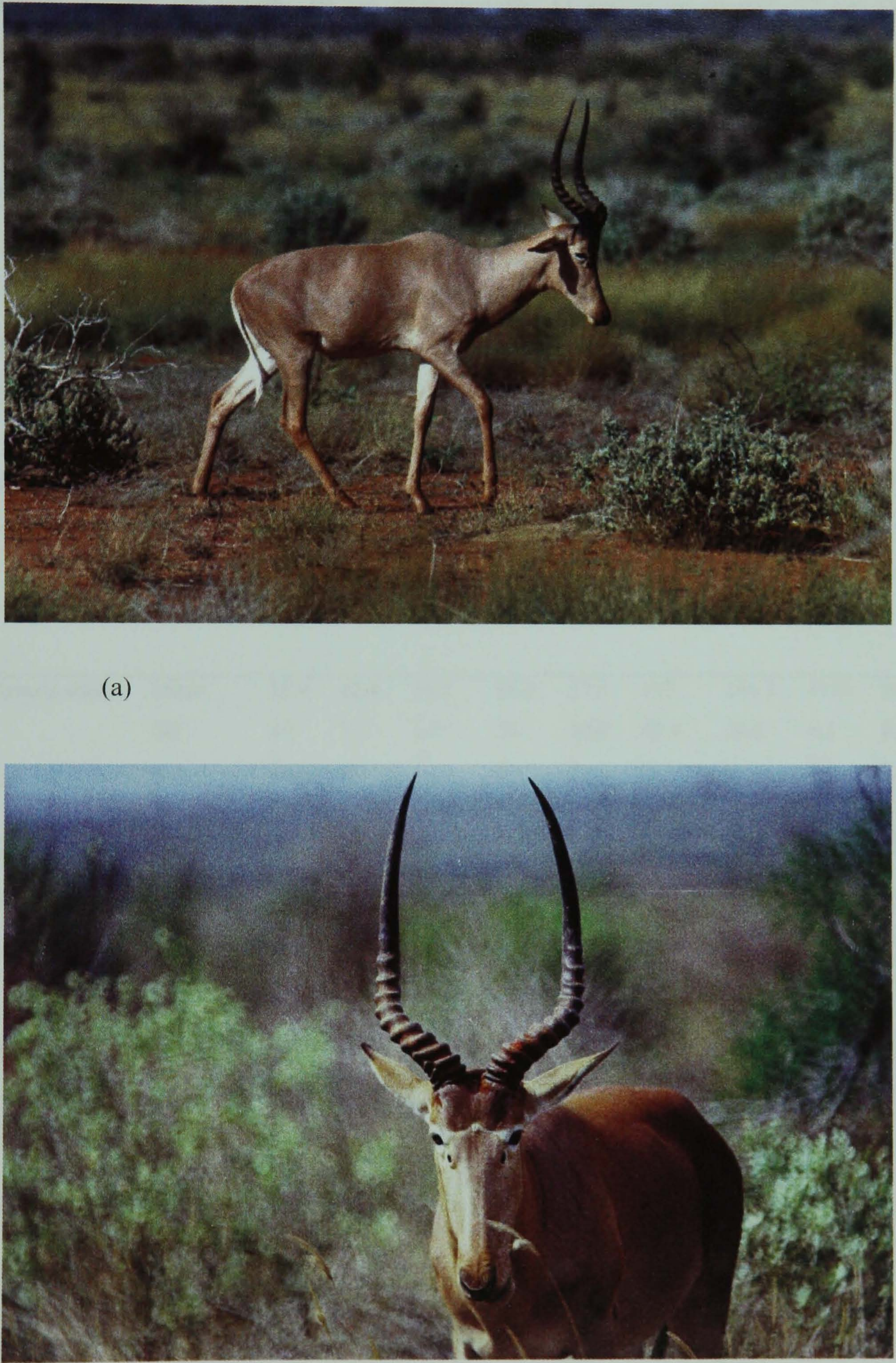
The hirola or Hunter's antelope (*Beatragus hunteri,* Sclater 1889) belongs to the subfamily Alcelaphinae (which includes the hartebeest *Alcelaphus spp.*, wildebeest *Connochates spp.*, and the topi and related species *Damaliscus spp.*) of the family

Bovidae. The hirola is one of the smaller members of the Alcelaphinae. Based on its general morphology, it was variously assigned as a subspecies (*D. lunatus hunteri*) of the topi (Haltenorth & Diller, 1977; Walther, 1990), a congener (*Damaliscus hunteri*) of topi (Sclater, 1889; Ansell, 1972; Grubb, 1993), and as the only extant member of the genus *Beatragus* (Kingdon, 1997; Pitra et al., 1997; Estes, 1999). Current karyotypic (Kumamoto et al., 1996) and mitochondrial DNA (Pitra et al., 1997) analyses support the view that the hirola is distinct from both *Alcelaphus* and *Damaliscus*, and that it is best referred to as *Beatragus hunteri*. Its large pre-orbital gland and muzzle differ from those of *Alcelaphus* and *Damaliscus* (Kingdon, 1997). *Alcelaphus* and *Damaliscus* are the only bovids so far known that have lost the female urine testing habit referred to as flehmen (Estes, 1991); however, close observations on hirola indicate that they display flehmen behaviour, although this behaviour is less conspicuous than in other ungulate species (Andanje & Goeltenboth, 1995).

1.2.2 Physical description

Detailed descriptions of hirola have been provided by Sclater (Sclater, 1889), Dracopoli (Dracopoli, 1914), Dorst (Dorst & Dandelot, 1970) and Kingdon (Kingdon, 1997). Hirola resembles the hartebeest but its withers are relatively less elevated above the hindquarters. The horns lack a basal pedicle and have a distinctive inverted white chevron between the eyes. Hirola have white "spectacles" around the eyes, whitish undersides, predominantly white inner ears and tail, large pre-orbital glands, and lyrate, very sharp horns similar to those of the impala (*Aepyceros melampus*). The tail reaches down to the top of the hocks and the coat is uniform yellowish brown or rufous-tawny. Both sexes look alike, although males are larger, their horns are thicker and their coats are slightly darker, becoming slate-grey with age (Figure 1.1). Calves are paler, more sandy-brown than adults, with a less glossy coat; the calves are strikingly similar to those of hartebeest and topi.

Several authors have recorded hirola body measurements. Body weight: 80-118 kg, head and body length: 120-200 cm, tail length: 30-45 cm, shoulder height: 100-125 cm, horn length: 55-72 cm (Kingdon, 1982). Body weight: 73 kg, shoulder height: 99 cm,



(a)

(b)

Figure 1.1: Photographs of male hirola showing (a) the side view and (b) the face.

horn length: 61 cm (Dorst & Dandelot, 1970). Head and body length: 173 cm, tail length: 36 cm, ear length: 19 cm, horn length: 44 cm, horn spread: 32 cm (Butynski, 2000). I took additional measurements from fresh carcasses encountered in Tsavo and Garissa and from translocated hirola and the data are presented below (Table 1.1).

Table 1.1: Hirola body measurements (cm) of the 1996 translocation group (from Garissa) and from carcasses recovered in Tsavo East National Park. HL = head length; HnL = horn length; No.R = number of rings; SH = Shoulder height; BH = breast height; BL = body length; TBL = total body length; TL = tail length; HW = horn width; G = girth.

Sex/Age	Statistics	HL	HNL	No. R	SH	BH	BL	TBL	TL	HW	G
Male adults	Mean	36.5	55.4	13.8	75.3	72.0	128.3	178.7	37.8	31.4	124.0
	SD	3.9	3.8	1.9	28.4	24.3	67.8	17	2.6	5.6	15.2
	n	4	12	4	3	3	4	3	4	8	4
Female adults	Mean	31.9	42.4	14.1	56.5	57.6	117	166.7	37.0	24.4	124.7
	SD	3.7	7.7	1.3	33	30.0	42.4	26.6	4.3	8.6	25.1
	n	7	14	7	4	3	5	6	8	13	7
Male 7-12 months olds	Mean	28.8	28.1	1.25	-	-	94.7	149.8	33.5	11	90.3
	SD	1.9	4.0	1.5	-	-	17	20.4	6.4	3	6.6
	n	4	4	4	-	-	3	4	4	4	4
Female 7-12 months olds	Mean	27.5	27.9	2.5	52	90	88	143.5	31.4	12.3	94.7
	SD	5	18.0	0.6	38.1		23.1	26.2	2.4	2.5	9.2
	n	4	6	4	3	1	3	4	4	4	3

1.2.3 Distribution and range size

Hirola are probably more generalized ecologically than either *Damaliscus* or *Alcelaphus* and are believed to be the relic population of a formerly wide-spread group of species (Kingdon, 1982). Fossil evidence indicates that *Beatragus* was once in Eastern Africa (Ethiopia, Djibouti, Kenya, Tanzania) and probably ranged into South Africa (Kingdon, 1982). All records of the extant species indicate that their traditional range lies somewhere to the south of Garissa town in Kenya, 30-50 km inland, from and parallel to the Indian Ocean, east of the Tana River, to the north of Kismayu on the west of the Juba River in Somalia (Sclater, 1889; Ritchie, 1932; Dracopoli, 1914; Bunderson, 1976; Stewart & Stewart, 1963; Sidney, 1965; Kingdon, 1997; Grimwood, 1963; Grimwood, 1964; Donaldson, 1964), (Figure 1.2). Bunderson (Bunderson, 1977) estimated that hirola occupied 12,000 km^2 in Kenya and 2,000 - 3,000 km^2 in Somalia, giving a total range of 14,000-15,000 km^2.

1.2.4 Hirola population changes

The hirola (*Beatragus hunteri*) is categorized as "critically endangered" under criterion A1a of IUCN Red List Categories, 1996, having demonstrated a 90% percent population reduction between 1973 (13,729 individuals) and 1996 (1504 individuals). As such, hirola is recognized as the most severely threatened monotypic (Kumamoto et al., 1996) species of antelope in sub-Saharan Africa (after the scimitar-horned oryx - *Oryx dammah* - if any are left in the wild (Smith, 1998).

Estimates of hirola population size have varied greatly between different studies (Table 1.2). These differences are probably due to a number of factors, including the time of the survey (wet versus dry season), before and after calving, survey methods, the portion of the hirola population sampled and the distribution of the animals (Butynski, 2000). However, while taking account of this variation, the trend in the population since 1977 is clearly downward (Wargute & Aligula, 1993; Ottichilo et al., 1995; Magin, 1996b, Figure 1.3).

1.2.5 Habitat preference and food

The hirola are distributed north of the humid savannahs and forests of the coastal hinterland, areas that are essentially free from tsetse fly (Bunderson, 1985). To the north, their range is bounded by waterless semi-desert *Acacia* steppes with only sparse

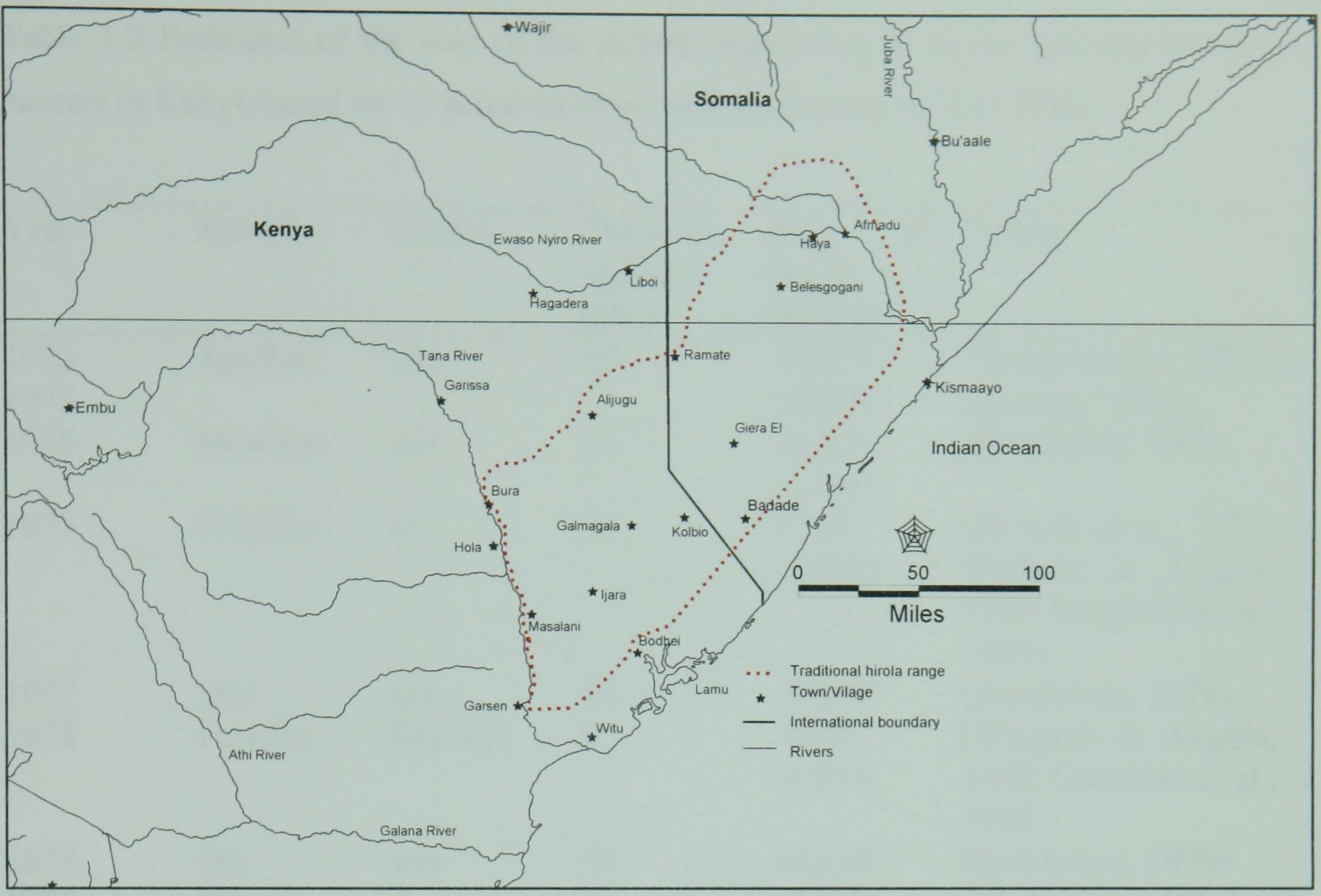


Figure 1.2: Map of parts of Kenya and Somalia showing the traditional distribution range of hirola. Data based on Bunderson (1981) and Pratt and Gwynne (1977).

grass cover (Kingdon, 1982). Lack of grass rather than aridity *per se* may set the northern limit of the range (Kingdon, 1982) while tsetse fly may set the southern limit (Bunderson, 1985).

Hirola are adapted to arid environments that receive an annual rainfall of 300 - 600 mm. They prefer open to lightly bushed grassland and wooded savannahs with scattered trees and shrubs of low stature (Bunderson, 1981). The highest densities have been recorded in *Digitaria milanjiana/Chloris mossambicensis/Dobera glabra* wooded-bushed grasslands, on well-drained white, sandy soils.

Hirola disperse throughout their natural range during the wet season. In the dry season, the distribution is more clumped due to the scarcity of pasture. Bunderson (Bunderson, 1985) described two main centres of dry season concentration, one near the Tana River and one in the Arawale Game Reserve, west of Hulugho, in the central northeast part of the range.

Table 1.2 Estimates of the size of the natural population of hirola antelope *Beatragus hunteri* in Kenya based on 15 aerial surveys conducted from 1973 to 1996.

Year	Months	Season	Transect spacing (km)	No. of hirola (95% C.I)	Source
1973	Apr/Jun	wet	10	13,729	(Watson et al., 1973)
1973	-	-	-	10,000	(Duncan, 1974)
1976	May/Jun	wet	10	14,180 (1,730)	(Bunderson, 1976)
1977	Feb/Mar	wet	10	2,278 (1,089)	(Dirschl et al., 1978; Wargute & Aligula, 1993; Grunblatt et al., 1995)
1977	Dec	dry	10	15,950	(Bunderson, 1979)
1978	Feb/Sep	Dry/wet	5	7,729 (1,840)	(Wargute & Aligula, 1993; Grunblatt et al., 1995)
1978	Jan	wet	10	14,835	(Bunderson, 1979)
1980	Jul	dry	5	13,000	(Williamson, 1987)
1981	Nov	dry	5	13,488 (2,461)	(Wargute & Aligula, 1993; Wargute, 1994)
1983	Apr/May	wet	5	10,843 (3,823)	(Wargute & Aligula, 1993; Grunblatt et al., 1995)
1985	Mar	dry	5	1,595	(Wargute & Aligula, 1993; Grunblatt et al., 1995)
1988	Feb-April	wet	5	1,585 (SE 571)	(Grunblatt et al., 1989; Wargute & Aligula, 1993)
1993	Mar	wet	5	1,725 (482)	(Wargute & Aligula, 1993)
1995	Jul	dry	1-2	302	(Ottichilo et al., 1995)
1996	May	wet	2-5	1,504 (654)	(DRSRS, 1977)

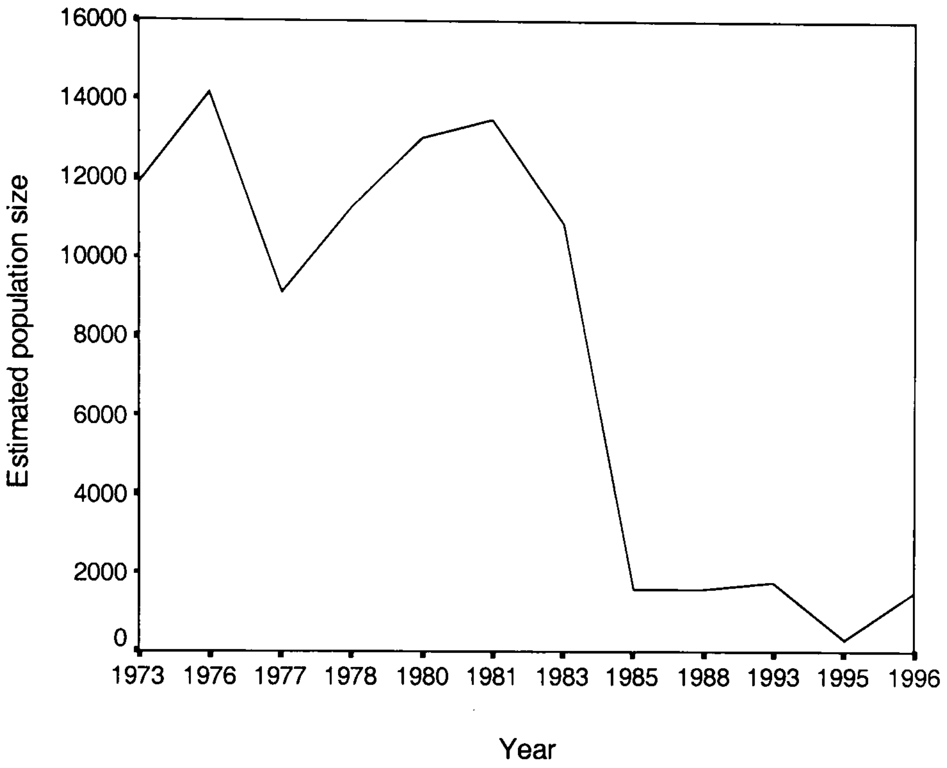


Figure 1.3: Changes in the size of the natural population of hirola in Kenya from 1973 to 1996 as determined by aerial surveys. Data from DRSRS and Butynski (Butynski, 2000).

Hirola are primarily grazers but Bunderson (Bunderson, 1985) states that browse may provide an important dietary supplement in the dry season. The animals also select short green grass when available, with a high ratio of leaves to stem (Andanje & Goeltenboth, 1995). In contrast, Kingdon (Kingdon, 1982) states that hirola are "strictly grazers" and considers forage quantity to be more important than quality. According to Kingdon (Kingdon, 1982) and Andanje (Andanje & Goeltenboth, 1995) hirola feed on the dominant grasses of the region, including coarse grasses, particularly *Chloris myriostachya, Cencrus ciliaris,* and *Digitaria* species.

1.2.6 Home range, territory and social organization

Mature males occupy and actively defend territories of several kilometres in extent when on good quality pasture (Bunderson, 1985). Males also associate in bachelor herds of 2 - 38 animals (Bunderson, 1985). Hirola are often found in the company of other animals such as topi (*Damaliscus lunatus*) (Kingdon, 1982), Grant's gazelle (*Gazella granti*), Zebra (*Equus burchellii*), and oryx (*Oryx beisa callotis*) (Andanje, 1997). They avoid close association with kongoni (*Alcelaphus buselaphus*), which occurs in the same range and utilises similar resources, perhaps indicating competition. Family groups have home ranges, which may encompass the ranges of several adult males (Andanje, 1997). However, information is lacking on male territoriality, how they are selected and how they relate to the ranges of groups of females with their young. One possibility is that males may abandon active territory defence at low population densities and follow groups of females throughout their range, as is the case in kongoni and other antelopes (Gosling, 1986).

Groups of females with young range from 5 - 40 with a mean group size of 7 - 9 (Bunderson, 1985; Andanje & Goeltenboth, 1995) and are most often in the company of a mature male. Such herds are relatively sedentary, though they will move away from an area as resources diminish (Kingdon, 1982). Mixed aggregations of breeding and bachelor herds numbering up to 300 have occurred in the past, particularly at the end of dry season when isolated showers produced patches of green vegetation (Bunderson, 1985). Sub-adults leave nursery herds and occupy peripheral areas where they form small mixed or single sex herds of up to three individuals (Andanje, 1997). Female sub-adults often join an adult male. However further information is needed on the age at which sub-adults leave the nursery herds, and on how they eventually join, or perhaps, establish new herds.

1.2.7 Reproduction

Hirola are seasonal breeders, most calves being born at the beginning of the short wet season in late September, October and November (Kingdon, 1982), after a gestation period of about 7.5 months (Smielowski, 1987). A similar calving period has been observed in Tsavo (Andanje, 1997). However, details of the seasonal frequency of reproduction, levels of recruitment and survival have not been established. The causes of juvenile mortality and its variation have yet to be established.

1.2.8 Predation

According to Kingdon (Kingdon, 1982) hirola are preyed on by lions (*Panthera leo*), and probably cheetah (*Acinonyx jubatus*) and hyaena (*Crocuta crocuta*). These species are also major predators of the related hartebeest, with lions preying mainly on adults and cheetah and hyena being major predators of the calves (Gosling, 1974). This study attempted to assess the mortality of hirola of differing ages due to these predators with a view to assessing their importance and of determining any seasonal effects. The hirola range contains migratory species, such as zebra, and their presence as alternative prey may influence the predation pressure on hirola. Other smaller predators such as black-backed Jackal (*Canis mesomelas*), caracal (*Felis caracal*) and serval cat *(Felis serval*) could take young hirola while lion, cheetah and hyeana could take both young and adults.

1.2.9 Conservation efforts

There is no doubt that the numbers of hirola have declined both in number and range. They are also known to occur in only two sites worldwide. In order to revitalize measures to conserve the species, the Kenya Wildlife Service through the IUCN Antelope Specialist Group, commissioned a study of the available information on the species with the aim of using it to make a rapid species recovery plan. The manuscript was completed in 1996 (Magin, 1996b). The overall key recommendations were i) to improve protection and management in the natural range and ii) to establish effective conservation of translocated populations in Kenya.

The recovery plan led to the revitalization of the National Task Force, which had been in existence for some time. The new body was called the Hirola Task Force (HTF) and was composed of government organizations, NGO's and private individuals who shared the common goal of conserving hirola in Kenya.

The first significant step to be taken by the HTF was to implement one of Magin's recommendations, namely a further translocation from the natural range to boost a previously translocated group in Tsavo East National Park. The survivors of the 1963 translocation had bred up to about 70 animals, despite a more general decline in grazing herbivores in the local ecosystem. This further translocation was intended to enable a closer scientific study of the species, and to boost the genetic composition of the Tsavo population in order to help ensure the persistence of the only ex-situ population of hirola. The present study also forms part of Magin's (Magin, 1996b) recommendations. It was realized that little was known about hirola ecology compared to other large East African ungulates, and future conservation actions could not be carried out effectively without basic biological information on the species.

1.3 Aims and objectives of the study

1.3.1 The objectives of this study were to:

1. Identify population limiting factors so that they can be manipulated in practical conservation programs.
2. Compare hirola ecology in Tsavo (the only *ex-situ* population) and Garissa (the only natural population) to provide an informed basis for planning a conservation strategy for hirola.
3. Evaluate the importance of the *in-situ* protected areas e.g., Arawale and TPNR to help determine whether they should be re-instated or not.

3.1 This study aimed to determine:

1. Group and population composition and dynamics (births, deaths, movements).
2. Diurnal behaviour patterns (including foraging and competition for shade).
3. Range quality, structure and composition (types of forage and shade plants).
4. Patterns of predation (predators, spatial variation).
5. Ungulate community structure (association and competition).
6. Food plant selection and quality (nutrients and diet overlap).
7. The operation of limiting factors in Garissa through comparable field information and through information provided by hirola community scouts.

Chapter II:

The Study Areas

2.1 The Study Areas

Data were collected at two sites within Kenya, both of which are described here. Most study time was spent on the free-ranging introduced population of hirola in Tsavo East National Park (Figure 2.1). Tsavo East is part of Tsavo National Park, the largest protected area in Kenya which lies within 40, 000 km^2 of the Tsavo ecosystem. Periodic comparative study was carried out in Garissa, the natural range for hirola, a pastoral rangeland of over 20,000 km^2 between the Tana River and the Kenya-Somalia border, an area prone to banditry and political unrest (Figure 2.1).

2.2 General overview of the study sites

2.2.1 Degree of protection

Only a small section of Tsavo East National Park, around Voi Town and the Taita Hills, has been fenced to protect the farming Taita Community against crop raiding by elephants, especially in the dry season. The rest of the park is unfenced but is protected by the Kenya Wildlife Service rangers through regular ground and aerial patrols. Due to good security, infrasture and the availability of big game, the park is one of the most popular tourist destinations in the region. On the other hand, the Garissa hirola range lies within a vast unprotected and unfenced Somali pastoral community grazing land with sparse infrastructure and frequent insecurity threats from bandits. The only available security personnel are for government civil administration purposes and wildlife receives little effective protection.

2.2.2 Terrain and flora

Except for the low Yatta Plateau and a few isolated granitic hills, most of Tsavo East National Park consists of flat, relatively uniform plains ranging between an elevation of 600m to the West and 150m to the East. The vegetation is predominantly "bush" or "thicket" which varies from "dense" to "light" in cover and sometimes contains scattered trees. The open areas support a diverse herb layer (Greenway, 1969). Similarly, the Garissa hirola range is flat or gently undulating and lies between an elevation of 40 m

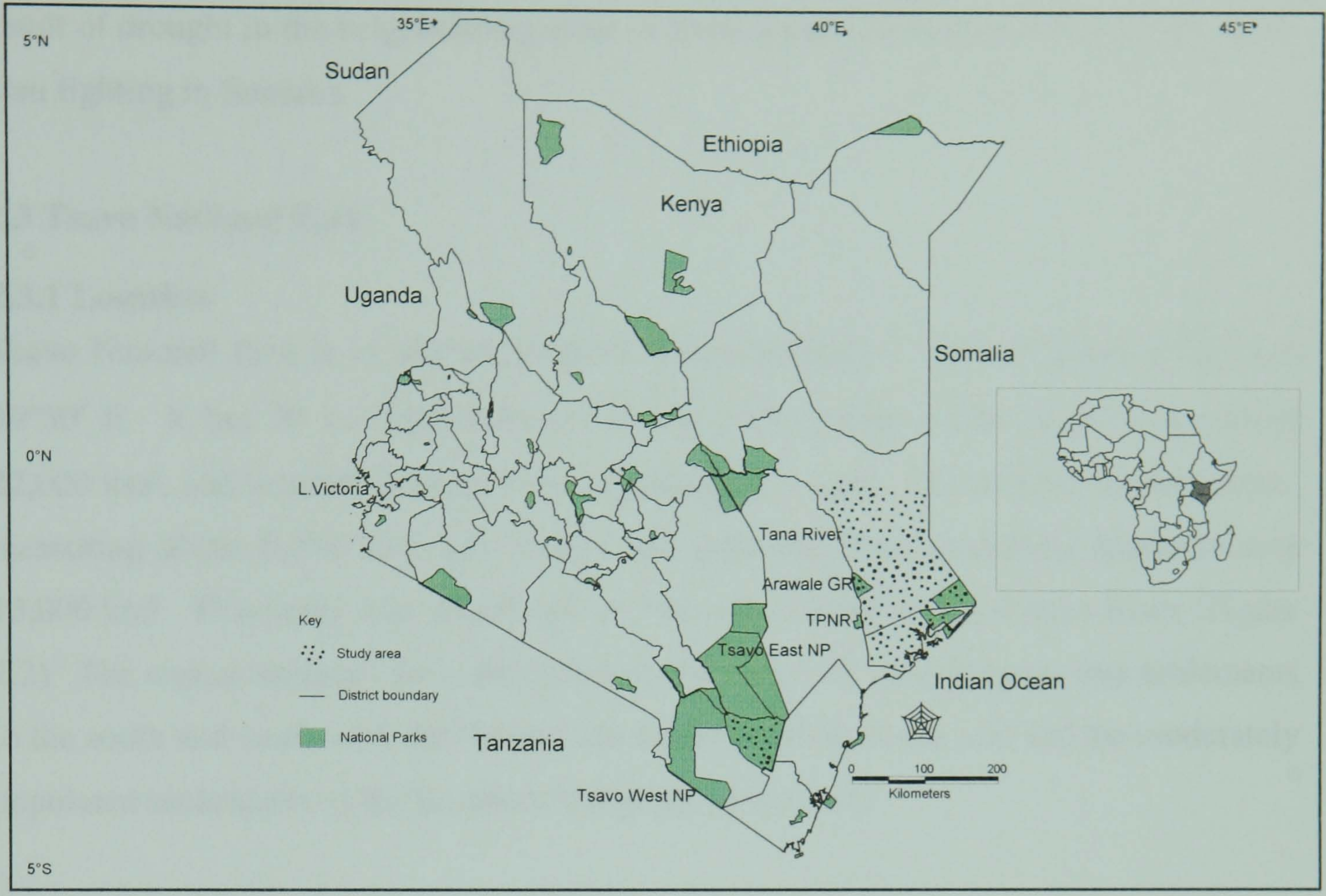


Figure 2.1: Map of Kenya showing the two study sites, National Parks, and district boundaries. Inset: Map of Africa showing the position of Kenya.

(towards the Tana River) and 220m (towards the Kenya/Somali border). The predominant vegetation types within the natural range of hirola vary from forest/wooded grasslands in the south to open bushed grassland in the central area and dry thorn bush in the north (Bunderson, 1979).

2.2.3 Wildlife and livestock

Tsavo East National Park is dominated by elephants whereas the Garissa hirola range is dominated by the livestock of the Somali pastoralist (See Chapter **VI**). Although a majority the hirola in Tsavo occur inside the park, their range is encroached by cattle from the neighbouring ranches during the dry season. On the other hand, due to lack of protection and proximity to the Kenya/Somalia border, the Garissa hirola range has lost most of its wildlife, especially elephants and rhinos, through poaching. Due to a large increase in the human population, there has been a general increase in the number of livestock. Occasionally large herds of livestock also move into the hirola range as a result of drought in the neighbouring areas or from Somali herdsmen in flight from inter-clan fighting in Somalia.

2.3 Tsavo National Park

2.3.1 Location

Tsavo National Park is located in southern Kenya between 2° and 4° S and 37°30′ and 39°30′ E. It lies 70 to 250 km from the coast. The National Park area covers about 22,000 km^2, and is subdivided into two administrative units: Tsavo West National Park, measuring about 9,000 km^2 and Tsavo East National Park measuring approximately 13,000 km^2. This study was undertaken in Tsavo East south of the Galana River (Figure 2.2). The region borders Tsavo West Park to the west, the Taita Ranches and settlements to the south and southwest, the Galana and Kulalu ranches to the east and the moderately populated settlements of the Kamba tribal group to the north.

2.3.2 Relief, climate and drainage

The Tsavo area is situated only a few degrees south of the equator. The distribution of rainfall is roughly related to the movements of the tropical convergence zone, which produces two alternating dry and rainy seasons around the time of the equinoxes (Brown & Cocheme, 1969). These are a long dry season from June to October, the short rains in November/December, a short dry season from January to March and the long rains in April/May (Figure 2.3 and 2.4). However, this pattern is quite variable and often modified by out-of-season rains or dry spells. Temperatures are fairly constant over the year with mean monthly maxima of 30^0 C and minima of 20^0 C (Wijngaarden, 1985). Rainfall in Tsavo East N.P. is generally erratic in spatial and temporal distribution and averages 300-600 mm p.a.; there is a high probability of severe drought every 10 years. Tsavo East N.P. is mostly flat (300-500 m a.s.l.) except for the low Yatta Plateau and a few isolated granitic hills which attact occasional rainstorms.

Edaphic conditions are uniform, water is geographically restricted in the dry season, and the vegetation is severely degraded in many areas, particularly along rivers where animals tend to concentrate during the dry season. Most of the area consists of flat, relatively uniform plains, developed on various kinds of parental material. It contains the

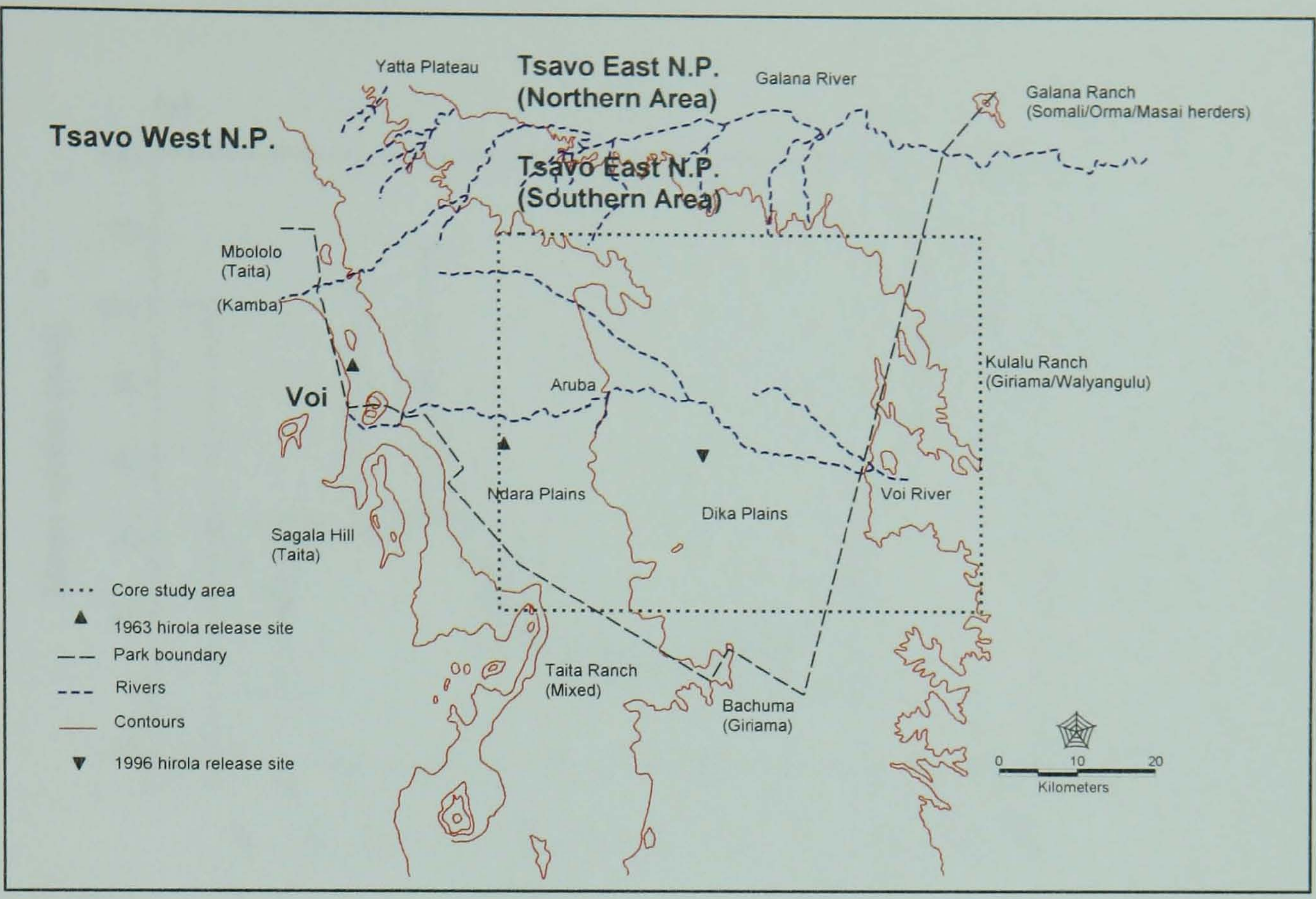


Figure 2.2: Map of Tsavo East National Park south of the Galana River showing the location of the study area (located to the southwest of the hirola's natural range).

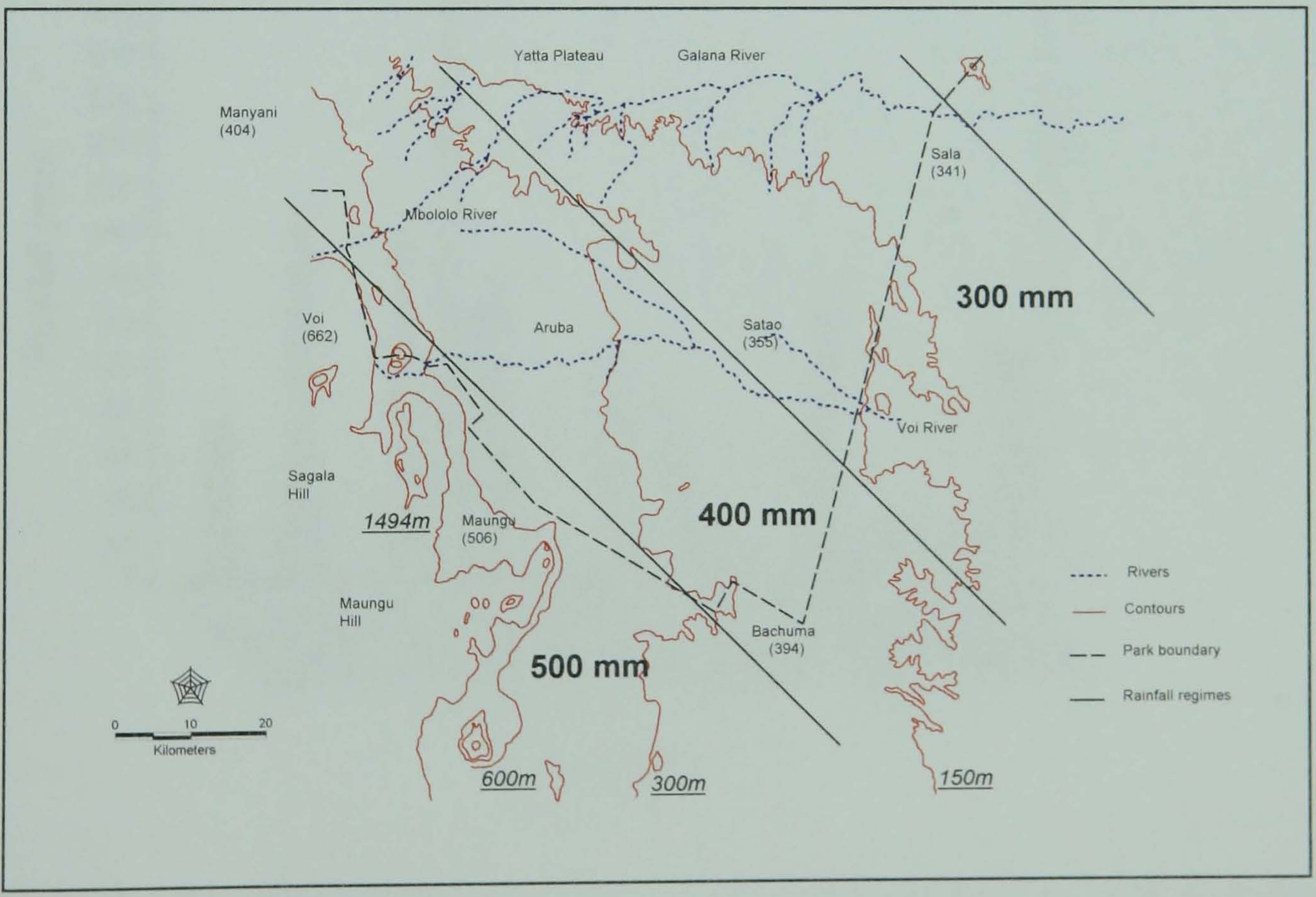


Figure 2.3: Map of the Tsavo East National Park study area showing mean annual rainfall isohyets (mm) and altitudinal contours (italics and underlined).

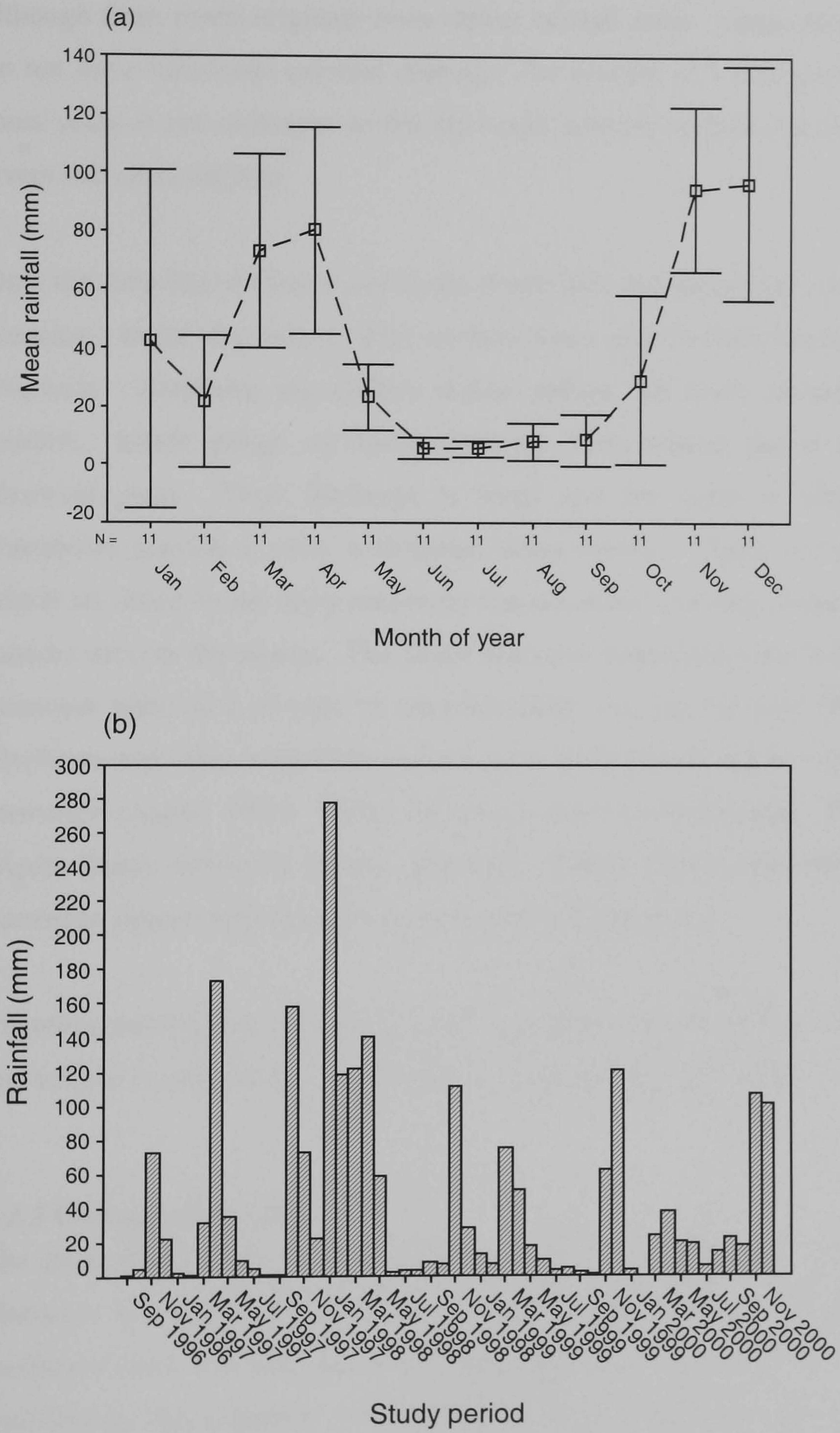


Figure 2.4: Monthly rainfall trends in Tsavo East National Park south of the Galana river (a) between1990 and 2000, and (b) during the study period (1996 to 2000). Values in (a) are monthly means±2SE.

drainage basins of the Tana (Tiva), the Athi-Tsavo-Galana, Voi and Umba Rivers, although these rivers originate from higher rainfall areas. Large parts of the Tsavo area do not have functional external drainage: the amount of water generated by run-off in most years is not sufficient to fill the broad alluvial valleys and thus reach the major rivers that cross the area.

Only the Athi-Tsavo-Galana and Umba rivers flow the entire year. The Tiva and Voi are seasonal. In the dry season, they contain water only beneath the surface of the sandy riverbeds. Elephants dig shallow holes making the water accessible to most other wildlife. Small springs are found along the Yatta plateau and in some places on the dissected plain. Their discharge is small and the water is often saline. Natural waterholes provide a more widespread water source. These are shallow depressions which are filled in the rainy season by run-off water and may contain water for several months into the dry season. The larger and more important water holes are found on the erosional plain at a density of approximately one per 10 km^2 (Wijngaarden, 1985). Elephants and other wallowing animals have probably played an important role in their formation (Ayeni, 1975). Other sources of water are man-made. These includes dams (Aruba Dam), boreholes (Ndara, Mukwaju, Aruba), piped water (Mzima pipeline), and numerous dugout waterholes along the game viewing roads.

In general environmental conditions in Tsavo East N.P. can thus be characterised as harsh and subject to extreme fluctuations both within and between years.

2.3.3 Geology and soils

The geomorphology of the Tsavo ecosystem is dominated by the occurrence of extensive planation levels of both erosional and sedimentary origin (Wijngaarden, 1985). A number of erosional surfaces can be identified, but only the latest, the Nyika level of the end-Tertiary age, is present over large areas. Remnants of the older surfaces are found at the base of Chyulu Hills and Yatta Plateau (Wijngaarden, 1985). The Chyulu Hills are relatively recent volcanic hills composed of basalts and in places covered by coarse pyroclastic deposits. The Yatta Plateau consists of a protective cap of Miocene phonolites, only approximately 10m thick, and overlying gneisses of the basement system rocks. The erosional plains are developed on a variety of rock types, such as the basement system rocks and the Duruma sandstones.

Eastwards of approximately the 300m contour line, accumulation processes have formed the landscape. These sedimentary plains are developed on Plio-Pleistocene "bay deposits" of an unconsolidated clay and saline nature. Towards the major rivers, the landscape has been dissected relatively recently, as shown by the gently sloping dissected topography towards the rivers and the V-shaped valleys. Within this extremely flat plain, a number of inselbergs occur, some more than 100m high. They consist of a quartzitic type of basement system rock, making them more resistant to weathering and erosion. Where the basement system rock consists of crystalline limestone, they often form low elongated ridges. The soils of Tsavo show a wide range in depth, colour, drainage, condition, structure, chemical and physical properties. However, extreme differences in texture are uncommon and most soils have a sandy-clay texture in the subsoil (Wijngaarden, 1985).

2.3.4 Vegetation types

2.3.4.1 Forest

This habitat consists of riverine or swamp forest types and occurs along the Galana and Voi rivers in Tsavo East N.P. It consists of stands of trees, which attain a height of 18 m, with crowns touching or intermingling and sometimes freely inter-laced with lianes. The trees have simple or buttressed boles and some of them are evergreen. The forest floor is covered with herbs and shrubs where light penetrates. Common trees found in this habitat include *Dobera glabra, Newtonia hildebrandtii, Acacia elatior*, and *Kigelia africana.* Common shrubs include *Azima tetracantha, Capparis sepiaria, Pluchea dioscordis, Salvadora persica, Combretum ukambensis, Cordia goetzei, Gardenia jovis-tonantis, Lawsonia inermis, Vernonia hildebrandtii* and *Meyna tetraphylla* (Appendix 1) Occasionally, pure stands of *Hyphaena coriacea* measuring about 15m high occur, especially along and on the tributaries of the Galana River.

2.3.4.2 Woodland

This habitat consists of three vegetation layers: the mostly deciduous tree layer measuring about 9 m high with a canopy of about 18 m, the open ground layer of bushes and grasses and a herb layer of annual and perennial species. The perennial species are tufted and rarely grow above 90 cm high. The common tree species found in this habitat include *Cassia abbreviata, Delonix elata, Platyceliphium voense, Melia volkensii, Acacia tortilis, Acacia reficiens, Acacia thomas*ii and *Adansonia digitata* as an occasional emergent. The bush species include *Grewia vilosa, Erythrochlamys spectabilis* and *Euphorbia spp.* The ephemeral grass species include *Aristida spp., Brachiaria eruciformis, Bracharia leersoides* and widely spaced perennials such as *Cenchrus ciliaris, Chloris roxburghiana Eragrostis caespitosa* and *Schmidtia bulbosa.*

2.3.4.3 Wooded grassland

This habitat consists of perennial grasses and other herbs with either evergreen or deciduous, grouped or scattered, armed or unarmed, trees and shrubs that cover less than 50% of the ground. The grasses may be densely procumbent or matted, or may grow in patches, tufts or clumps attaining a height of up to 120 cm. The wooded grassland habitat has been subdivided into three types. The grouped-trees/grassland habitat consists of stands of *Acacia spp., Melia volkensii, Delonix elata, Commiphora spp. Dobera glabra* and *Platycelithium voense*, among grass species such as *Chloris roxburghiana Cenchrus ciliaris, Sporobolus helvolus, Cynodon dactylon, Digitaria spp.* and *Schimidtia bulbosa.* The scattered-trees/grassland habitat consists of trees such as *Melia volkensii, Platycelithium voense, Commiphora spp.* with very occasional *Euphorbia robechii* or *Adansonia digitata.* The grass species are similar to those found in the grouped-trees/grassland habitat. The shrub or dwarf-trees grassland is wide spread. The shrub component of this habitat include *Boscia coriacea* (which is found throughout Tsavo East N.P.), *Dobera glabra, Balanites orbicularies, cadaba heterotricha, Terminalia parvula, Terminalia spinosa, Platycelithium voense* and *Commiphora spp.*

2.3.4.4 Grassland

This habitat consists mainly of grasses and other herbs that are generally perennial, sometimes with evergreen or deciduous trees or shrubs, either very scattered or in small isolated groups, in either case not covering more than 10% of the ground. The grasses may be mat-like, forming a dense or thin carpet, in clumps or tussocks, close or widely spaced or they may be perennial forming a continuous ground cover; the sward height ranges from a few centimetres up to about 120 cm. The main grass species include *Brachiaria deflexa, B. leersoides, Cenchrus ciliaris, Digitaria macroblephara, D. rivae,* *Latipes senegalensis, Panicum maximum, Aristida adscensionis, Chloris roxburghiana, Tetrapogon tenellus* and *Sporobolus helvolus.* The common shrubs in this habitat include *Acacia bussei, Cadaba heterotricha, Combretum aculeatum, Commiphora spp., Terminalia orbicularis, Boscia coriacea, Acacia tortilis, Caesalpinia trothae, Caucanthus albidus, Cassia longiracemosa, Ehretia teitensis* and *Thylachium thomasii.* There is hardly any pure grassland in Tsavo East N.P., that is, habitat without any trees or shrubs.

2.3.4.5 Swamp vegetation

Swamps occur, where free water accumulates on the surface for some periods of the year. Sites with this kind of vegetation in Tsavo East N.P. include Kanderi and Aruba dam areas, where water is permanent and at the scattered water holes and wallows where water is seasonal. On sites with permanent water, the trees and shrubs species include *Newtonia hildebrandtii, Thylachium thomasii, Salvadora persica*, and scattered bush clumps of *Echbolium revolutum, Maerua denhardtiorum, M. subcordatum.* The dominant grasses include *Cynodon dactylon, Cenchrus ciliaris* and *Bothrocloa redicans.* The scattered water holes and wallows may have clumps of shrubs of *Lawsonia inermis, Ziziphus mucronata* or *Gardenia jovis-tonantis*, and occassionally *Tamarindus indica* and *Kigelia africana.* If the water rapidly evaporates or is quickly dispersed by drinking or wallowing animals, the bare ground is first invaded by annuals such as *Glinus setiflorus*, and later *Echinochloa haploclada* or *Sporobolus helvolus*, with occasional *Cyperus distans.*

2.3.4.6 Bushland

This habitat consists of more than 50% cover of shrubs or small trees growing densely together. Tall trees such as *Adansonia digitata, Delonix elata, Melia volkensii*, may be present, occasionally in clumps, more often as widely scattered individuals. Herbs, ephemeral or succulent, or both, and grasses not above 100 cm tall, mostly annual or short-lived perennial, form the ground cover under deciduous bushland. Several different bushland communities occur in the park and variation in species composition is related to soil type and drainage (Greenway, 1969; Wijngaarden, 1985). Generally, on bright orange-red loam soils adjacent to granitic intrusion, the shrub and small tree species include *Dirichletia glaucescens, Euphorbia engleri, Hymenodction parvifolium, Commiphora riparia, Strychnos decussata, Lannea elata, Adenia globosa, Premna* *resinosa, Boswellia hildebrandtii, Bauhinia taitensis, Sesamothamnus rivae, Calyprotheca somalensis* and *Grewia fallax.* The second community occurs on brown sandy clay loam soils and consist of shrubs and small trees of is composed of *Combretum aculeatum, Dobera glabra, Cadaba heterotricha, Caesalpinia trothae, Acacai tortilis, Sericocomopsis hildebrandtii* and *Ehretia teitensi* among others. The third community, a rather open bushland habitat occurrs on buff-brown sandy loam and includes consists of *Acacia bussei, Acacia mellifera, Boscia coriacea, Combretum aculeatum, Commiphora africana, Cordia monoica* and *Grewia tembensis.* Other common bushland communities include *Bauhinia teitensis* thicket, *Ochna inermis* thicket, *Givotia gosai* thicket and *Anisotes parvifolius* thicket.

2.3.5 Wild and domestic animals of the study area

The common wildlife species in the region are elephants (*Loxodonta Africana*), African buffalo (*Syncerus caffer*), Burchell's zebra (*Equus burchellii*), Coke's hartebeest (*Alcelaphus buselaphus*), waterbuck (*Kobus ellipsiprimnus*), Grant's gazelle (*Gazella grantii*), Impala (*Aepyceros melampus*), hippopotamus (*Hippopotamus amphibius*), Giraffe (*Giraffa camelopardalis*), lesser kudu (*Tragelaphus imberbis*), gerenuk (*Litocranius walleri*), warthog (*Phacochoerus aethiopicus*), fringe-eared oryx (*Oryx beisa callotis*)and eland (*Taurotragus oryx*) (Appendix 2). Common domestic animals kept on the surrounding ranches include, indiginous cattle (*Bos indicus*), sheep (*Ovis aries*), goats (*Capra hirtus),* and donkeys (*Equus asinus*). Large carnivore species found in the area include lions (*Panthera leo*), spotted hyena (*Crocuta crocuta*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), and black-backed jackal (*Canis mesomelas*).

2.3.6 People and land use

Much of Tsavo is unsuited to crop farming. Livestock ranching is the most economically viable project on the surrounding land. The ranches are either owned by the Agricultural Development Corporation (ADC) or by individuals (private or group ranches). The pastoral Orma to the east, the Kamba in the north and the Masai to the west and south occasionally use them as dry season feeding grounds. Only the climatically more favorable Taita Hills are occupied and settled by the agriculturalist Taitas. Semi-permanent agriculture and pastoralism does occur in the north between the Kamba and the remnant Waliangulu and Giriama tribesmen along the Galana and Voi Rivers (Figure 2.2).

2.4 Garissa District.

2.4.1 Location

The study area lay in Kenya between 0°50'^{S} and 2°45'^{S} and 39°50'E and 41°40'E. This area encompassed approximately 20,000 km² mainly in the Lamu and Garissa districts, but including a narrow strip of the Tana River District next to the river (Figure 2.5).

The Indian Ocean and the Tana River were the boundaries of the study area to the south and west. To the north, conditions become rapidly more arid and less favorable to hirola. The eastern side is marked by the internal boundary between Kenya and Somalia. This area contains all of the current known natural range of the surviving hirola population (Chapter I, section **1.2.3**).

2.4.2 Relief and Drainage

The area is flat or very gently undulating. Because of the flat terrain, there is little run-off and many areas are susceptible to flooding during the wet season. The entire region lies between 0-110m a.s.l. with a SE to SW increasing gradient of 135 cm/km (Bunderson, 1981). This gradient is particularly noticeable on the flood plains of the Tana River, whose waters originate from the highlands several miles to the north of the study area. Although the Tana River is the longest and largest river in Kenya, it is not part of the internal drainage system in this area. Existing drainage is confined to small and highly seasonal water courses ('luggas'), which flow in a southeasterly direction towards the Indian Ocean (Figure 2.5).

2.4.3 Geology and soils

Soils of the region are formed from the tertiary and quaternary sediments (Kenya, 1970). Because of flooding and the prevalence of black cotton soils, the area is often inaccessible by vehicle during the rainy season.

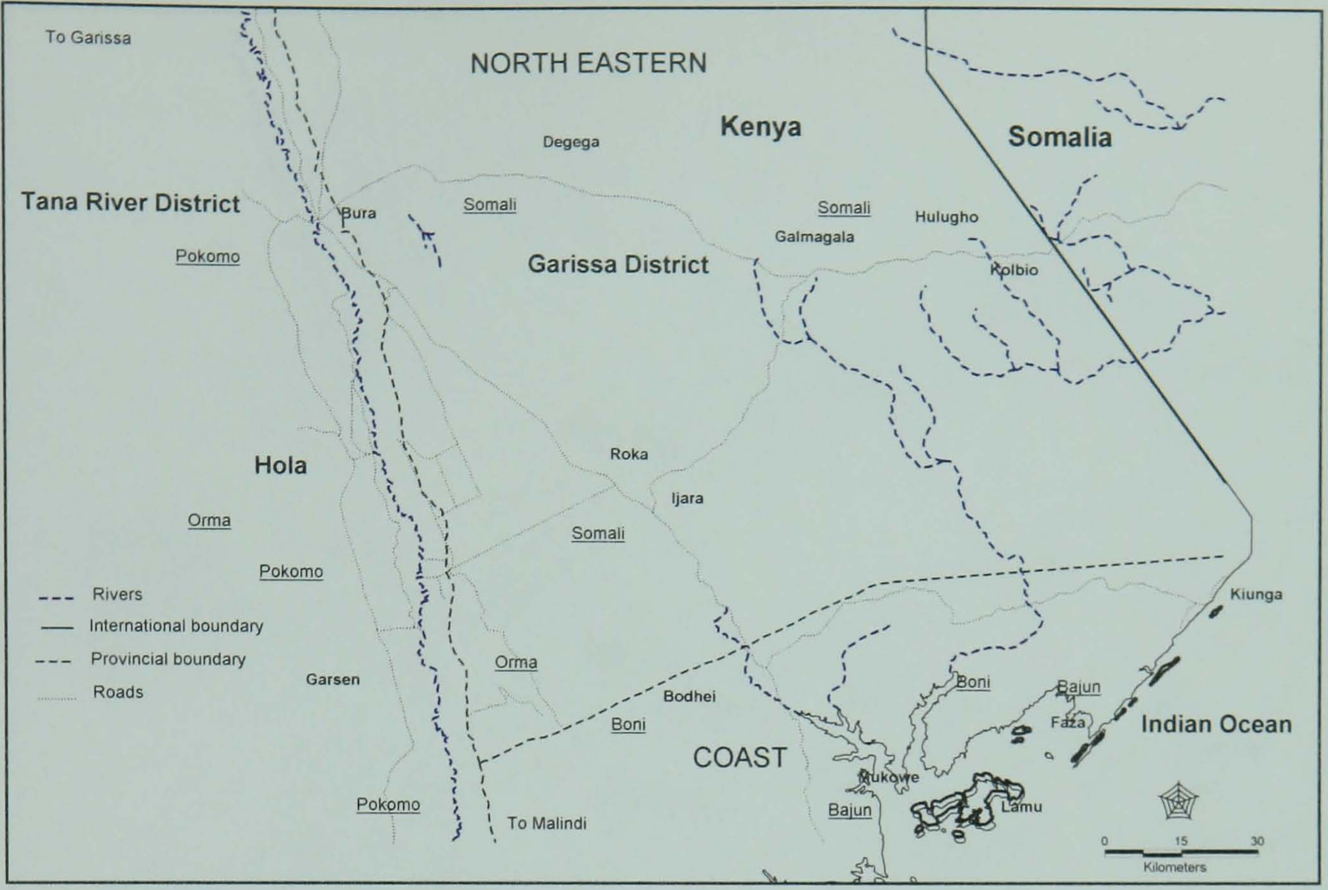


Figure 2.5: Map of the Garissa study area showing towns, villages and tribal groups.

2.4.4 Climate

The study area lies within 1-3 degrees of the equator and is close to sea level. Temperature and evaporation rates are thus high throughout the year and change little from north to south. In contrast, rainfall and relative humidity fall considerably, and progressively, when moving inland from the coast.

Rainfall is the most important attribute of climate in East Africa because of its effect on primary production. In the Garissa study area, rainfall varied considerably from north to south ranging from 397mm per year at Bura to 1072 mm at Lamu in the south (Figure 2.6). The mean annual pattern of rainfall is characterized by a bimodal distribution, with the exception of a narrow strip along the coast where a single season prevails.

The long rains fall in April to July and the short rains in November and December (Figure 2.7). Distinct dry seasons occur between the wet seasons, the most severe being from January to March. Although the onset of the wet and dry seasons is more or less

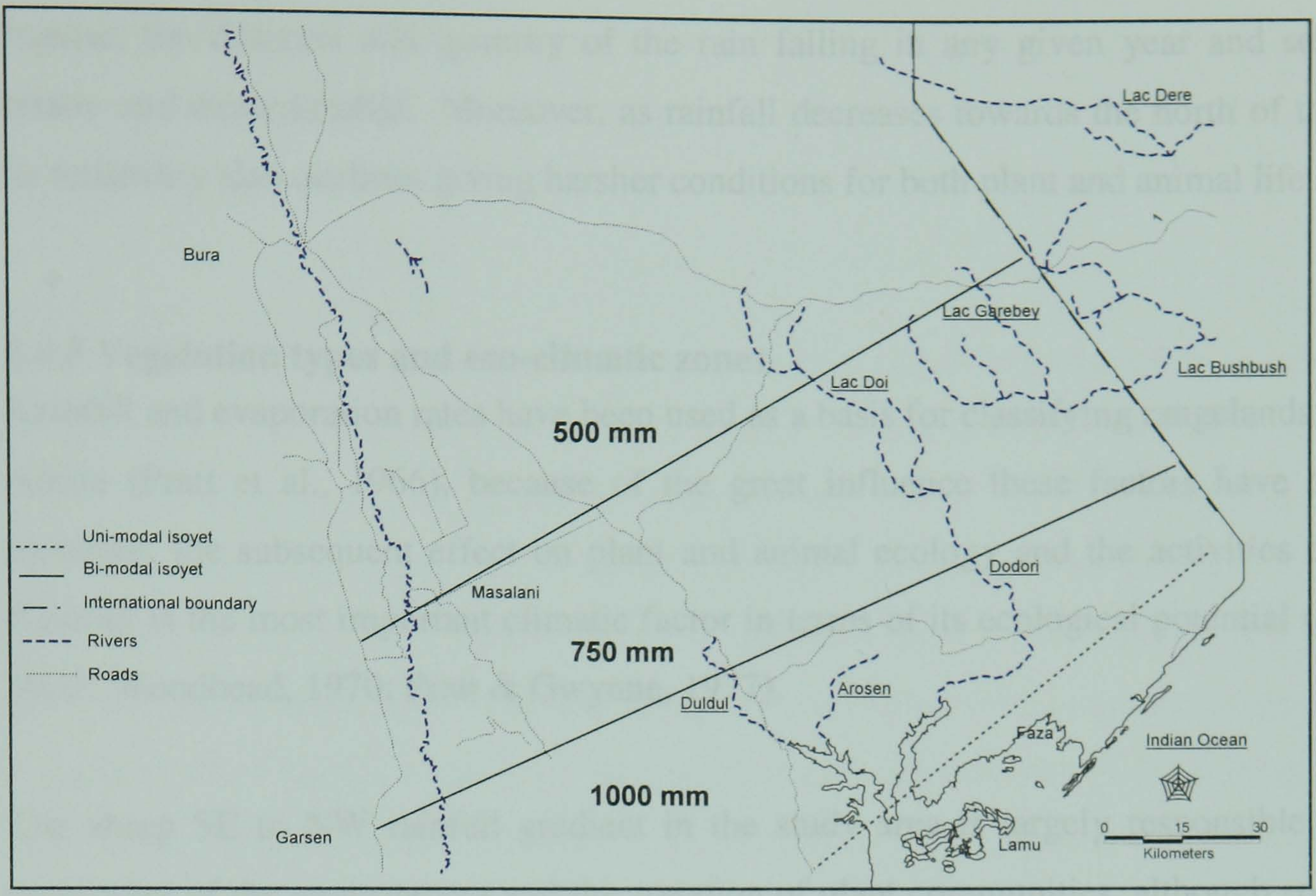


Figure 2.6: Map of the Garissa study area showing mean annual rainfall (mm) in different localities and major drainage lines (underlined)

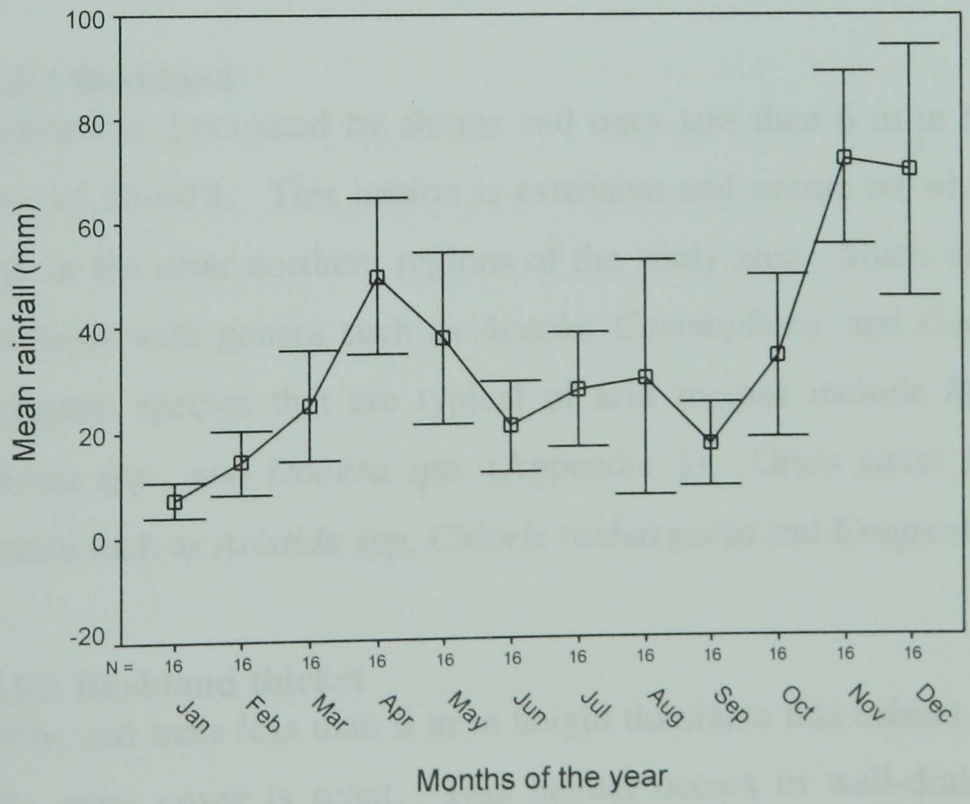


Figure 2.7: Average patterns of rainfall through the year in the Garissa hirola range between 1970 and 1985, Data from Bunderson (Bunderson, 1985). Values are means ±2SE.

regular, the duration and quantity of the rain falling in any given year and season is erratic and unpredictable. Moreover, as rainfall decreases towards the north of the area, its reliability also declines giving harsher conditions for both plant and animal life.

2.4.5 Vegetation types and eco-climatic zones

Rainfall and evaporation rates have been used as a basis for classifying rangelands in East Africa (Pratt et al., 1966), because of the great influence these factors have on soil, moisture, the subsequent effect on plant and animal ecology and the activities of man. Rainfall is the most important climatic factor in terms of its ecological potential (Brown, 1963; Woodhead, 1970; Pratt & Gwynne, 1977).

The sharp SE to NW rainfall gradient in the study area is largely responsible for the variability of the environment and the zonation of plant communities, although soil types and ground water also contribute to this variation. The rainfall gradient leads to a general trend of forest and lush grasslands in the south to semi-arid bushlands and bush grasslands in the north. According to Bunderson, (Bunderson, 1981), the main vegetation types are the following:

2.4.5.1 Bushland

Bushland is dominated by shrubs and trees less than 6 m in height and with a canopy cover of 25-60%. This habitat is extensive and occurs on white sandy clays and black clays in the drier northern regions of the study area. Much of the woody vegetation is deciduous with genera such as *Acacia, Commiphora*, and *Combretum*, being common. Evergreen species that are typical of arid regions include *Boscia spp., Cadaba spp., Maerua spp.*, and *Dobera spp.* (Appendix 1). Grass cover is poor and composed of annuals such as *Aristida spp, Chloris roxburgiana* and *Eragrostis spp.*

2.4.5.2 Bushland thicket

Shrubs and trees less than 6 m in height dominate this habitat with a canopy cover over 60%; grass cover is scant. This habitat occurs in well-drained reddish sands and is dominated by *Euclea divinorum* and *Haplocoelum foliolosum*. Other shrubs and small trees present include *Sideroxylon diospyroides*, *Croton pseudopulchellus*, *Hunteri zeylanica*, *Grewia plagiophylla* and *Lannea spp.* Although most trees and shrubs are below 6 m, emergents such as *Tamarindus indica* and *Afzelia cuanzensis* are present at heights of about 10 m. This habitat type occurs along the Boni forest and along parts of the coast.

2.4.5.3 Bushed grassland

This habitat consists of grassland with scattered trees and shrubs under 6 m in height and with a canopy cover of less than 25%. The most extensive bushed grassland occurs on seasonally waterlogged black cotton soils. Grass cover is of intermediate height, generally continuous, but with patches of bare ground. The dominant grass is *Schoenefedia transiens.* Other common grasses include *Chrysopogon plumulosus, Chloris roxburgiana, Dactyloctenium aegyptium, Tetrapogon bidentatus*, and *Sporobolus helvolus*, which often form pure stands in small depressions of impeded drainage. Deciduous shrubs dominate the woody vegetation, and these include *Grewia tennex* and C*ombretum volkensii* as principal species. The major trees are the stunted form of *Dobera glabra* and *Acacia zanzibarica.*

2.4.5.4 Wooded grassland

This habitat consists of grasslands with scattered or groups of large trees having a canopy of less than 25%. Woody vegetation averages 10-15 m in height and is primarily evergreen, although some deciduous trees and shrubs are present. Grass cover is fairly dense and uniform and increases with increasing rainfall. This habitat occurs on poorly drained black cotton and sandy clays and the largest expanse forms a mosaic with the Boni forest. *Panicum infestum, Panicum maximum, Hyperrhenia rufa, Heteropogon contortus, Andropogon dummeri* and *Digitaria mombasana* dominate the herb layer, with *Diospyros cornii, Lannea stuhlmannii, Dobera glabra*, and *Terminalia spinosa* being the principal trees. *Echinochloa haploclada* often forms pure stands of grass over 2 m in height on inundated clays along seasonal drainage lines and in swamps.

2.4.5.5 Wooded-bushed grassland

This habitat has a prominent grass layer with scattered or groups of trees and shrubs of low stature, and a woody canopy cover of less than 20%. This vegetation type is transitional in physiognomy and composition between arid bushed grassland in the north and the wetter, wooded grasslands of the south. The zone consists of almost exclusively well-drained white sandy clays, mainly occurring in a narrow strip along the northern fringe of the forest belts from Tana River to Somali border. The grass layer in the habitat includes *Digitaria milanjiana, Chloris mossambicensis, Sporobolus pyramidalis, Chloris roxburgiana* and *Eustachyus paspaloides.* The major tree species are *Dobera glabra, Acacia bussei, Salvadora persica.* Common shrubs include *Grewia tenax* and *combretum volkensii.*

2.4.5.6 Forest

The forest habitat is characterized by a closed canopy and an abundance of trees over 10 m high. The main trees are evergreen although some deciduous genera such as *Albizia, Terminalia, Acacia* and *Combretum* occur. These forests include the evergreen rainforest around Witu, and the dryland Boni forest, which forms a discontinuous belt with wooded grassland from the Tana River to the Kenya-Somali border. Common trees in the Witu rainforest include *Sterculia appendiculata, Ficus depauperata, Erythrophleum guineense*, and *Dalium orientale*, while those occurring in the Boni forest include *Diospyros cornii, Albizia amara, Afzelia cuanzensis, Brachylaena hutchinsii, Combrtum schummanii, Oldfieldia somalensis, Olea africana,* and *Terminalia prunoides.*

2.4.5.7 Woodland

The woodland habitat contains trees ranging up to 18 m high, which are interspersed with shrubs. The woody canopy cover is greater than 25% and grasses are abundant in the understory. The habitat has well-drained, reddish-white sandy soils, with clumps of trees and shrubs dominated by *Diospyros cornii* and *Euclea divinorum*, respectively. The areas between clumps of trees support short to medium height grassland with *Adropogon amplectens* and *Eragrostis superba* as principal species.

2.4.5.8 Gallery forest

The gallery forest varies in composition depending on the soil type, susceptibility to flooding, and climate. This habitat occurs along the Tana River between Bura and Garsen. It occurs on brown loamy clay soils, and up to about 50 m from the river. It is dominated by *Acacia elatior, Albizia gummifera, Ficus sycomorus, Mimusops fruiticosa, Populus ilicifolia* and *Trichilia roka* with emergents such as *Diospyros mespiliformis* and *Sterculia appendiculata.*

2.4.5.9 Bushland

The bushland habitat is found close to forest along the Tana River between Bura and Garsen. Bushland is usually dense with a canopy of about 4-5 m, and occasionally some tall trees such as *Dobera glabra* and *Garcinia livingstonei*. This habitat occurs on brown clay soils, is subject to heavy flooding and is dominated by *Terminalia brevipes*, a deciduous shrub. Other common species include *Lawsania inermis, Thespecia danis, Phoenix reclinata,* and the poisonous *Exocaecaria veninifera*.

2.4.5.10 Grassland

Grasslands are composed mainly of grass species and support a woody canopy of less than 5% cover. This habitat is found only on the Tana River flood plains, although smaller patches occur in swamps and drainage lines. The grasses are tall and perennial, growing on brown alluvial clays, caused and renewed by seasonal floods. Dominant grasses include *Echinochloa haploclada, E. pyramidalis, Panicum maximum*, and *Setaria holstii*. Pure stands of *Sporobolus helvolus* often develop in swamp areas of heavy clays. A common woody plant in the habitat is *Acacia stuhlmannii*.

2.4.5.11 Wild and domestic animals of the study area.

Common domestic animals include, cattle (*Bos indicus*), sheep (*Ovis aries*), goats (*Capra hircus*), camels (*Camelus dromedarius*), and donkeys (*Equus asinus*). Wildlife species common in the region are hippopotamus (*Hippopotamus amphibius*), hirola (*Beatragus hunteri*), reticulated giraffe (*Giraffa camelopardalis reticulata*), African buffalo (*Syncerus caffer*), Burchell's zebra (*Equus burchellii*), waterbuck (*Kobus ellipsiprimnus*), topi (*Damaliscus korrigum*), lesser kudu (*Tragelaphus imberbis*), gerenuk (*Litocranius walleri*), warthog (*Phacochoerus aethiopicus*), and eland (*Taurotragus oryx*) (Appendix 2). Coke’s hartebeest (*Alcelaphus buselaphus*) a possible competitor of hirola (Kingdon, 1982), is absent. Large carnivore species found in the area include lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*), cheetahs (*Acinonyx jubatus*), leopards (*Panthera pardus*), and wild dogs (*Lycaon pictus*).

2.4.5.12 People and land use

Much of the study area is unsuited to agriculture. This leads to a preponderance of nomadic Orma, and Somali herdsmen of Hamitic origin. The Somalis occupy the extensive bush regions of the north, while their long time rivals, the Orma, are restricted to the Tana River flood plains of the south. Neither tribe uses the central portion of this distribution because the area is infested with tsetse fly. The only people occupying this central region are the Waboni, a small, ancient tribe, previously hunters and gatherers who have now adopted shifting cultivation.

Other people in the study area include small communities of agriculturalist and fishermen. These are the Pokomo along the Tana River and the Swahili, Bajun, and Arabs on the cost and offshore islands. However, the amount of crop production is limited and has remained at subsistence level. The main crops include bananas, cassava, maize, mangoes, coconuts and rice.

Chapter III:

Methods

3.1 General study techniques

This study was conducted mainly in the field, between September 1996 and December 2000. A large part of the work involved systematic searching for hirola in Tsavo (*ex-situ* range) and Garissa (*in-situ* range). Systematic (searching and locating each individual hirola group) data collected included i) group composition, dynamics and movement, ii) diurnal behaviour patterns, iii) group range quality, vegetation structure and composition, iv) ungulate community structure and composition, and v) food plant selection and quality. *Ad hoc* data were collected on predators and their kills and some additional information was collected by radio collaring lions and cheetah, the principle preadtors of hirola.

Finding hirola in Tsavo involved searching by vehicle, aircraft and by radio tracking. Sighting reports by other people, including KWS staff and tour drivers sometimes helped locate particular groups. A total of 660 days were spent in the field in Tsavo and 100 in Garissa. This constituted a total of 7920 ground-work hours in Tsavo and 1200 in Garissa. In addition, 148 hours were spent searching for hirola from the air in Tsavo and 32 hours in Garissa. A total of 674 group contacts were made with a total observation time of 2696 hrs in Tsavo. In Garissa, 122 group contacts were made. In total 66,000 km was covered on the ground in Tsavo and 27,000 km in Garissa.

The biggest problem in Tsavo was the difficulty in finding widely scattered hirola and often many hours were spent searching for particular groups. In Garissa, apart from the difficulty of sighting animals, bad roads and insecurity were major difficulties. On every trip to Garissa, I was accompanied by at least 6 armed rangers as a precaution against armed bandits and to prevent the research vehicle and equipment from being hijacked and stolen by Somali militia. These problems made visits to Garissa both costly and dangerous. Further, a combination of bad roads, and the prevalence of black cotton soils, made the range inaccessible by car at the peak of the wet season.

3.2 Population dynamics

3.2.1 Monitoring groups and individuals

A key technique in the Tsavo study was to locate and count all groups and individuals at regular intervals. The information collected for each group included the location, the identity of known individual (see **3.2.1.2**), and the age and sex structure. In Garissa, similar information was collected except that it was not possible to devote the time needed to identify individuals. In each study area, air searches were conducted, whenever an aircraft was available, to locate hirola groups. When groups were located from the air, I followed them up by ground inspection to collect more detailed data.

3.2.1.1 Location

A GARMIN 12 XL GPS was used to collect UTM (Universal Transverse Mercator – WGS 84, Zone 37 Southern Hemisphere – the study region) coordinates of the location of hirola groups for range mapping. Identifiable groups of hirola were tracked visually or by radio tracking to determine their ranging area. In Tsavo, 10 hirola were fitted with Telonics radio collars for radio tracking (White & Garrott, 1990). The antenna and receiver were fitted to the research vehicle or aircraft. Radio signals were detected from about 30 km by aircraft although, on the ground, the signal range was only 1 – 10 km. The signal range was highest in raised locations with sparse vegetation and lowest in flat areas with dense tall vegetation. Stronger signals were received during the dry season compared to the wet season. The activity of a radio collared animal also affected the signal: when animals were lying, the transmitter signals were generally weak or absent.

Attempts were made to identify and monitor the movement patterns of all adult males in order to establish their behavioral mating strategies (resource-defence territoriality or following) in relation to the size and movements of groups of females and their young. This information, in addition to group sightings was gathered continuously to help establish home ranges, seasonal movements, core areas, group interactions, range overlap, and habitat and microhabitat usage.

3.2.1.2 Individual identification

Individuals with distinct markings such as scars and broken horns were described and named. Some individuals were tagged, ear-notched and collared. Color photographs were taken using a 600mm lens and a Nikon camera to record detailed identifying features, including horn shapes. Hirola adults demonstrated some variation in horn shapes although this was sometimes confusing if an animal was still growing (Figure 3.1). In some species, e.g., Coke's hartebeest (Gosling, 1974), ear notches and other scars caused by fighting can be used to help identify individuals (although the primary method of identification in this related species was from variation in horn shape and grooves). However, hirola typically have a smooth unblemished pelage with remarkably few ear nicks or tears.

Additional information collected included observations on all forms of individual interaction especially agonistic interactions. Field observations indicated a high level of interaction between individuals, especially during shading times. Competition was particularly intense for high quality shade trees and information on such contests was used to help assess the importance of shade as a limiting factor for hirola groups.

3.2.1.3 Numbers age and sex structure

Individuals were aged using successive categories of horn development (Figure 3.1). "0 –3 month olds (calves)" were designated as individuals without horns or with horns just protruding. "4 – 6 month olds (6 months olds)" were individuals with straight horns, just exceeding ear-length. "7 – 9 months olds" were individuals with horns measuring approximately 30cm, and just beginning to curve inwards. "9 –12 months olds (yearlings)" were individuals whose horn tips had started pointing inwards and widening from the center. "13 – 15 month olds" were individuals whose horn tips had reached near maximum proximity showing a clear oval (rugby ball) shape from a front view. "16 months olds and above (2 year olds)" were individuals whose horn tips were beginning to diverge and the base angles had started to show. Adults were individuals with spread out horns with the mature shape either formed or almost formed.

Sexing hirola in the field required careful and prolonged observation. Adult male and female hirola are broadly similar in appearance and inexperienced observers generally find them difficult to distinguish. Hirola males have small light coloured testicles that are suspended high up within the thighs. The penal sheath has very little hair and cannot easily be seen. Opportunities for sexing hirola, especially the calves, are when they are

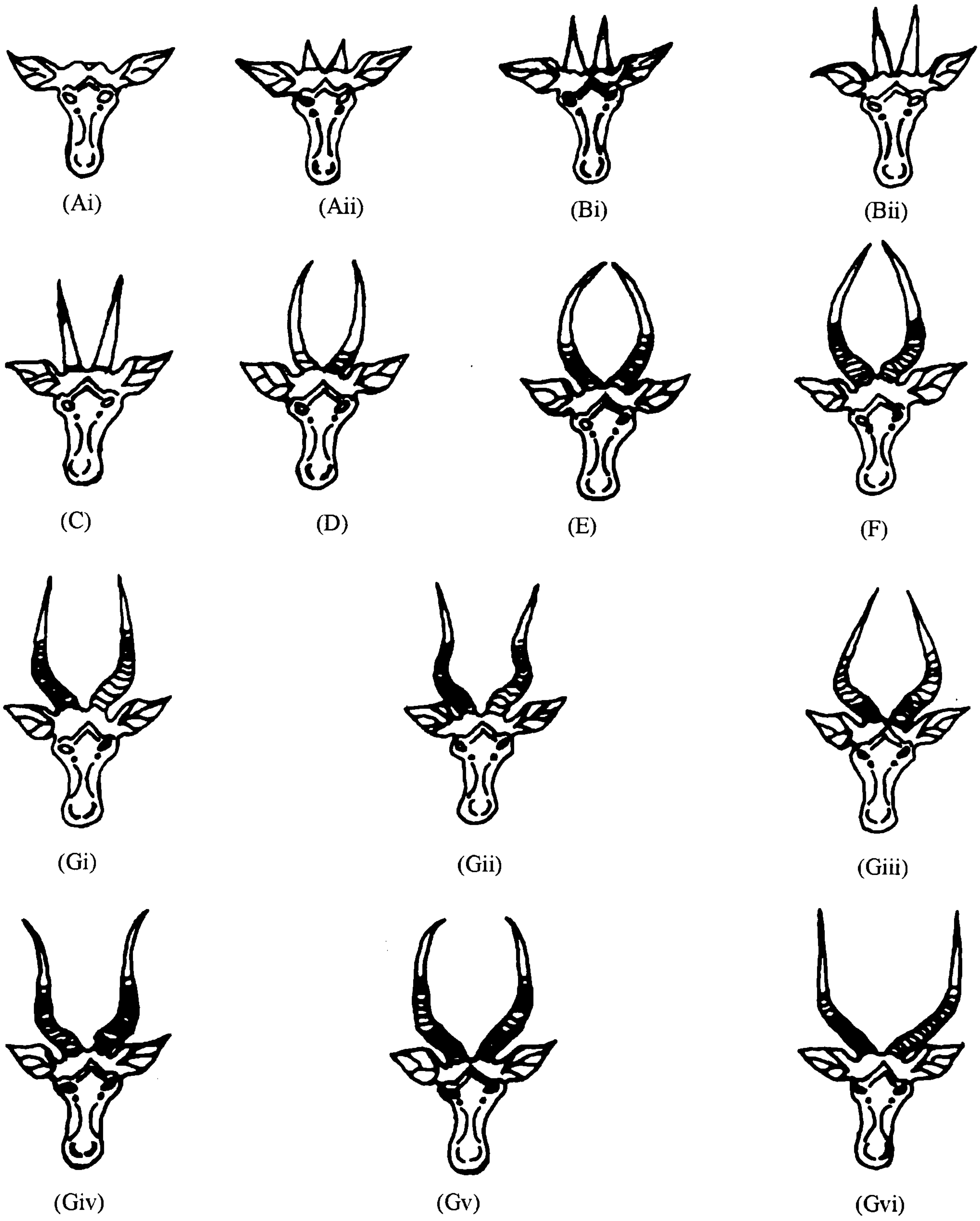


Figure 3.1: Aging hirola in the field using horn development: Ai – Aii = 0 – 3 months old (calves); Bi – Bii = 4 – 6 months old (6 months olds); C = 7 – 9 months old; D = 10 – 12 months old (yearlings); E = 13 – 15 months old; F =16 months old and above (2 year olds). Gi – Gvi = horn shape variations among adult hirola.

urinating and when they expose their genitals while scratching with the hind feet or when walking or running away from the observer. Sexing hirola was carried out by careful observation of individuals using a Leica 8 x 42 binoculars. In Tsavo, hirola groups were frequently observed and sexed and calves were repeatedly observed during diurnal behaviour observations and as they developed to yearling stages. In Garissa, since hirola groups were often located only once per visit, sexing was ascertained by observing a group for at least 30 minutes and following it whenever it moved and carefully observing the sex of each individual, especially the calves and young.

Additional information collected included evidence of births and deaths, exchange of members between groups, signs of predation and predator attacks such as claw and teeth scratches on individuals, state of alarm of a group and whether the group had been scattered. This information was gathered as frequently as possible to help establish population size, age and sex composition during different years and seasons, and to monitor birth, calf development, mortality and recruitment (the number of individuals reaching the adult stage) among hirola.

3.2.1.4 Associated species

Preliminary field observation indicated that hirola associated with other herbivores including Grant's gazelle, common zebra, giraffe, Coke's hartebeest, fringe-eared oryx, and eland. Observations in the Mara-Serengeti region of Kenya and Tanzania (Sinclair, 1985) indicate that predation and competition played a major role in shaping the ungulate community structure. To investigate the significance of such associations for hirola, every time a group of hirola was sighted, a record of the associating species and the degree of association was made. Associations were divided into three classes namely, "close" (when individuals of an associating species were mixed among a hirola group), "nearby" (when an associating species was observed within 100 m of a hirola group but were not mixed, and "aggregate" (when an associating species was between 100 and 500 m from a hirola group).

3.3 Behaviour

3.3.1 Ad hoc long-term observations of behavior

Whenever groups were located and watched with the aim of recording demographic data, *ad hoc* records were collected of any social behaviour observed. Such records included observation of mother offspring behaviour (to monitor the development, mortality, and the dispersal of young), agonistic behaviour (intra and inter specific), mating strategies (including the relationship between bachelor males and the males that accompanied family groups), interactions within and between groups (including the occasional joining of neighbouring groups and the exchange of individuals between groups) and anti-predator defence strategies (how groups reacted to the presence of predators). Although attempts were made to collect night hirola activity patterns on full moon and dark nights, observation group soon ran off. During these attempts, target study group was located as early as 1700hrs and monitored into the night. However, after nightfall, lion roaring, alarm sounds of other ungulates after suddenly noticing the car, the sound of elephants breaking branches, and generally any slight twig breaking sound made them run or slowly start drifting away and out of view. Attempts to start the car and follow made them run further and could not be relocated.

3.3.2 Diurnal behaviour pattern

In order to quantify diurnal variation in activity and social behaviour within hirola groups, single groups were followed from dawn (or as soon as they could be located) until nightfall. Scan samples (Altmann, 1974) were taken at 10min intervals from all visible individuals. These data were collected during dry seasons (January and July/August) and in wet seasons (April/May and November/December). However, it was not easy to acquire this data in the way planned. First, the target study group could rarely be found by 0600 hrs: sometimes a group was located as late as 1200 hrs or was never sighted at all. Secondly, some groups were less habituated and always drifted away or ran when closer approach was made. Thirdly, as a result of occasional disturbances from predators, other herbivores, tour vehicles and sometimes as a result of the spontaneous movement of hirola into thick bushes, the otherwise good observation days were terminated. However, data were collected on 6 groups for both wet and dry seasons and the undisturbed behaviour recordings were averaged to obtain a 12 hour behaviour pattern. A total of 50 behaviour data days were achieved in the wet season giving a total of 368 hrs. In the dry season, a total of 57 behaviour data days were acquired accounting for 459 hrs. The following information was recorded:

General activity pattern:- Data collected included resting (standing/lying), drinking, grazing, urinating, defaecating, ruminating (standing or lying) and moving (walking, running).

Social activity patterns:- Data collected included, grooming another individual, agonistic behaviour, scent marking, social play, reproductive behaviour and mother-offspring behaviour.

Shade utilisation:- Records were made of shade use by every individual. These data included information on whether the weather was sunny or overcast, and, if sunny, whether each individual was in the sun or shade. Shade tree or shrub species were recorded and the number of hirola sharing each shade tree.

3.3.3 Vigilance

A general measurement of the vigilance of an animal is to monitor the behaviour of "head up" during grazing or resting (Underwood, 1982; Elgar, 1989; Quenette, 1990). Data on hirola vigilance were collected as a special exercise between August 1999 and August 2000 to help determine the anti-predator significance of associated species. When groups of hirola were selected for study, care was taken not to disturb the animals and to watch them from the furthest point possible. Records were made of whether they were alone or with an associated species. Scan data (Altmann, 1974) were recorded every five minutes. Records were made of whether an animal had its head down or up when resting or grazing. These data were collected for all visible individuals in the association. Samples of the same data were taken on hirola groups of varying sizes and associates of varying numbers. The types of groups sampled were, hirola on their own, hirola associated with Grant's gazelle (the Tsavo hirola's main associated species) and Grant's gazelle on their own.

3.4 Feeding

3.4.1 Habitat surveys and mapping

Surveys were carried out on the resources and other characteristics of hirola home ranges to provide a basis for comparing reproductive success and survival among hirola groups. Range surveys were carried out twice a year during the rainy season (March-May) and the dry season (June-August) for both study sites, immediately following diurnal behaviour pattern sampling. This enabled information to be collected on the exact range area used by a group. Thirty sample points were randomly selected from within each hirola group range. Randomization was achieved by selecting a point at the center of the range, then randomly selecting a direction of movement from the 8 compass directions, moving 200 or 500 m depending on the size of the range and bush cover, and sampling. This step was undertaken at every point until 30 sample points were achieved. At each sampling site, a 20 m^2 quadrat was set. In each quadrat, data were collected at two levels: (i) within the entire quadrat, all woody species of height above and below 1.8m and crown diameter (CD) greater and less than 5 m were described, and (ii) in a $1m^2$ area at the centre of the main quadrat, all herb and grass species, their height and percentage cover were described. A total of 270 sample points were taken per season in Tsavo giving a total of 540 sample points while in Garissa, 60 samples per site were taken giving a total of 360 sample plots. Later, a thorough ground and/or aerial survey was carried out to determine and map all transient waterholes in each hirola range using UTM GPS coordinate readings.

3.4.2 Food plant selection

3.4.2.1 Field observation

Sampling was carried out on all the group ranges in Tsavo in order to give a more accurate representation of food plant selection. Attempts were made to contact groups early in the morning when they were actively feeding. Care was taken to prevent any disturbance, by watching the group graze from the furthest point possible. These data were collected only in areas where hirola were observed to be feeding without associates to avoid any confusion with evidence of feeding by other species when vegetation was sampled. Because of the hot sun in Tsavo, earlier plant bites by other species were dry and easy to differentiate from the hirola's fresh bites. Hirola were left to graze in a patch for at least 30 minutes before sampling. Thereafter, $1m^2$ quadrats were laid randomly in the patch used. The number of quadrats laid in each area varied depending on area size and vegetation homogeneity. In each quadrat, a record was made of: (1) the number of grass/herb tufts per plant species, (ii) the number of tufts eaten per plant species, (iii) the plant parts eaten, (iv) the number of bites per plant species, and (v) the bite height per plant species. The plants were later identified. In total, at least 30 quadrats were sampled per group per season for all hirola groups in Tsavo giving a total of 270 points in the wet season and 270 points in the dry season.

3.4.2.2 Faecal plant tissue analyses

In order to cross-check on these field observations of feeding, microscopic faecal analyses (Storr, 1961; Stewart, 1965; Stewart, 1967) was performed on fresh faecal samples collected on every group per season. Although this technique has several shortcomings, it was a useful method for confirming the range of plants eaten by hirola, particularly in the natural range (Garissa).

During sampling of habitat structure, all grass/forb material encountered in the ranges occupied by any group of hirola were collected for reference material. Leaves were cut into 15 mm lengths and boiled in 10% nitric acid in a flask inside a fume chamber (Storr, 1961). The cuticle layer was removed, stained lightly with haemotoxylin, and permanently mounted on a microscope slide. Both the adaxial and abaxial surfaces of the plant cuticles were photographed to obtain a reference collection of colour prints.

Faecal pellets were collected from Garissa from all groups that were sighted and in Tsavo from all available groups between 1998 and 1999 for both dry and wet seasons. From every hirola group, faecal pellets were collected from at least five individuals and/or defecation units (piles of faeces from one defaecation). All pellets in a pile were collected in a disposable plastic bag, crushed and mixed, and then a small sample put in a 10% formalin solution for preservation. Once back in the lab, formalin was drained from the sample, and the sample was digested in 4 ml concentrated nitric acid over low heat for about two minutes. The sample was then made up to 100ml with distilled water, boiled and stirred. The resulting mixture was centrifuged for 15 minutes at 2000 rpm and the supernatant discarded. The remaining bleached cuticle fragments were stored in 5 ml FAA (25% distilled water, 60% absolute alcohol, 10% formalin, and 5% glacial acetic acid) prior to analysis.

During analysis, the sample was stirred and a sample pipetted onto and spread out on a microscope slide, stained with haemotoxylin, covered with a slide cover and observed at x400 magnification. Tissue was identified by adaxial/abaxial cell shapes and layering, density and cell layers of epithelial hairs and numbers, layout and shapes of stomatal cells using the reference photographs. The proportion of tissues identified in a sample were determined by calculating areas (using the eye piece micro-scale) of each tissue type and by summing to estimate the amount in the diet. Analyses of Tsavo faecal pellets were used to confirm systematic field feeding observations. In Garissa, it was not possible to carry out systematic field observations of feeding behaviour because of the security situation, but a total of 80 samples were taken for faecal analyses, 40 in the wet and 40 in the dry season to determine plant selection and to quantify usage. Each season samples were taken from all the known hirola sites in Garissa.

The faecal tissue analysis technique is limited because it is carried out on relatively indigestible material (Storr, 1961; Stewart, 1965; Stewart, 1967). Herbivore forage digestibility studies indicate that as grass swards mature, they increase in biomass and decrease in quality as they accumulate structural carbohydrates (Waite, 1963). Mature, poorly digestible grass often passes through the digestive system with little absorbtion (Illius & Gordon, 1992) whereas young high-quality grass is mainly digested and absorbed (Baile & Forbes, 1974). Thus, the analysis of faecal plant tissue in a selective grazer such as the hirola will often underestimate plant species selection as most consumed plants are digested and absorbed and only a few indigestible ones are excreted in the faeces.

3.4.3 Nutrient analyses

The aim of this procedure was to determine the nutritive quality of hirola food plants within the different study sites and variations between seasons in relation to hirola reproduction and survival.

3.4.3.1 Plant nutrients

Material for plant nutrient analyses were collected during habitat surveys and mapping (See **3.3.1**). Samples of grass species were collected on both study sites in each area used by hirola during the wet season (April – June) and during the dry season (July – September). A total of 30 grass food plants per season and per study site were analyzed for % nitrogen, % phosphorus, % potasium and % calcium. Unfortunately, calorific determinations were not carried out and this needs to be done in the future. Whole plant (leaf, stem, shoot, flowers) samples was taken, taking care not to contaminate with soil. All collected grass species were sun-dried. The same species collected in different sites of each study area were combined, and a representative species sample of 100 g taken for analyses at the Kenya National Agricultural Research Laboratories (KNARL), Nairobi.

It was not possible to carry out detailed investigation of nutritional requirements on captive animals and such work will be needed in the future to understand the energy requirements of hirola, and how this may limit the population in their natural environment.

3.4.3.2 Faecal nutrients

In both study sites, collection of faecal material was made from each family group. A composite sample was made of fresh material from the locality where a hirola group had spent the night. All heaps of pellets within the sampling area were located. From the heaps, four pellets were collected using a pair of forceps and placed in a porous bag. Care was taken not to contaminate the sample with soil. The samples were then sun dried while in the field to avoid rotting. A total of 20 samples were taken at each study site per season. In the lab, the samples were further dried in the oven at 50°C for 24 hours. Thereafter 100 g from each sample were packed in airtight bags and send to KNARL, Nairobi, for analysis.

3.4.3.3 Analyses of nutrients

Analysis of the mineral content of plant and faecal material was carried out on 5 sets of a thoroughly mixed small sample of 0.1 g to obtain an average figure for mineral content. The sample was "wet digested" with sulphuric acid and hydrogen peroxide. This provided the base material on which to carry further analyses.

Nitrogen: Measured on Auto Analyzer, results were multiplied by 6.25 to give % Crude Protein dry matter (%CP).

Phosphorus: Measured on an Auto Analyzer and converted to % phosphorus dry matter (%P).

Potassium: measured with a Flame Atomic Absorption Spectrometer, and converted to % potassium dry matter (%K).

Calcium: measured with a Flame Atomic Absorption Spectrometer, and converted to % Calcium dry matter (%Ca).

3.5 Community structure

The size and composition of the large ungulate community within the hirola range was estimated for both study areas. In Tsavo, ten 15 km road transects were established. Every month on the last day, beginning June 1998 to June 2000, I drove these transects between 6 and 10 am and 4 to 6 pm for two days in order to encounter most animals during their active feeding moments of the day. Animals within 200 m (maximum sighting distance) on either side of the transects were counted, aged, their occupied habitat sampled (see **3.3.1**) and levels of association with other species recorded. Similar but more concentrated transects were undertaken in Garissa in June 1999, and March and August 2000. A total of 20 15 km transects were completed per visit to Garissa.

3.6 Predation

During the course of the study, all sightings of predators and their kills in Tsavo were recorded. Data were collected on species, number, location (GPS), species killed and the age of the carcass. While such data cannot be used to estimate levels of predation, they give some indication of variation in the risk of predation within the Tsavo study area and in particular, between the ranges of the different hirola groups. An attempt was made to determine the seasonal ranging patterns of lions and cheetah in Tsavo. One female lioness from the Aruba pride (which contained 11 individuals) and from the Satao Camp pride (containing 9 individuals) and a female from a cheetah family at Sato Airstrip (6 individuals) were collared. Predators from these sites were selected as their range was believed to cover a large part of the known hirola ranging areas. The predators were collared in February 1999 and monitored (radio tracked) through the wet and dry season and uncollared in October 1999. During the monitoring period, records were made of all known prey species killed and the ranging area of each using GPS points from sighting locations.

In Garissa, data on predation were collected by hirola community scouts, from within their grazing range. Whenever mortality occurred, the scouts collected and kept the skulls as evidence and noted the location of the incident. During my visits to the range, I verified the data by visiting the carcass sites or by the presence of fresh skulls (although sometimes hyenas stole the skulls from where some scouts had stored them).

3.7 Poaching

Data on poaching activities was collected in both Tsavo and Garissa. In Garissa, these data was collected by hirola community scouts and constituted an important activity in their work. Prior to the collection of these data, there had been numerous reports about hirola poaching on the natural range. The hirola scouts recorded incidents that they witnessed or that were reported to them by other members of their community. In cases where they acquired information from someone else, they visited the scenes to confirm the incident. They also collected and kept any available material as evidence. During my visits, I confirmed some cases by visiting the sites in the company of the individual hirola scout or by observing fresh samples from the dead hirola that they had collected. Most of the remains involved stomach contents that were difficult to verify, but sometimes the head and lower feet were found. Often, the hirola scouts had to dig these out as some poachers buried the remains to hide evidence. In Tsavo, information about poaching was gathered by the Kenya Wildlife Service (KWS) field security surveillance team and I was informed of any incidences that occurred within the hirola range, if I did not already know about it.

3.8 Analyses of data

All data were entered onto Excell spreadsheets and then sorted in preparation for statistical analyses. Both non-parametric and parametric statistical tests were used where appropriate (Sokal & Rohlf, 1981). Data analyses followed standard techniques supported by SPSS for Windows version 10.0. The Kolmogorov-Smirnov one-sample test and general histograms was used to determine whether data were normally distributed. Most tests are reported with their two-tailed probability values at the 0.05 probability level. All maps have been generated using MapInfo Professional Windows version 5.0 with projections in UTM (Universal Transverse Mercator – WGS 84, Zone 37 Southern Hemisphere – the study region). Sample data are detailed in appropriate sections where needed.

3.8.1 Population dynamics

Due to the occasional separation of individuals from natal groups at different times of the day and season, hirola group sizes were obtained by taking the highest number of individuals observed in a group after every four months period of consistent group sightings. A comparison with the null hypothesis of equal number of ages and sexes within groups and between years were analysed using χ^2 tests (Sokal and Rolf, 1981). Pearson correlations were used to determine the relationships between calving and group structure.

3.8.2 Social organization and behaviour patterns

Hirola social grouping were derived from monthly percentage sightings of varying group composition during the study period. Activity time budgets were analyzed as follows: the number of records of each behaviour category during each hour from all animals in the group were counted and converted to percentages. This percentage activity category was subjected to Log10 transformation prior to analysis. Each behaviour category was analysed for significant difference between groups and seasons (wet and dry) using One-Way Anova (**SPSS 10.0**).

3.8.3 Ungulate community structure

Mean species density were calculated from two year road count data. Biomass was calculated using published mean body weights (Coe et al., 1976) of the species encountered. Monthly ungulate data were converted to percentages and later subjected to Log10 transformation prior to analysis. Data on the various kinds of association with hirola (i.e., close, near and aggregate – see **3.2.1.4**) were converted to monthly percentages and subjected to Log10 transformation. One-way Anova was performed to determine significant differences between individual associates species in relation to kinds of association with hirola. Student-Newman-Keul's test was used to rank the importance of each species in terms of its association with hirola.

3.8.4 Community ecology

Home range size and the degree of overlap of home ranges were calculated using the soft-ware package RANGES V (ITE, 1996). The 90% minimum convex polygon (Hayne, 1949; Kenward, 1987) was arbitrarily defined as the home range (Burt, 1943). This eliminated areas of the range that were entered by hirola groups on rare occasions. The general home range for each group was calculated from data points for the entire study period. Core feeding area were manually calculated from digitized study area base maps using MapInfo professional 5.0, by visually identifying clustering sites with more that 15 group sightings.

Records of each vegetation data parameter (see **3.4.1**) in each group range/site per season were counted and converted to percentages. These percentage vegetation categories were subjected to Log10 transformation prior to analysis. One-way Anova was performed to determine significant differences between different vegetation categories and hirola group ranges, and study sites. Student-Newman-Keul's test was used to rank vegetation categories among hirola group ranges/sites.

Hirola bite height data was analyzed by averaging all bite height records for wet and dry season from field feeding observations. Data on all food plants observed from field data and from faecal analyses and their availability on the range was converted to percentages. These percentage food plant use and availability were subjected to Log10 transformation prior to analysis. Ivlev's Electivity Index (Ivlev, 1961) was used to determine species preference in relation to its availability.

$$Ei = (ri - ni)/(ri + ni)$$

Where (Ei) = Ivlev's electivity measure for species (i)

(ri) = Percentage of species (i) in the diet

(ni) = Percentage of species (i) in the environment

Electivity varies from (-) 1.0 to (+) 1.0, where values between 0 and (+) 1 indicate preference and values 0 and (-) 1 indicate avoidance. Pearson correlations were used to indicate any linear relationship in selectivity between seasons and greenness levels.

Food plant nutrients are known to vary with seasons of the year as plants sprout, mature and dry (Mannetje, 1984). Similarly, different plants have varying nutrient values and different sites can vary in overall nutrition qualities. Data on plant and faecal nutrient contents between Garissa and Tsavo were compared within sites, between sites and between seasons using One-way Anova.

3.8.5 Limiting factors

Both descriptive and parametric statistics were obtained for population trends, poaching, disease, predation, group ranging characteristics and reproductive and dispersal behaviour. In order to determine the relationship between factors affecting hirola groups in Tsavo, a regression analyses of dependent factors (group size, number of females per groups, calf mortality, carcasses per group range, emigration and immigration) and independent factors (predation effects, habitat structure, food availability, range characteristics and effects of associates). Stepwise multiple regression was carried out to help determine the key independent factors affecting a certain dependent variable.

Chapter IV:

Hirola Population Dynamics

4.1 Introduction

The population size and structure of a species is critical for its long-term survival. Information about these matters may also be critical for determining the risk status of a species and for defining targets for its recovery, or reduction in its risk of extinction (Ballou, 1983). The hirola is one of the world's most endangered large mammals, having suffered a 90% population reduction between 1973 and 2000 within its natural range. A population that has suffered such a dramatic reduction is likely to suffer from both demographic (variation in the population's births, deaths, and sex ratios caused by normal random variation among individuals), and genetic (loss of genetic material through inbreeding) problems (Ballou, 1983).

There has been much debate about the population levels above which a species is likely to persist in the medium and long term. According to Franklin (Franklin, 1980), a minimum of 50 individuals could tolerate inbreeding depression, whereas 500 individuals is the minimum population that can allow free rein to evolutionary processes. However, given the varying influences on species dynamics (i.e., differing levels of environmental stochasticity, behavioural and demographic adaptations, etc), it has also been suggested (Soule, 1987b) that there can be no single rule of thumb nor magic number for the safe minimum size of populations.

The effective population size (the size of an ideal population that loses genetic variance at the same rate as does the real population) is an important consideration for small populations (Caughley, 1994). The structure of the population influences the population's survival through the effects of unbalanced age distribution and sex ratio on its rate of increase. An effective population size is a population with an even sex ratio and a stable age distribution that has the same net change in numbers over a year as the population of interest (Goodman, 1980). As a first approximation, effective population size is equal to or less than the number of breeding individuals. However, effective population size is controlled by the number of the less common sex: the higher the number of the less common sex, the less offspring will be closely related, and the less likely is the loss of genetic variation during transfer of genetic material from parent to progeny. The contribution of an effective population size to the next generation has a Poisson distribution, the fundamental property of which is that the variance equals the mean. If the variance of offspring production among individuals exceeds the mean number of offspring produced per individual, the effective population size will be smaller than the census size (Wright, 1940). An extreme sex ratio may have a significant effect on a population's ability to increase from low numbers, enhancing that ability when females predominate and depressing it when males dominate (Goodman, 1980).

In large-herbivore populations, environmental variation and density dependence co-occur and have similar effects on various components of fitness (Gaillard et al., 2000). Regardless of the source of variation, adult female survival generally shows little year-to-year variation (coefficient of variation (CV) < 10%), the fecundity of prime-aged females and yearling survival rates show moderate year to year variation (CV<20%), and juvenile survival and the fecundity of young females show strong variations (CV>30%). Old females show senescence in both reproduction and survival. The immature stage, despite a low relative impact on population growth rate compared with adult stage, may be the critical component of population dynamics of large herbivores (Gaillard et al., 2000). There are a number of individual adaptations that effect the survival rates of newborn animals in a population. Some grazing herbivores in Tsavo have a more synchronised breeding peak than browsers, and this may be related to seasonal changes in food quality (Leuthold & Leuthold, 1975) such that calves are born at a time when there is enough high nutrient forage for the lactating female. According to Jarman (Jarman, 1974), the type of food, feeding style, body size, and anti-predator behaviour among antelopes are interrelated, so that species whose social systems involve large herds have more synchronized breeding than those that live in small groups. As a result, sedentary predators are overwhelmed with prey for a short period and can only take a fraction of the newborn. Solitary species have less need for such as measures as they rely on crypsis to escape predators (Jarman, 1974).

Lions, the major predators in Tsavo, are territorial, except in periods of extreme hardship (Parker et al., 1990). Lions must therefore endure wide fluctuations in the local densities of certain prey species, relying on resident species during lean periods. Studies on lion prey selection in Kruger National Park showed that lions selected the most abundant small to medium sized ungulates namely impala, wildebeest and zebra (Funston et al., 1998). Local prey densities can vary dramatically on a weekly or even daily basis, especially in the case of migratory species (Scheel, 1993). These variations can thus cause increased predation pressure on species such as the hirola that remain in an area with resident predators and with reduced numbers of alternative prey.

Age, sex, reproductive status and body condition can influence the antipredator behaviour of an individual (FitzGibbon & Lazarus, 1995a). The various classes of individuals (fawn, adolescent, adult; male and female; territorial and non-territorial, females with young of varying ages, etc) vary in their risk of predation as a result of their behavioural and morphological characteristic. Such characteristics influence both the probability that an individual is selected as a target and its chance of surviving an attack (FitzGibbon & Lazarus, 1995a). This study aimed to explore the population dynamics of hirola in the Tsavo and Garissa population, with an emphasis on identifying potential limiting factors.

4.2 The Tsavo population

4.2.1 Numbers and distribution

It was not possible to locate all of the hirola groups every month in Tsavo because animals were widely scattered and often hidden in scrubland. To examine population trends over the study period, the highest number of individuals sighted per group within each four month period between September 1996 and December 2000 were summed to give a continuous overall population estimate. Thus the variations observed in this analysis is of actual individuals that were observed from individual group sightings within this period. Because of hirola's usual behaviour of individuals occasionally separating from the natal groups, such individuals may have been excluded from the analysis if any were out of the group at the time of sighting. A total of 10 hirola groups (M1 = Mukwaju 1, M2 = Mukwaju 2, MK = Mackinnon, A3 = Alpha 3, B1 = Balguda 1, B2 = Balguda 2, VR = Voi River, DK = Dakota, DH = Dida Harea, SAT = Satao) were found and monitored in Tsavo East NP. The groups occurred in distinct family units in an area around the Dika Plains (Figure 4.1). Between 1996 and 2000, the lowest total number was 59 (April 1997) while the highest was 90 (December 1996; Figure 4.2).

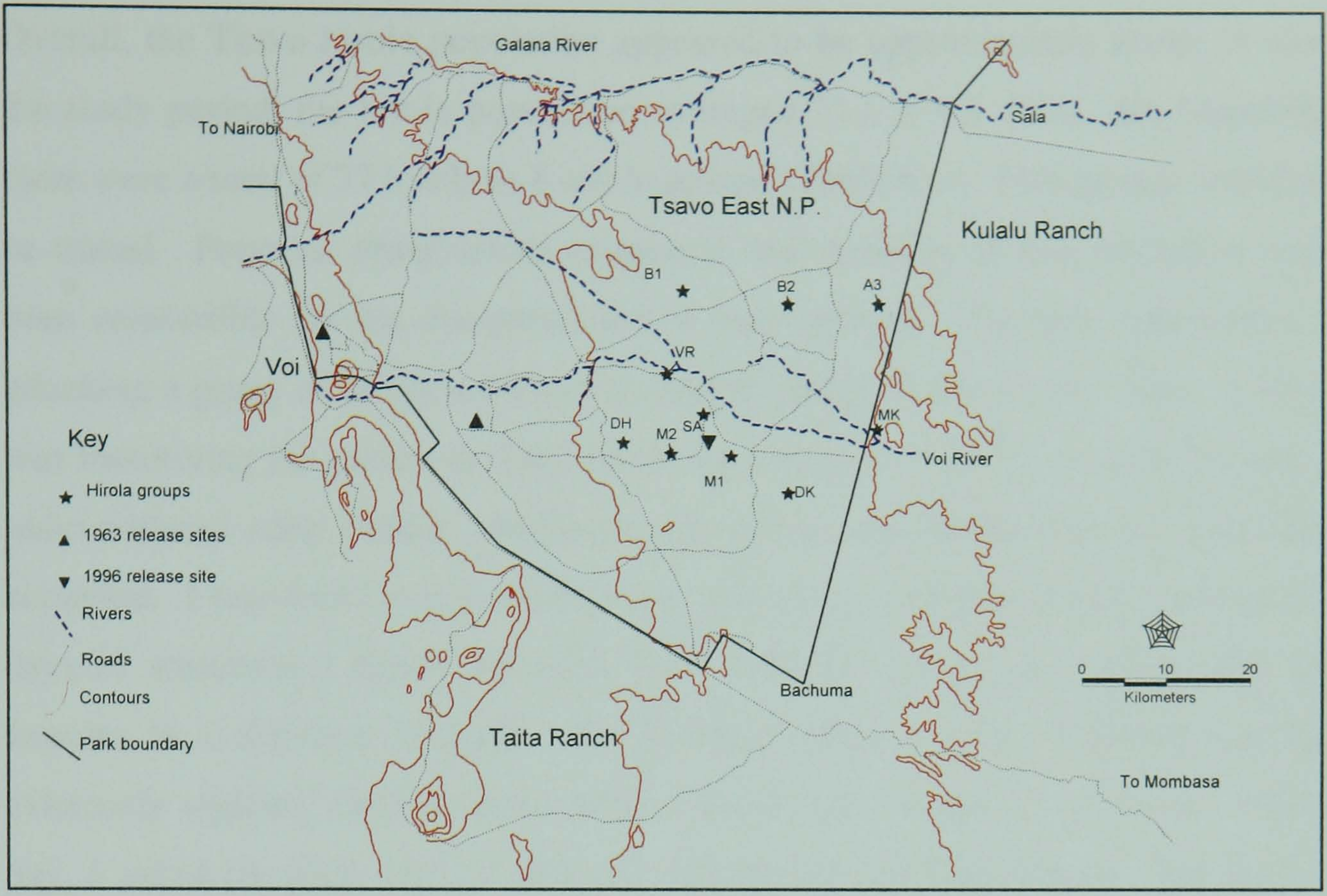


Figure 4.1: The centre point of the range of hirola family groups in Tsavo East National Park between September 1996 and December 2000.

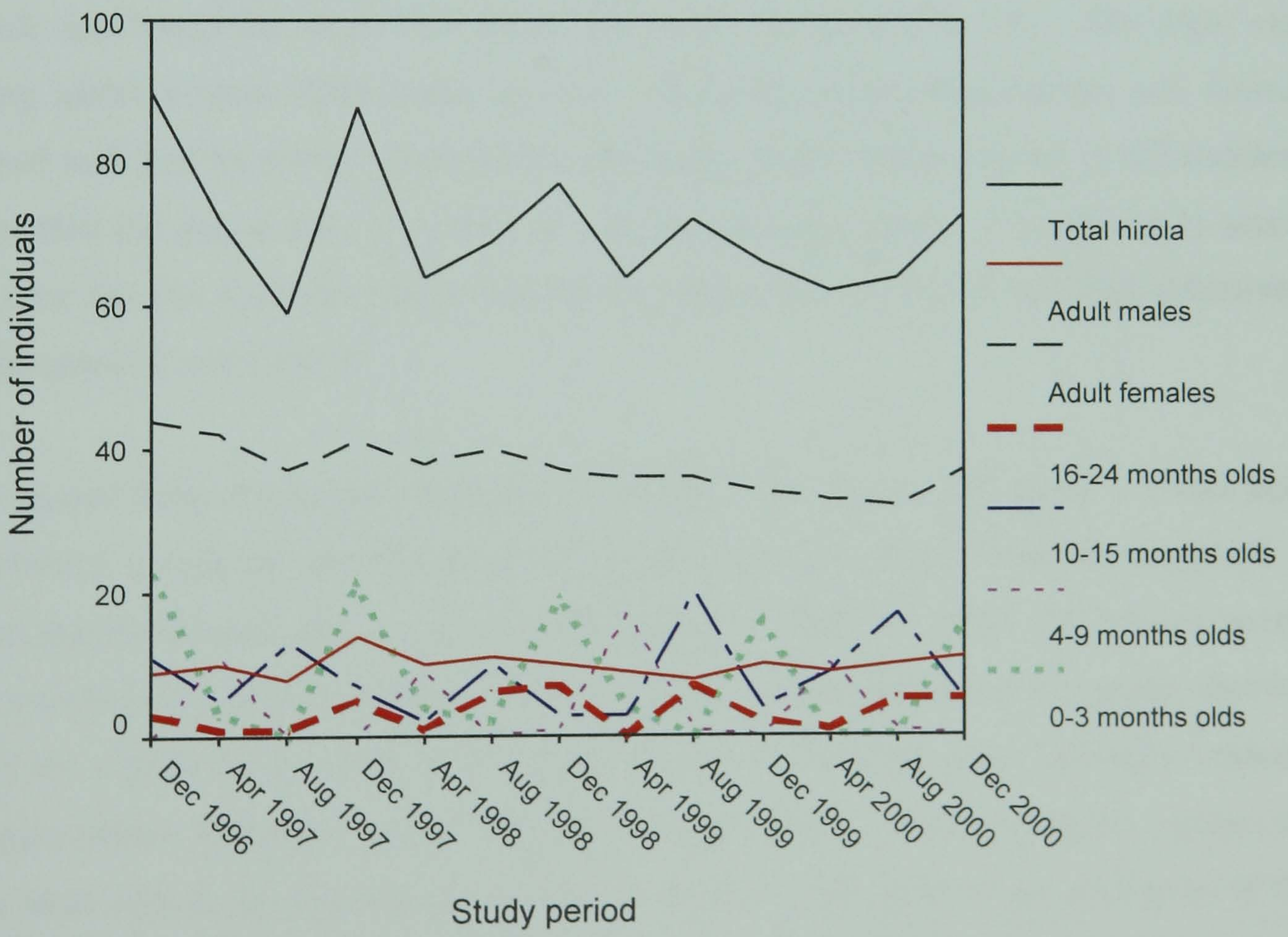


Figure 4.2: Variation in the total number of hirola in Tsavo East National Park between 1996 and 2000.

Overall, the Tsavo hirola population appeared to be approximately stable in size. Over the study period, the hirola population averaged 71.1 ± 9.3 (SD). By December 2000, there were a total of 77 hirola in 8 stable groups (Table 4.1). Two groups could no longer be traced. Previous observations suggested that episodes of lion predation might have been responsible for the disappearance of these groups. The first observation of lions attacking a group of hirola involved on the DK group, in December 1996. At this time, I was monitoring the group on daily basis and was able to locate it easily because it had a radio-collared adult female. Suddenly, the group was absent from the area that it had occupied. I searched for it in all the core areas that it had previously used and after two days of searching I found the adult male from the group, now alone, and two adult females in a different location. All of these animals were displaced and they were extremely vigilant, running away when I made any attempt to approach. On the third day, I asked the park pilot to help me relocate the collared female. We flew over the range in the morning and after 30 minutes I detected the signal, about 10 kms from where I had last seen the group. The pitch of the signal indicated that this female was dead. After circling around the signal, we sighted a pride of 10 lions. Later I visited the site by vehicle and found the skull, two lower limbs and the hoof of a calf. The lions were resting under a bush 500m from the site. The area around the carcass was heavily marked with lion footmarks, resting sites and scats. Within three months of this incident, I relocated the group male once and the two lone females twice. I continued to search this area but the scattered individuals never regrouped and the group thus effectively disappeared as a social unit.

The second lion attack was observed in March 1998 on the M2 group. I had been monitoring a collared heavily pregnant female from the group with the intention of observing the calving process and tagging the calf. This was achieved but two weeks after calving, and when the female was temporarily in isolation from the group, she was killed by a pride of 13 lions (9 adults and 4 cubs). The lion pride had been roaming around a central waterhole within the group's range. When I encountered the carcass, the lions were still at the site though they had consumed almost all of the carcasses of the female and calf. The only identifiable remains were half of the calf's skull, the skull of the adult female and the rib cage and the radio-collar. This group had a small home range and, surprisingly, they remained in this range during and after this predation incident..

Table 4.1: Total number and composition of hirola groups in Tsavo East NP during December 2000. L/ads = lone adults: L/sads = lone subadults.

Group ID's	Total group size	Males					Females				
		Adults	16-24 Months olds	10-15 Months olds	04-09 Months olds	0-3 Months olds	Adults	16-24 Months olds	10-15 Months olds	04-09 Months olds	0-3 Months olds
A3	6	1	0	0	0	0	3	0	0	0	2
B1	8	1	0	0	0	0	4	0	1	0	2
B2	6	1	0	0	0	1	4	0	0	0	0
DH	12	1	0	0	0	1	6	1	0	1	2
DK	-	-	-	-	-	-	-	-	-	-	-
M1	9	1	0	0	0	1	5	0	0	0	2
M2	-	-	-	-	-	-	-	-	-	-	-
MK	9	1	0	0	1	1	5	0	0	0	1
SAT	9	1	0	0	0	1	4	1	0	0	2
VR	7	1	0	0	0	1	4	0	0	0	1
L/ads	3	3	0	0	0	0	0	0	0	0	0
L/Sads	7	0	3	4	0	0	1	0	0	0	0
Pop. Size	77	11	3	4	1	6	36	2	1	1	12

One month after this incident, I encountered the same pride of lions under a bush with the remains of another young female from the same hirola group. A further search for the group revealed three isolated females, and later, and again in isolation, the male. Two of the lone females later joined the neighbouring DH group. No other members of this group were seen again. After the El Nino rains, a bush fire in December 1998 opened up the range and I was able to find four other fairly old hirola skulls including that of the group male, who could be identified from his characteristic horn shape.

4.2.2 Group size, Age and sex structure

Monthly observations on individual family groups showed no significant variation in size over the study period (Figure 4.3) (F = 0.633, df = 49, 126, $P > 0.05$). Groups varied from 2 to 15, with a mean of 7.3 ± 2.6 SD. Occasionally two neighbouring groups joined up and grazed together for a maximum recorded period of two weeks. The largest such grouping observed in Tsavo was 17 animals. Hirola groups tended to peak in size just before the calving season (due to an influx of maturing females and of other adult females) and during the actual calving season (due to the influx of new calves, Figures 4.3 & 4.4).

Overall age ratios varied according to season. In order to quantify this variation, age and sex structures data for the months of August (just before the onset of calving) and December (just after the peak calving season) were analyzed for the entire study period. Before calving, the population consisted of adults, 16-24 months olds, 10-15 month old animals, 4-9 months old animals and 0-3 months old calves in the ratio of 91:9.5:30:1:1 respectively (Table 4.2). Comparing these data with the null hypothesis of equal numbers of animals in each age class showed significant variation between classes (χ^2 = 1688.2, df = 4, $P < 0.01$) (Table 4.2). Inspection of the above ratios suggested that this variation was mainly due to a bias towards adults and yearlings (Table 4.2). The age structure during this period did not vary between years (χ^2 = 15.7, df = 12, $P > 0.05$). After the calving period, the population consisted of adults, 16-24 months old animals, 10-15 months old animals, 4-9 months old juveniles and 0-3 months old calves in the ratio of 82:7.3:10:1:32.3 respectively. This population age structure composition differed

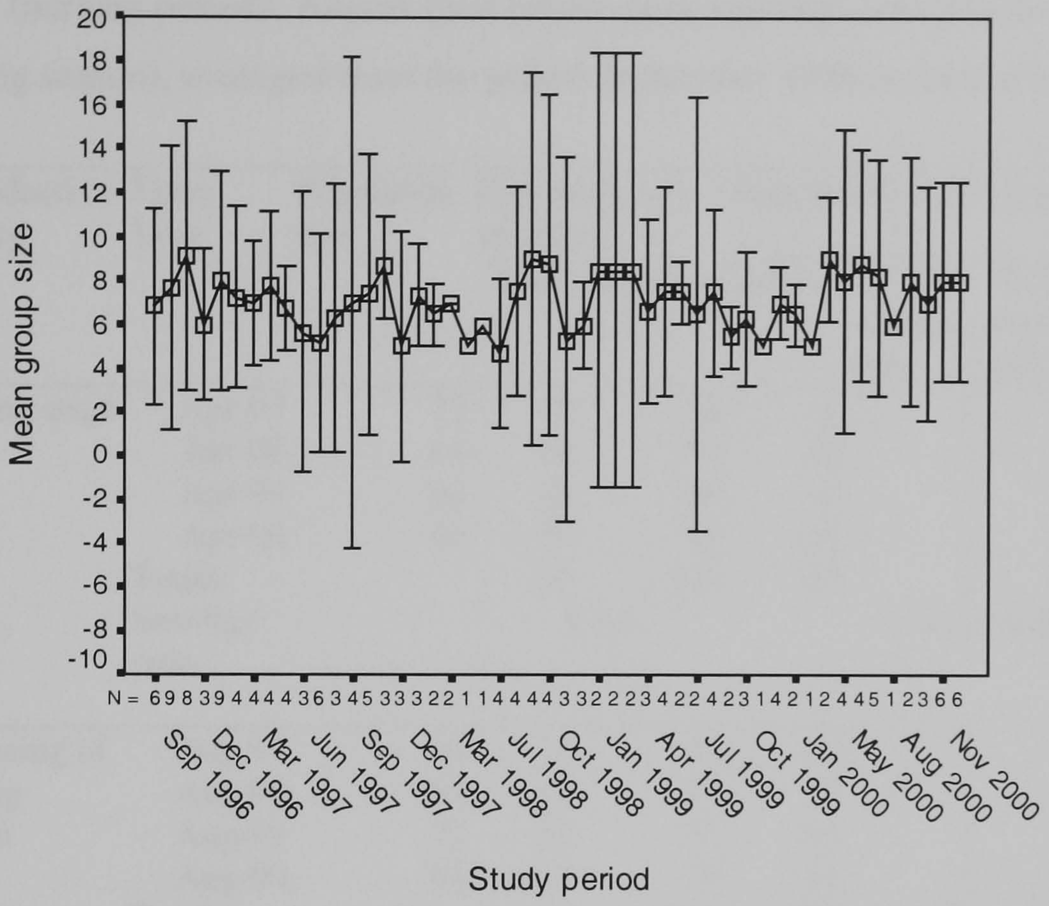


Figure 4.3: Overall variation in the total number of hirola per group in Tsavo East National Park between 1996 and 2000. Values are means ± SD.

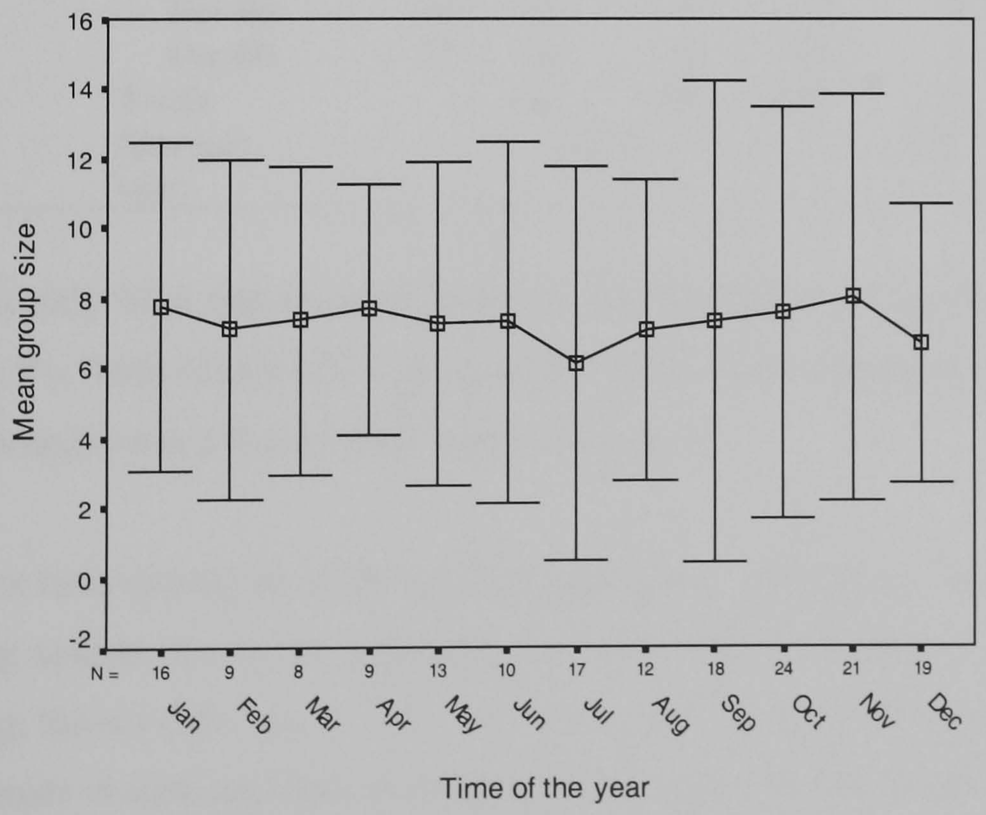


Figure 4.4: Overall annual variation in the total number of hirola per group in Tsavo East National Park between 1996 and 2000. Values are means ± SD.

Table 4.2: The sex and age structure of the Tsavo hirola population during the months of April (nursing period), August (just before peak calving), and December (just after peak calving season), averaged from the period September 1996 to December 2000.

Reproductive activity	Time/ Year	Population size	Population sex structure		Population age structure				
			Male	Females	Adults	16-24 months olds	10-15 month olds	4-9 months olds	0-3 month olds
Nursing stage	Apr-97	72	15	56	52	1	5	11	3
	Apr-98	64	15	49	48	1	2	9	4
	Apr-99	64	16	49	45	0	3	17	0
	Apr-00	62	20	42	42	1	9	10	0
	Totals		66	196	187	3	19	47	7
	Sex/Age ratio		1:3.0		63.3:1:6.3:15.7:2.3				
Beginning of calving season	Aug-97	59	14	45	45	1	13	0	0
	Aug-98	69	16	55	51	6	10	0	2
	Aug-99	72	21	52	44	7	20	1	0
	Aug-00	64	17	49	42	5	17	1	0
	Totals		68	201	182	19	60	2	2
	Sex/Age ratio		1:3.0		91:9.5:30:1:1				
End of peak calving season	Dec-96	90	24	66	53	3	11	0	23
	Dec-97	88	23	65	55	5	7	0	21
	Dec-98	77	22	55	47	7	3	1	19
	Dec-99	66	18	47	44	2	4	0	16
	Dec-00	77	24	51	47	5	5	2	18
	Totals		111	284	246	22	30	3	97
	Sex/Age ratio		1:2.6		82:7.3:10:1:32.3				

significantly from that expected from the null hypothesis of equal number ($\chi^2 = 1974.2$, df = 4, $P < 0.05$) (Table 4.2) and inspection of the ratios suggested that the main source of this variation was a bias towards adults and calves.

The sex ratio among the entire hirola population was biased towards females. Before the calving season, the hirola population sex ratio was 1 : 3 (male : female) whereas after calving, the sex ratio was 1 : 2.6. A comparison with the null hypothesis of equal number of animals in each sex class showed that the population was biased towards females both before ($\chi^2 = 7.9$, df = 1, $P < 0.01$) and after calving ($\chi^2 = 4.9$, df = 1, $P < 0.05$) (Table 4.2).

A comparison of sex ratio variation between years showed no variation either before ($\chi^2 = 0.84$, df = 3, $P > 0.05$) or after calving ($\chi^2 = 0.84$, df = 3, $P < 0.05$).

4.2.3 Calving

Records of new calves were collected during routine visits to groups. However, some females lost their calves soon after birth. For example, in October 1997, a female from the M1 group gave birth and lost her calf after 6 days, in November 1998; a female from the VR group gave birth and lost her calf after 3 days and in August 2000, a newly calved young female lost her calf after a day. Such losses raised problems in assessing calving rates because some hirola groups such as MK, B1, B2, and A3, were generally difficult to locate and some calves undoubtedly died before they could be recorded. It was easy to assess pregnancy in mature hirola females as gravid individuals looked rather emaciated with protruding ribs and sunken bellies. However, such assessments were less clear on younger females, and so it was difficult to tell if a young female had produced and then quickly lost a calf to predators. This source of bias was confirmed by a positive correlation between the number of sightings of each hirola group during the calving season and the number of calves recorded from each group (Pearson $r = 0.342$, $n = 45$, $p < 0.05$, Figure 4.5). Thus the number of calves recorded were an underestimate of the total number born. The number of calves recorded per year in Tsavo ranged from 16 (in 1999) to 23 (in 1996), with a mean of 18.3 ± 2.8 (± SD, n = 5). These apparent calving rates (calves per adult female) varied between years from a minimum of 0.48 (in 1999) to a maximum of 0.53 (in 2000). Overall, recorded calving rate was 0.51 ± 0.017 (n = 5, ± SD), (Table 4.3). Adult females generally appeared to be in excellent condition (except when they were lactating) and, if it is assumed that all adult females calved, then about 48.6% of calves born would have died before they could be detected.

Hirola had a distinct calving season in Tsavo. Calving occurred between August and March each year with a peak in November and October (Figure 4.6). Calving coincided with the average period of onset of the short rains. However the short rains were extremely variable, sometimes starting late and sometimes occurring only sporadically. As a result, calves were often born in dry conditions with little or no fresh grass or water, or shade, for both the calves and the lactating females. Females could give birth and

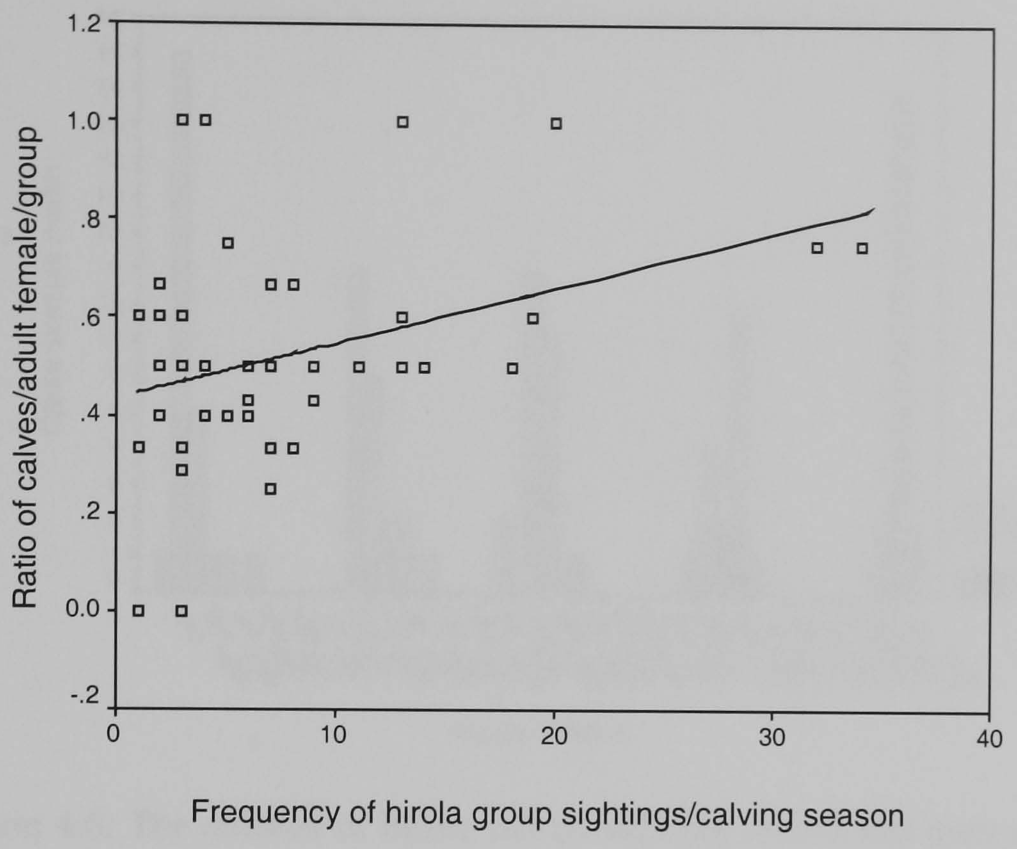


Figure 4.5: Relationship between the frequency of sighting of Tsavo hirola family groups in realtion to the ratio of calves per adult females per group. The relationship suggests that some calves were missed when groups were observed less frequently.

Table 4.3: Annual births, deaths and recruitment of hirola in Tsavo between 1996 and 2000.

Factor	Sex	Year					Total
		1996	1997	1998	1999	2000	
No. of births	Female	15	15	12	9	12	63
	Male	8	6	7	7	6	34
	Totals	23	21	19	16	18	97
No. adult females		44	41	37	33	34	
Calving rate		0.52	0.51	0.51	0.48	0.53	
Mortality (upto 6 months age)	Female	9	8	5	5	2	29
	Male	3	2	3	2	1	11
	Totals	12	10	8	7	3	40
Recruits (survival to 2 years +)	Female	2	5	3	3	5	18
	Male	3	3	4	4	3	17
	Totals	5	8	7	7	8	35

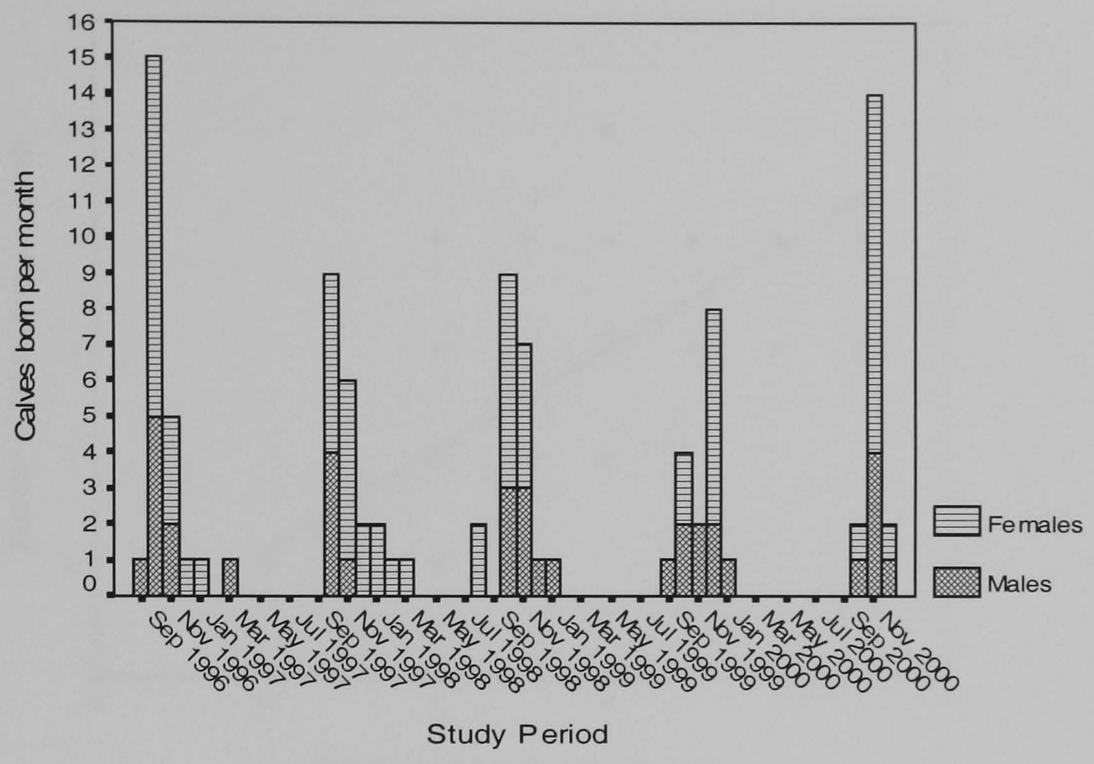


Figure 4.6: The number of hirola calves born per month and their sex ratio in Tsavo East National Park between September 1996 and December 2000.

remain for up to a month without significant rainfall. During these periods, fewer calves survived and lactating females often looked emaciated.

The sex of all calves seen was recorded and sex ratios were calculated (see Chapter III, section 3.2.1.3).). Overall, calf sex ratio was 1 : 1.85 (males : females) (Table 4.3). A comparison with the null hypothesis of equal number of calves in each sex class showed that calf sex ratios did not differ significantly from unity ($\chi^2 = 0.129$, df = 1, $P > 0.05$). There was also no significant differences in sex ratio between years ($\chi^2 = 1.065$, df = 5, $P > 0.05$). Similarly, offspring sex ratio did not differ among the family groups ($\chi^2 = 8.26$, df = 9, $P > 0.05$).

Calving rates showed large variation between groups. As expected, the number of calves per group per year was related to the number of adult females (Pearson $r = 0.83$, $n = 72$, $P < 0.01$, Figure 4.7). However, there was considerable unexplained variation in calving among different groups (Figure 4.8) which will be considered later (Chapter **VII**). The number of calves per group ranged from 1 to 4, with an average of 2.1 ± 0.9 (± SD).

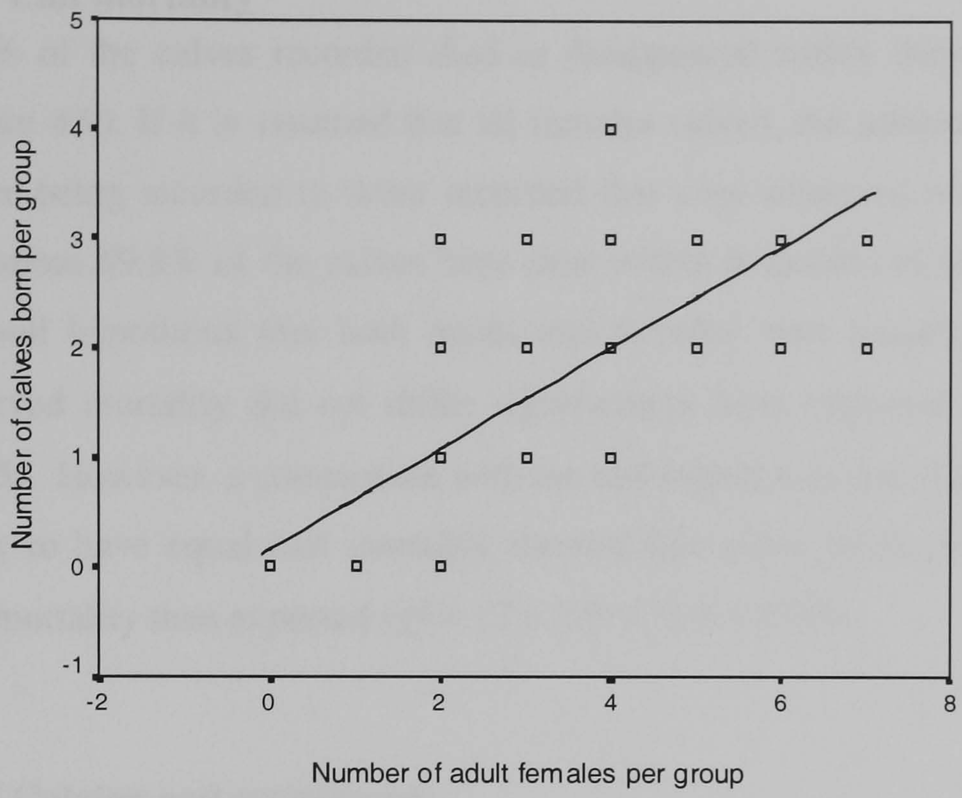


Figure 4.7: Relationship between the number of calves born per group and the number of adult females per family group in Tsavo between September 1996 and December 2000.

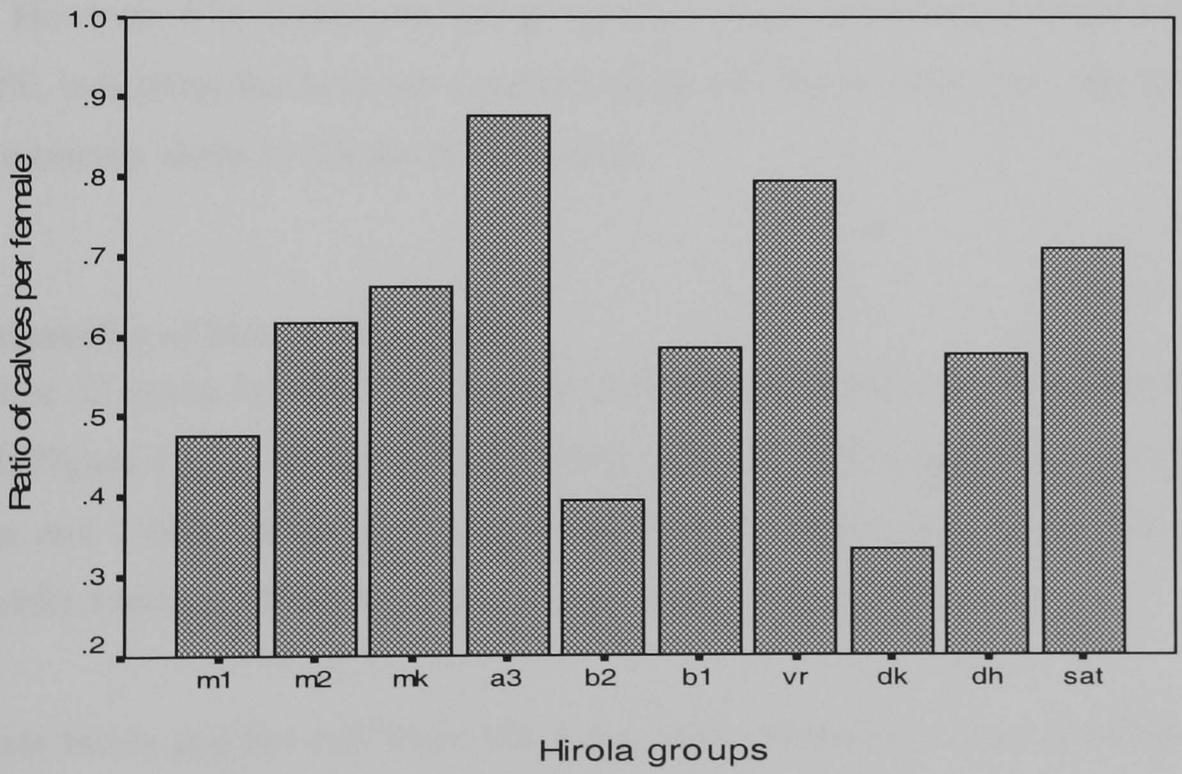


Figure 4.8: Variations in calving rates per hirola family group in Tsavo between September 1996 and December 2000.

4.2.4 Calf mortality

41.2% of the calves recorded died or disappeared within their first six months of life (Figure 4.9). If it is assumed that all females calved, the addition of the calves that died before being recorded to those recorded that were observed would lead to the estimate that about 69.8% of the calves born died within 6 months of birth. A comparison with the null hypothesis that both males and females were equally likely die showed that observed mortality did not differ significantly from expected ($\chi^2 = 0.776$, DF = 4, $p > 0.05$). However, a comparison with the null hypothesis that different hirola groups were likely to have equal calf mortality showed that some hirola groups experienced higher calf mortality than expected ($\chi^2 = 17.6$, DF = 9, $P < 0.05$).

4.2.5 Calving and recruitment

Observations on hirola groups indicated that for most of the time, the groups were predominantly composed of adult individuals. After the calving season young of less than a year old were added. Very few young adults were observed among groups. If only the calves observed are considered, then about 34.9% survive to maturity (Figure 4.10). However, if it is assumed that all females calved, recruitment would be estimated at 18.0%, indicating that between 6 months of age and about 2 years age (the notional age of recruitment), about 13.2% more hirola died.

4.2.6 Mortality of known individuals

A total of 52 hirola from 10 groups were identified and monitored (Chapter III, section **3.2.1.3**; Figure 4.11). By the end of the study period, 6 (2 adult female, 2 two year old females and 2 male calves, see section **4.2.1**) of the known individuals were killed by lions while a further 14 had disappeared and could not be accounted for.

A female hirola and her calf from VR group were observed to have diarrhoea but they recovered. Loss of individuals from groups occurred during the months of February and March (dry season) and October-November (short rains/calving season; Figure 4.11). A comparison of the sex and age structures of individuals dying and those alive indicated significant differences between sexes ($\chi^2 = 5.398$, DF = 1, $P < 0.05$) with a bias towards males and no difference between the ages ($\chi^2 = 0.294$, DF = 2, $P > 0.05$).

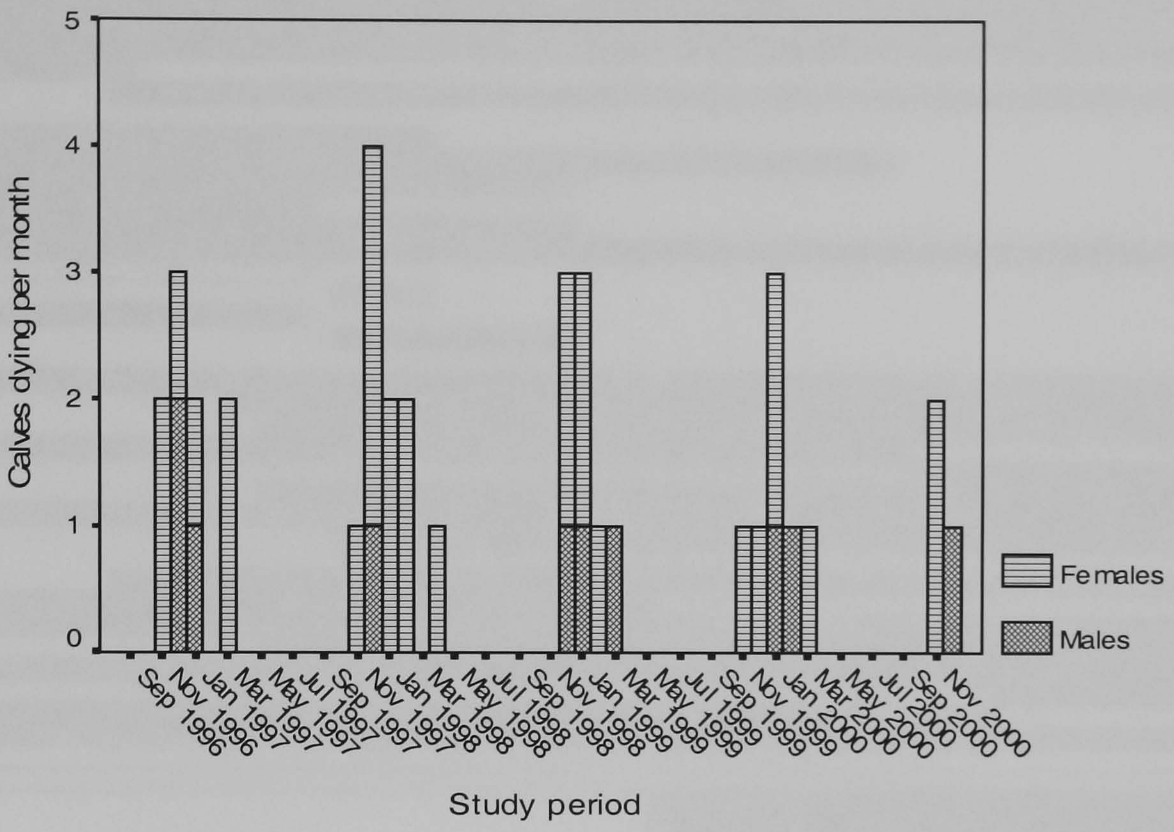


Figure 4.9: The number of hirola calves dying per month and their sex ratio in Tsavo East National Park between September 1996 and December 2000.

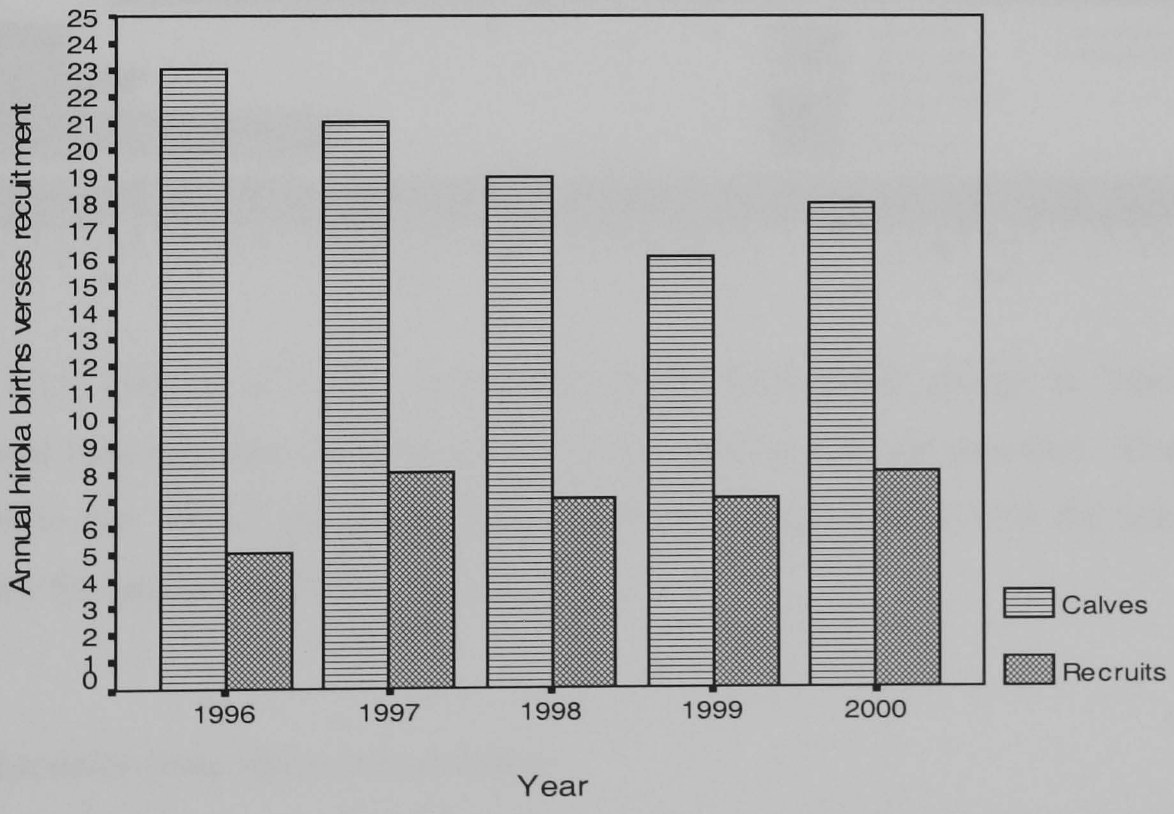


Figure 4.10: The annual numbers of hirola calves born and the numbers that recruited (ie those that survived to 2 years old) in Tsavo East National Park between September 1996 and December 2000.

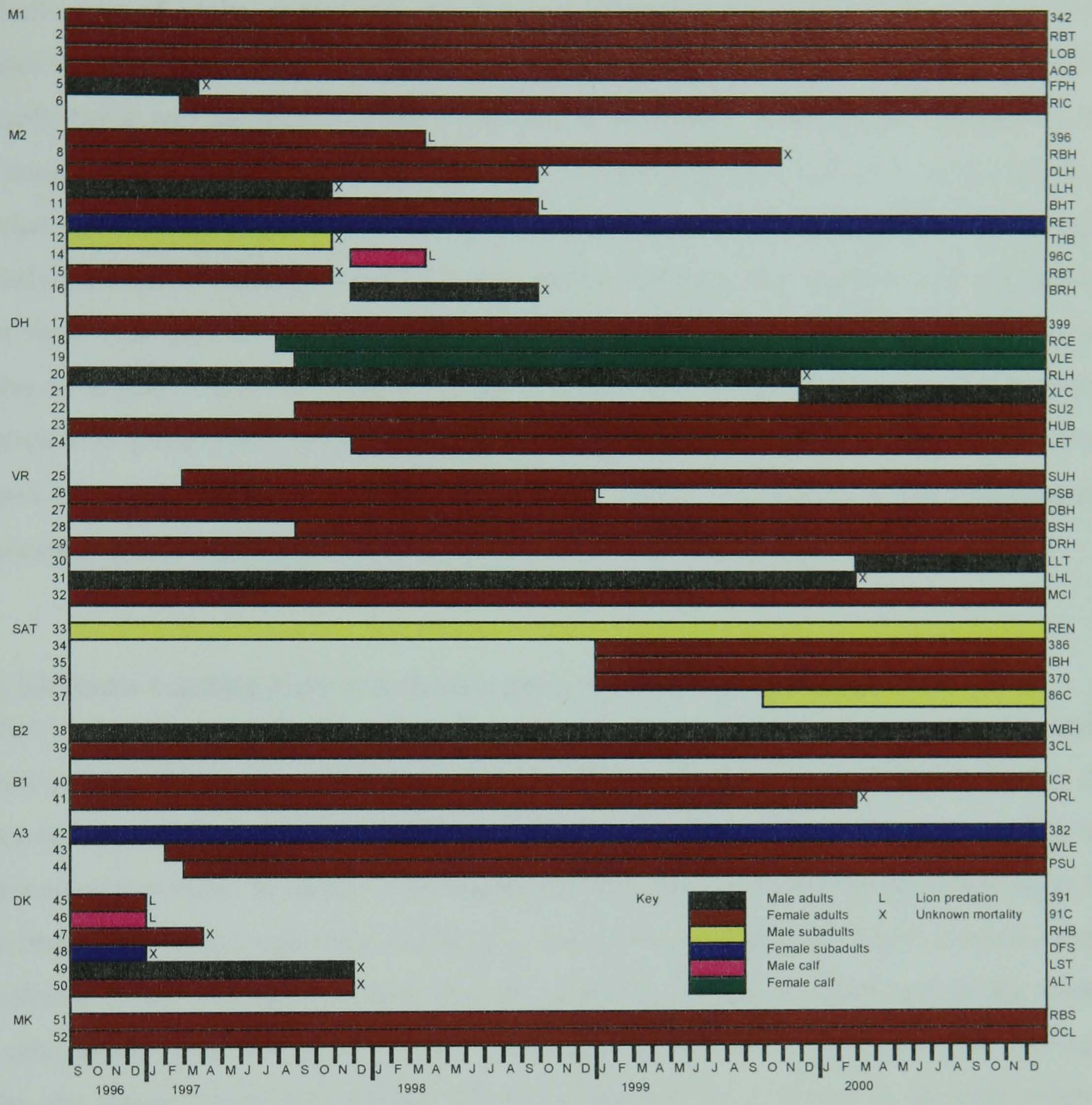


Figure 4.11: History of known hirola individuals from hirola groups in Tsavo East. Horizontal bars represent the period over which each animal was recorded. Codes and numbers to the left of the graph denote individual identification and the transmitter frequency for radio-collared individuals.

4.2.7 Mortality from observed carcasses

A total of 24 skulls were collected in Tsavo over the study period (Figure 4.12). The distribution of skulls found were not correlated with sightings of lions per hirola range (Pearson $r = 0.491$, n 9, $p > 0.05$), cheetahs (Pearson $r = 0.489$, $n = 9$, $p > 0.05$), leopards (Pearson $r = 0.516$, $n = 9$, $p > 0.05$), or hyaenas (Pearson $r = 0.572$, $n = 9$, $p > 0.05$). All skulls were of adults, except one of a 2 year old female. The skulls were easier to find after the 1998 fires, which reduced bush and grass cover. Most of the skulls were old and partly burnt and the time of death could not be effectively determined. The skulls of young animals were rarely found, probably because they were soft and easily eaten or otherwise destroyed. I recorded two cases in which an adult female and calf were killed. Only the skull of the adult female could be found, subsequently, together with fragments of skull from the calf. A comparison of the null hypothesis that the number of carcasses should simply reflect variation in group size (ie that deaths occurred randomly with respect to group size), showed that there was significant variation in carcass numbers between group ranges ($\chi^2 = 16.394$, $DF = 8$, $P < 0.05$). The source of this variation is considered in Chapter VIII.

4.2.8 Radio-tracking lions and cheetah and prey selection behaviour

Two lionesses, one from the Aruba Dam lion pride (1 adult male, 5 adult females, and two cubs) and the other from the Satao Camp pride (1 adult male, 6 female adults, 2 female subadults, 1 male subadult, and 4 cubs), were radio-collared and monitored for a period of 8 months. In addition to the lions, a female cheetah from a group of 4 (1 adult 1 subadult male and 2 subadult females) was collared and monitored. These animals were collared at the beginning of the long wet season in February 1999 and prides were continuously monitored up to the end of the long dry season in September 1999. During the dry season, lions tended to stay close to the major water bodies, particularly Aruba dam and Satao Camp waterhole. The water points attracted concentrations of water dependent prey species and also provided water for the lions. During this dry period, the large groups of zebra, oryx, Coke's hartebeest, elephants, buffaloes, and eland that were previously present, migrated to the hilly parts of Kulalu ranch and to the Taita/Ndara ranch. These areas received more rainfall than the hirola range and were thus greener, and, had plenty of uniformly distributed artificial water sources to support their cattle. In contrast, during the wet season, most potential prey, in addition to the returning migratory species, dispersed as water and forage were widely distributed. Thus lions could afford to use small ranges in the dry season. In the wet season, they had to forage more widely in order to encounter dispersed prey. Radio tracking data showed that both lion prides used much bigger areas in the wet season (57.22 ± 3.73 SD km^2) than during the

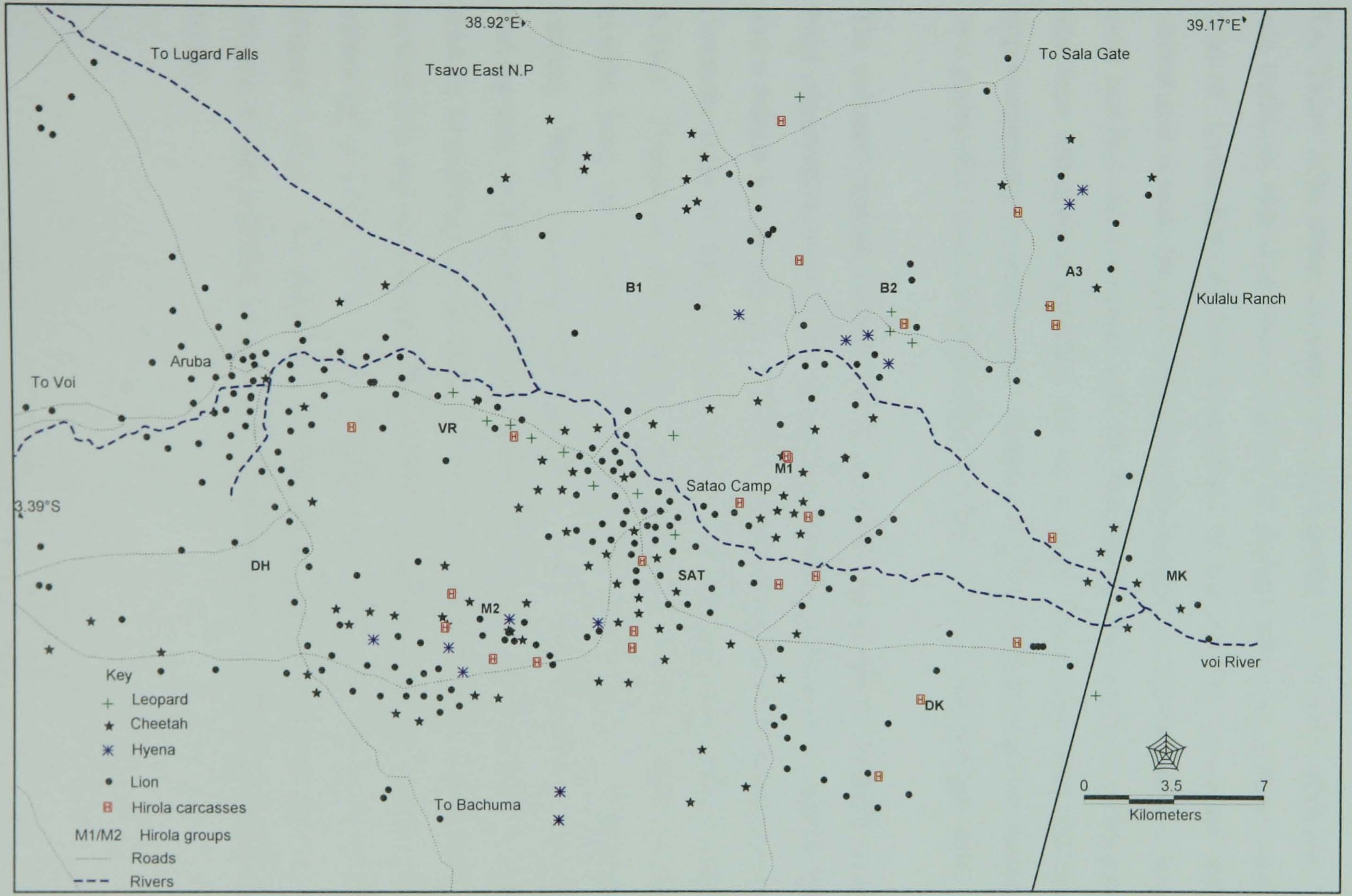


Figure 4.12: The location of hirola carcasses in relation to overall predator sightings in Tsavo East NP over the period September 1996 to December 2000.

dry season (30.01 ± 7.74 SD km^2) (Figure 4.13). The collared cheetah wandered extensively and because of the low frequency of encounters, seasonal ranging area could not be established; however, radio locations indicated a total ranging area of 701.6 km^2 (Figure 4.13). Collars were removed at the beginning of October 1999 because the transmitters had started failing and because the general public does not approve of seeing lions and cheetah with collars.

The Tsavo lions often scavenged on dead animals, especially elephants, hippos, giraffe and buffaloes that died from a variety of causes, including getting stuck in the drying mud of Aruba dam, disease or poisoned arrow wounds, (sustained while roaming in settled area outside the park during the dry season), or from traditional poachers. A lone male lion that was associated with the Satao pride male was seen picking up a dikdik that had been killed by a speeding van on a road. The Tsavo lions and cheetah also fed opportunistically on small prey. I observed a female lion from the Aruba pride feeding on a guinea fowl and a cheetah chasing a flock of yellow-necked spur fowl.

The collared cheetah ranged widely and close observations on kills were not possible. Four observations were made: a yearling female waterbuck, two young Grant's gazelles and a mature female impala. Collared lions were found feeding on or resting near fresh carcasses from 11 different prey species. 47 such carcasses were encountered (Figure 4.14a). Though no direct hunting and killing was observed, signs of the struggle was evident from the ground and from teeth and claw scratches on uneaten parts of the carcass. When camping at Satao Camp, I also sometimes heard the sounds of lions making kills (including the groaning of a buffalo being strangled). A comparison of the relative availability of the prey species as measured from road transect (Chapter III, section 3.5) and the number killed by lions indicated that some species were preferred to others ($\chi^2 = 19.72$, df = 8, $p < 0.02$), with buffalo and zebra constituting most prey (Figure 4.14a). An inspection of the lion carcasses indicated that most were adults (Figure 4.14b) and that a wider variety of species were killed in the dry season (Figure 4.14c).

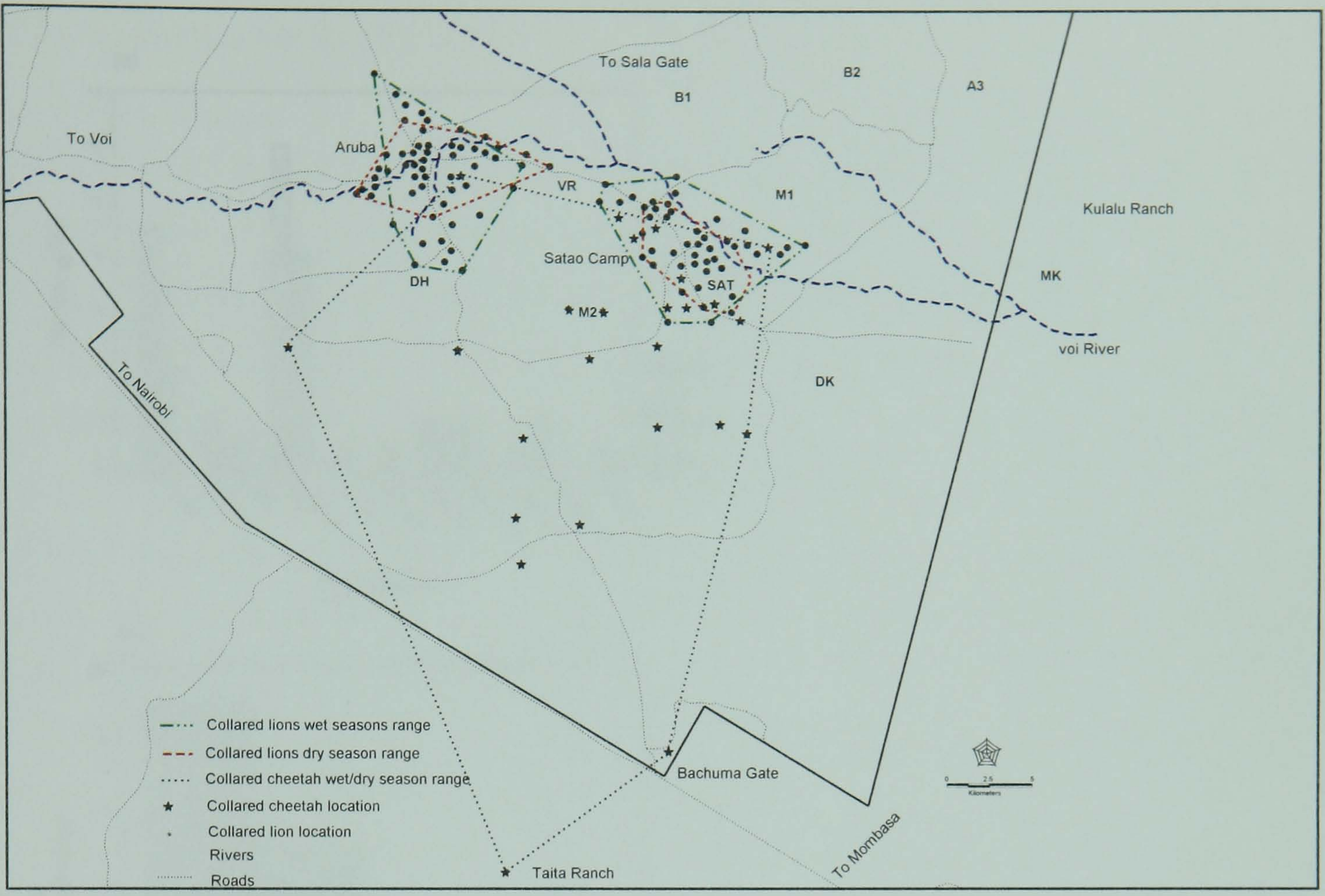


Figure 4.13: The ranges of radio-collared predators in the Tsavo East NP in the wet and dry season in relation to the location of hirola family groups between February and September 1999.

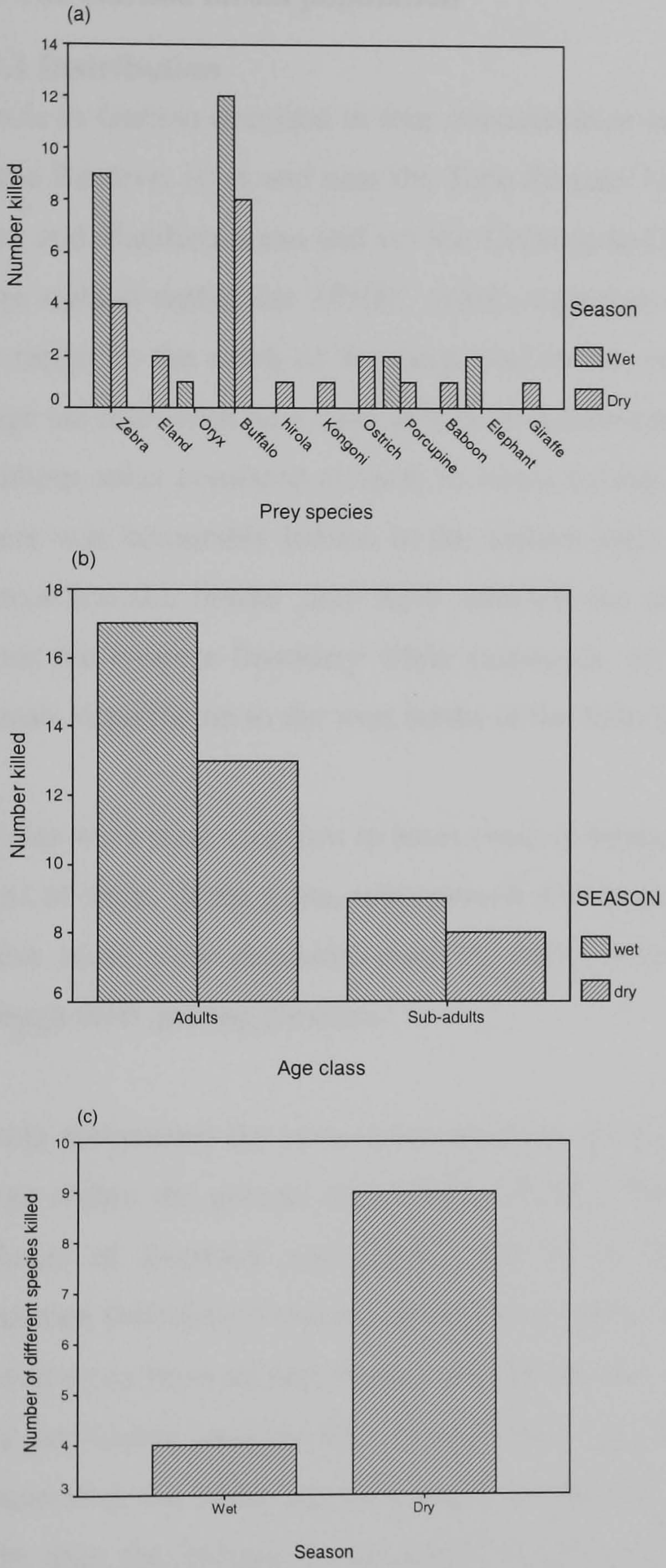


Figure 4.14: Prey selection by the prides of radio-collared lions in Tsavo Esat NP between February and September 1999. The graphs show (a) the range of species killed in the wet and dry season; (b) the age structure of the animals killed and (c) a comparison of the numbers of species killed in the wet and dry season. The data were collected between February and September 1999.

4.3 The Garissa hirola population

4.3.1 Distribution

Hirola in Garissa occurred in four concentration areas, namely i) to the south of Arawale Game Reserve, ii) in and near the Tana Primate National Reserve (TPNR), iii) the Roka, Ijara and Handaro areas and iv) the Galmagala-Gubis areas (Figure 4.15). Most hirola were sighted within the TPNR. Hirola sightings declined as one moved to the north of the range, to the south of the range and to the extreme east. The northern parts of the range are drier with bare open ground and clustered bush/shrub cover. The habitat of the southern areas consisted of bush to forest habitat interspersed with glades of tall grass. There was favourable habitat in the eastern areas but incidences of poaching along the Kenya-Somalia border may have affected the distribution of hirola. The Tana River forms the western boundary while eastwards, the natural hirola range extends into the Somali Republic up to the west banks of the Juba River.

Hirolas were most common in areas close to human settlements. They appeared to prefer areas of short, green grass, interspersed with bushes for shade and cover (Chapter **VII**). These areas were regularly used by cattle, which maintained the short grass habitat through their grazing pressure.

Hirola maintained the same concentrations across the seasons, but made slight shifts in range within the general area (Figure 4.16). These shifts appeared to be caused by i) influxes of livestock and people, and ii) by patchy rainfall. The pastoral Somali herdsmen shift their livestock in search for green pasture and water and hirola sometimes moved away from an area when livestock moved in. They generally moved either to the area previously used by the livestock or to an adjacent new area. Alternatively, they remained in the same area and spent the daylight hours in nearby areas of bushes. At night after the livestock were herded to the night camps (bomas) the hirola grazed in same areas that were used by the livestock). This degree of overlap probably created severe competition during the extreme dry season when livestock had to be grazed for extended periods and sometimes even at night.

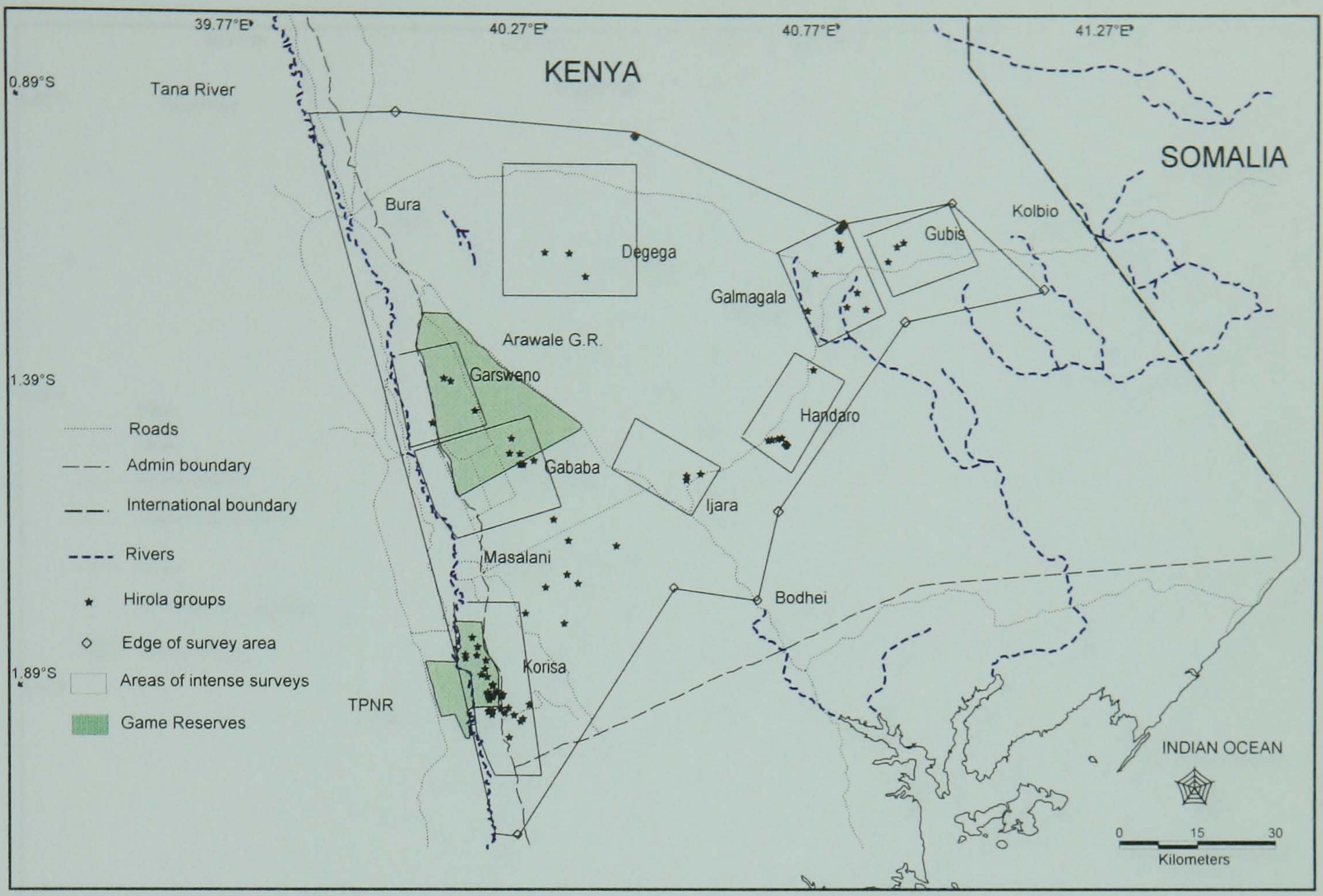


Figure 4.15: Map of Garissa area showing overall hirola distribution, concentration sites, and sampling blocks (residential sites for individual hirola scouts) between June 1996 and August 2000.

4.3.2 Population size

During my visits to the hirola natural range in Garissa, I attempted to visit and search every region in which hirola had been sighted or known to occur. However, these searches were limited and constrained by the danger from armed gangs in these areas, and sometimes by lack of access paths. The ground data were complemented by opportunistic visits to the region with KWS pilots on either security or other missions. In order to estimate the overall population size in Garissa, ground census data from 8 sites (namely Degega, Garsweno, Gababa, Korissa, Ijara, Handaro, Galmagala, and Gubis Figure 4.15) was used. These sites covered the entire hirola range and were reported on by hirola community scouts, who had a detailed knowledge of local hirola distribution. Using information about the location of hirola groups provided by the hirola scouts, a unit area was sampled at each location and all hirola encountered were counted. Every sampling block (Figure 4.15) was thoroughly surveyed at least once over the study period.

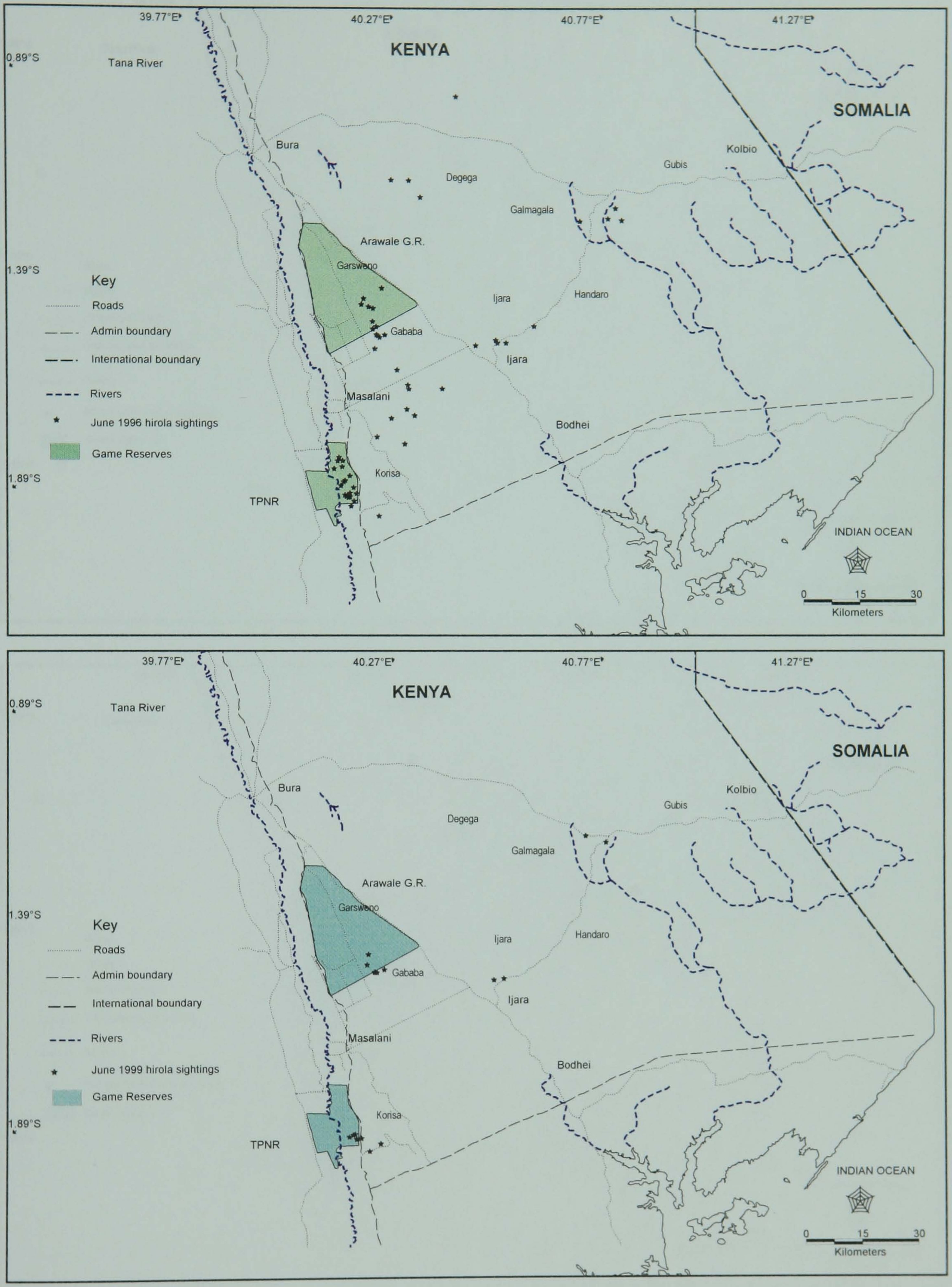


Figure 4.16: Sighting of hirola in the Garissa area during different survey periods. The occupation of Arawale G.R. and TPNR at different seasons indicates local seasonal movements of hirola groups.

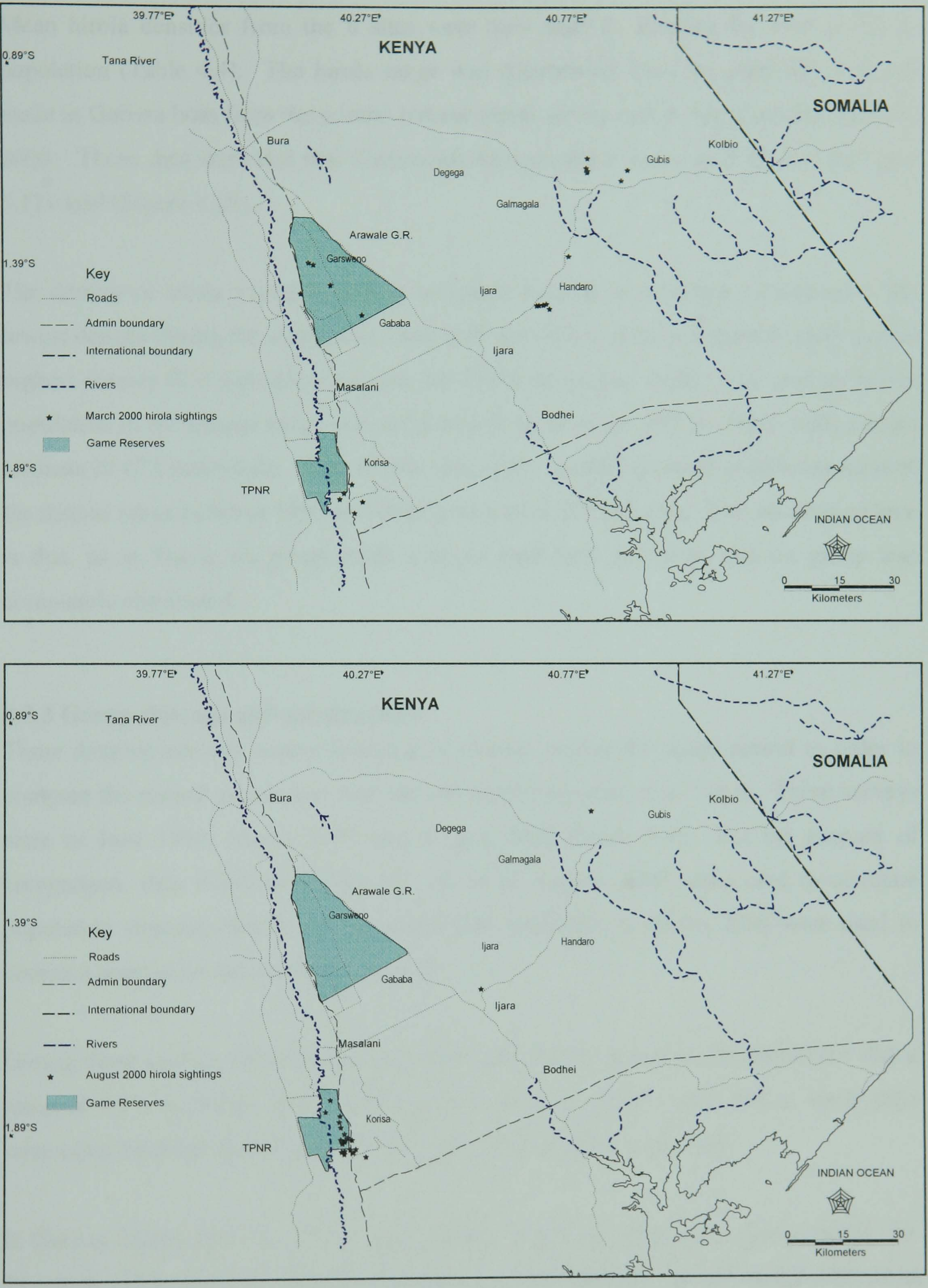


Figure 4.16: Cont.

Mean hirola densities from the 8 sites were then used to estimate the Garissa hirola population (Table 4.4). The hirola range was determined from the sightings of hirola made in Garissa both from the ground and the aerial survey carried out between 1996 and 2000. These data indicated that Garissa hirola occurred over an area measuring about 5,171 km^2 (Figure 4.15).

The density of hirola varied according to season because of seasonal movements. The lowest density during the study period was 0.02 hirola/km^2 at Bura in March 2000 and the highest density 0.53 hirola/km^2 around the TPNR in August 2000. The average hirola population in the natural range was estimated to be between 259 and 1085 with a mean estimate of 672 individuals. Overall, the sum of the animals counted in different parts of the natural range between 1996 and 2000 gave a total of 618 hirola. The assumption here is that, as in Tsavo, no group made a major shift from its range, and no group was completely eliminated.

4.3.3 Group size, age and sex structure

Three detailed surveys were conducted in Garissa during the study period in order to compare the natural population with the introduced population in Tsavo. These surveys were in June 1999, March 2000 and August 2000 (Table 4.4). For the purpose of comparison, data collected during the month of August 2000 were used to compare population structure before calving while data collected in March 2000 were used to compare population structure after calving.

During these surveys, the hirola groups sighted ranged from one to 25 individuals with a mean of 7.9 ± 4.15 SD. Single individuals sighted were often adult males, while pairs were often a mother and its young or an adult female and an adult male.

In Garissa, before the onset of calving, the population was found to consist of adults, 16-24 month old animals, 10-15 month old animals, 4-9 month old and 0-3 month old calves in the ratio of 24:7.6:7.8:1.6:1 respectively. Comparing these data with the null hypothesis of equal number of animals in each age class showed significant variation

Table 4.4: An analysis of hirola sampling sites showing numbers and densities during different sampling times in Garissa. (Gps = Number of hirola groups sighted, Nos = Total numbers of hirola seen, mGps = mean group size, Dty = Density per site)

Sampling Sites	Area (Km²)	June 1999				March 2000				August 2000				Mean Density
		Gps	Nos	mGps	Dty	Gps	Nos	MGps	Dty	Gps	Nos	MGps	Dty	
Korisa	350	8	53	6.6	0.15	3	14	4.6	0.04	17	151	8.9	0.43	0.21
Gababa	428	6	60	10	0.14	-	-	-	-	-	-	-	-	0.14
Garsweno	198	-	-	-	-	4	27	6.8	0.14	-	-	-	-	0.14
Bura	580	-	-	-	-	4	19	4.8	0.03	-	-	-	-	0.03
Ijara	172	2	15	7.5	0.09	3	14	4.7	0.08	3	25	8.3	0.15	0.11
Handaro	172	-	-	-	-	5	48	9.6	0.28	-	-	-	-	0.28
Galmagala	310	2	19	9.5	0.06	4	21	5.3	0.08	3	34	11.3	0.11	0.06
Gubis	208	-	-	-	-	2	9	4.5	0.04	-	-	-	-	0.08
Summary		18	147	8.2		25	152	6.1		23	210	9.1		0.13

between age classes (χ^2 = 907.9, df = 4, P < 0.01). Inspection of the above ratios suggested that this variation was mainly due to a bias towards adults and yearlings. Comparable data were collected in Tsavo at the same time and showed that the two populations had similar age structure (χ^2 = 7.637, df = 4, P > 0.05). Data collected from Garissa at the end of March 2000, showed that the population consisted of adults, 16-24 month old animals, 10-15 month old animals, 4-9 months old and 0-3 month old calves in the ratio of 45:1:7:16.5:1 respectively. This population structure composition differed significantly from that expected from the null hypothesis of equal number (χ^2 = 756.9, DF = 4, P < 0.01) and inspection of the ratios suggested that the main source of variation was a bias towards adults and 4 – 5 months olds. This age structure did not differ significantly from that recorded from the Tsavo hirola population during the month of March 2000 (χ^2 = 5.11, df = 4, P >0.05).

Data from Garissa on all individuals indicated that the sex ratio was 1:2.9 (male:female) before calving and 1:3.8 after calving. A comparison with the null hypothesis of equal numbers of males and females showed that the population was biased towards females both before (χ^2 = 5.5, df = 1, P < 0.05) and after the calving (χ^2 = 8.9, df = 1, P < 0.01). A comparison of the sex structure between the Garissa and Tsavo hirola population revealed no differences either before (χ^2 = 0.0, df = 1, P > 0.05) or after calving (χ^2 = 2.8, DF = 1, P > 0.05). Observations on hirola calves indicated a sex ratio of 1 : 1.8 (Males to females). This ratio did not differ from the expected 1:1 distribution (χ^2 = 0.125, df = 1, P > 0.05). The ratio of calves to adult females in Garissa was 0.46, while the ratio of 2 year olds (recruits) to adult females was 0.19.

4.3.4 Mortality and causes

Data on the causes and levels of mortality in the hirola natural range was collected at 4 monthly intervals from March 1998 to August 2000 (Table 4.5). Information was acquired by debriefing the local hirola community scouts in different localities in the hirola natural range and by going to the site to confirm a sample of the reports whenever possible. From the data obtained in this way, a total of 90 hirola were known to have died during the study period. According to the hirola community scouts records, the causes of mortality were poaching (24.4%), predation (37.7%) and disease (37.7%).

Table 4.5: The numbers of hirola reported to have died as a result of poaching (a), predation (b) and disease (c) in Garissa between March 1998 and August 2000. Information was provided by the Garissa community hirola scouts.

Sites	Mar - Jun 1998			Jul - Nov 1998			Dec 1998 –Feb 1999			Mar - Jul 1999			Aug - Nov 1999			Dec 1999 -Mar 2000			Apr – Aug 2000		
	a	B	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	C
Galmagala	0	0	1	2	4	8	0	0	2	2	2	0	1	0	0	0	1	0	0	0	0
Gubis	0	0	0	1	1	4	0	0	0	0	2	0	1	0	1	5	0	3	1	4	0
Ijara	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	1
Bura	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Handaro	0	1	3	0	2	1	0	0	0	0	1	0	0	2	0	1	2	0	0	0	0
Gababa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Garsweno	1	0	0	0	0	4	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0
Korisa	3	0	0	0	2	4	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0
Totals	4	3	5	3	9	21	0	1	2	2	6	1	2	3	1	6	4	3	5	8	1

According to the hirola community scout records, poaching of hirola was mainly carried out by armed Somali bandits (36.4%), the Kenya Police Reserve (KPR) (27.3%), the administration Police (AP) (31.8%), and the Kenya Army (4.5%). A total of 34 hirola were reported to have been kiled by predators during the study period. Predation by lions was reported to have contributed 79.4% while hunting dogs contributed 20.6%. These figures may have been an overestimate because diseased animals (see below) would have become vulnerable to predation or scavenged by predators after they were dead.

Observations made by hirola community scouts on hirola that died of disease soon after the El-Nino rains (the period after June 1998) indicated that they showed similar symptoms. The affected animals rapidly lost weight, had a nasal discharge and were soon unable to walk. When in this condition, they were quickly infested by ticks (red ear ticks) and were exposed to predation. According to the Gubis community hirola scout, a male hirola, that developed this condition in the backyard of his homestead (manyatta) was later killed by lions. Two further sick and disabled female hirola within the same area were later found dead and hyaenas were feeding on the carcasses. The scout was not able to establish whether the hirola had died and the hyaena was just scavenging or if the hyaena had finally killed them. Four other hirola were observed with similar symptoms but their fate was not determined. However a total of 21 carcasses were recovered by the community hirola scouts during the same period. Similar conditions were reported in livestock and other wildlife (buffalo, kudu, and topi). Sick and disabled livestock were kept under shade within the manyatta, where they could be guarded from predators, sprayed to kill ticks, provided with food and water, and treated with antibiotics (tetracycline). Some recovered after a while, but the weak animals died. The local community's outcry, because of their dying livestock prompted the investigation of the problem by the Kenya Veterinary Department and Kenya Wildlife Service, in collaboration with the local NGOs working in the area. According to Dr. Richard Kock's report to the Hirola Management Committee, blood samples collected from sick cattle indicated foot and mouth disease, though the possibility of other diseases such as rinderpest, East Coast Fever (ECF), trypanosomiasis, and contagious bovine pleuro-pnumonia (CBP), that are prevelant within the hirola natural range were not ruled out.

4.4 Conclusions

Research on introduced species, such as the Tsavo hirola population, have shown that they may increase in both numbers and range if the new environment is suitable (Channell & Lomolino, 2000). However, observations on the Tsavo hirola population show that the population has grown very slowly since its introduction nearly 40 years ago and that it is approximately stable. At the end of the study period, there were a total of 8 stable groups. Initially, 9 groups existed, but after predation on the DK and M2 groups, the surviving members dispersed and were never found again. Luckily a new group, SAT, was formed from a founder group of one adult male, one adult by predation by lions. Tsavo hirola occur in distinct and separate groups to the east of Aruba Dam, south of Balguda, west of the Kulalu Hills and north of the Bachuma gate. The total population of hirola in Tsavo over the study period averaged 71 ± 9.3 SD and despite some fluctuations the population appeared to be essentially static. By December 2000, a total of 77 hirola existed in Tsavo. Surveys in Garissa indicated that the population size ranged between 259 and 1085 individuals with a mean estimate of 672, in an estimated area of 5,171 km^2. The main concentrations of hirola in Garissa were on the east bank in Tana Primate National Reserve, south of the Arawale Game Reserve, and in the Ijara/Handaro and Galmagala/Gubis areas.

Hirola family groups were stable in number except during the calving season when new calves caused small and usually temporary increases in overall numbers. In Tsavo, the animals most likely to be separated from social groups were the adult males and females with their calves or yearlings. Hirola group sizes varied from 2 to 15, with a mean of 7.3 ± 2.6 SD in Tsavo while in Garissa groups varied from 1 to 25 with a mean of 7.9 ± 4.15 SD. Thus group sizes were similar in size in Garissa and Tsavo.

As expected, the population showed a varied age structure with more young animals during the calving season and more adults at other times of year. The age structure of the populations in Tsavo and Garissa was similar both before and after calving. Similarly the population sex ratios were biased towards females before and after calving in both populations. However, calf sex ratios were equal in both populations.

Herbivore species tend to calve just before or during the rain season when there is enough forage for lactating females and for weaning calves. Hirola showed a distinct calving season with some calves appearing between August and March. However, peak calving occurred towards the end of November and the beginning of October in Tsavo. The similarity in age structure between the Tsavo and Garissa population indicated that they calved at the same time of year.

Between 1996 and 2000, the ratio of calves to adult females averaged 0.51 ± 0.017 SD in Tsavo. This indicated that at least half the adult females gave birth, although this may be an underestimate due to the loss of calves before they could be recorded. In Garissa, the ratio of calves to adult females was 0.46. The numbers of calves born per group varied between groups according to the number of females they contained. If it is assumed that all adult females calved, then about 69.8% of the calves born must have died within their first 6 months. Using the same assumption leads to an estimate that about 18.0% of calves survived to the age of 2 years, thus indicating that a further 13.2% of the hirola died between six months of age and their eventual recruitment.

Most predators, including lions, are territorial and thus hunt and kill what is available within their territories at different times of the year. Observations on predators in Tsavo indicated that lions and cheetah occurred commonly within the hirola range, although hyaena and leopard were also regularly sighted. Lions used slightly larger territories during the wet season when prey species dispersed and smaller areas, during the dry season when the non-migratory resident species concentrated around water holes. Observations on the carcasses of 6 known hirola indicated that they had been killed by lions. Losses due to predators (mainly lions) were the principle known cause of death in both adult and young hirola and by extrapolation may have been the main source of mortality in the population. Tsavo hirola were generally in good condition and they appeared to be very healthy. Only two hirola, a mother and calf, were observed to have diarrhoea but they soon recovered. .

The hirola range in Garissa occurs in pastoral community land. The population might thus be expected to be a affected by both natural and human induced factors. Clearly the human pressures would be expected to be more severe than those affecting a species in a designated conservation area such as Tsavo. Information from the community hirola scouts indicated that mortality was caused by poaching (24.4%), predation (37.7%) and disease (37.7%) over the study period. Bandits were reported to poach most hirola followed by government security personnel (i.e., Kenya Army, Kenya Police, Administration Police, Kenya Police Reserve), and the Pokomo tribesmen. Predation reports indicated that lions contributed 79.4% while hunting dogs contributed 20.6% of total hirola predation. The effect of predation may have been overestimated because some of the animals reported as killed by predators may have died as the result of disease and then scavenged or killed when weakened by disease. Foot and mouth disease was identified in sick cattle that showed similar symptoms to those that the hirola community scouts had observed among hirola. This disease and other unidentified disease/s that were carried by livestock have been responsible for a significant proportion of the observed hirola mortality.

Chapter V:
Social Organisation and Behaviour Patterns

5.1 Introduction

Relatively little is known about hirola behaviour in comparison to other large East African ungulates, as it has never been the subject of a long term, single species study until the current work. A Game Department biologist, A.D. Graham, commenced a three year study of the general biology and ecological requirements of the hirola in the early 1960s, but had to abandon it within a few months due to political unrest in Garissa (Grimwood, 1963). Much of what was known when I began this study was due to the work of W.T. Bunderson, who conducted research on the interactions between wildlife and domestic livestock in the hirola's natural range area between 1975 and 1978.

According to Bunderson (Bunderson, 1985), mature male hirola in Garissa occupy and actively defend territories in areas with good quality pasture; these territories are up to 7 km^2 in size. The territories are marked with secretions from the pre-orbital glands, smeared onto vegetation and the ground. In addition, males display on "stamping grounds". The soil at these sites is scraped with the hooves and marked with dung, and the vegetation is slashed with the horns (Kingdon, 1982; Andanje & Goeltenboth, 1995; Dahiye, 1999). Non-territorial males associate in bachelor herds of 2-38 animals (Bunderson, 1985).

In Garissa, family groups range from 5 - 40 with a mean group size of 7 - 9 (Bunderson, 1985; Kingdon, 1982) and are most often in the company of a mature male. Hirola groups are relatively sedentary, though they will move to another area as resources diminish (Kingdon, 1982). Mixed aggregations of breeding and bachelor herds numbering up to 300 may occur particularly at the end of dry season when isolated showers produce patches of green vegetation (Bunderson, 1985). However information is lacking on the relationships between territorial and/or bachelor males with the family groups. Studies have shown that male mammals show a diverse array of mating bonds, ranging from obligate monogamy to group polygyny and promiscuity (Clutton-Brock, 1989). Further, mammalian mating strategies may vary between populations or even individuals of the same species (Gosling, 1986; Langbein & Thirgood, 1989; Prins, 1996). Which male strategy is adopted will largely depend on the availability and distribution of resources, the density of females and/or males, and the degree of breeding synchrony (Emlen & Oring, 1977; Gosling, 1986; Clutton-Brock, 1989; Langbein & Thirgood, 1989). Since hirola are now limited to a few isolated areas, this may have a bearing on their mating strategies. Males may abandon active territory defence at low population densities and follow groups of females throughout their range, as is the case in Coke's hartebeest and other antelopes (Gosling, 1986). Further, information is lacking on the relationship between different family groups including the extent to which they exchange members and on the formation of new groups. Similarly, there is no account of the daily behaviour patterns of hirola groups.

5.2 Social organization

In Tsavo, groups were found predictably within well-defined geographical ranges, in which they made local movements in search for suitable microhabitats. The groups usually consisted of one mature male, a number of mature females and their offspring. In other cases, groups of bachelor males were detected (Figure 5.1). There were also various types of isolated individuals (see below) and sometimes females isolated with their calves. A total of 8 different types of hirola groupings were observed (Table 5.1).

Table 5.1: Total sightings of different types of hirola group between September 1996 and December 2000.

Group type	Composition	No. of individuals	N	%
5.1.1	Family groups	2 - 14	383	70.6
5.1.2	Single adult female + calf	2	15	2.8
5.1.3	Single adult female + yearling	2	15	2.8
5.1.4	Lone sub-adults	1	42	7.7
5.1.5	Mixed sex sub-adult groups	2 - 4	5	0.9
5.1.6	Adult male + sub-adult female	2 - 5	18	3.3
5.1.7	Bachelor groups	2 - 12	29	5.4
5.1.8	Lone males	1	34	6.3
	Summary		541	100

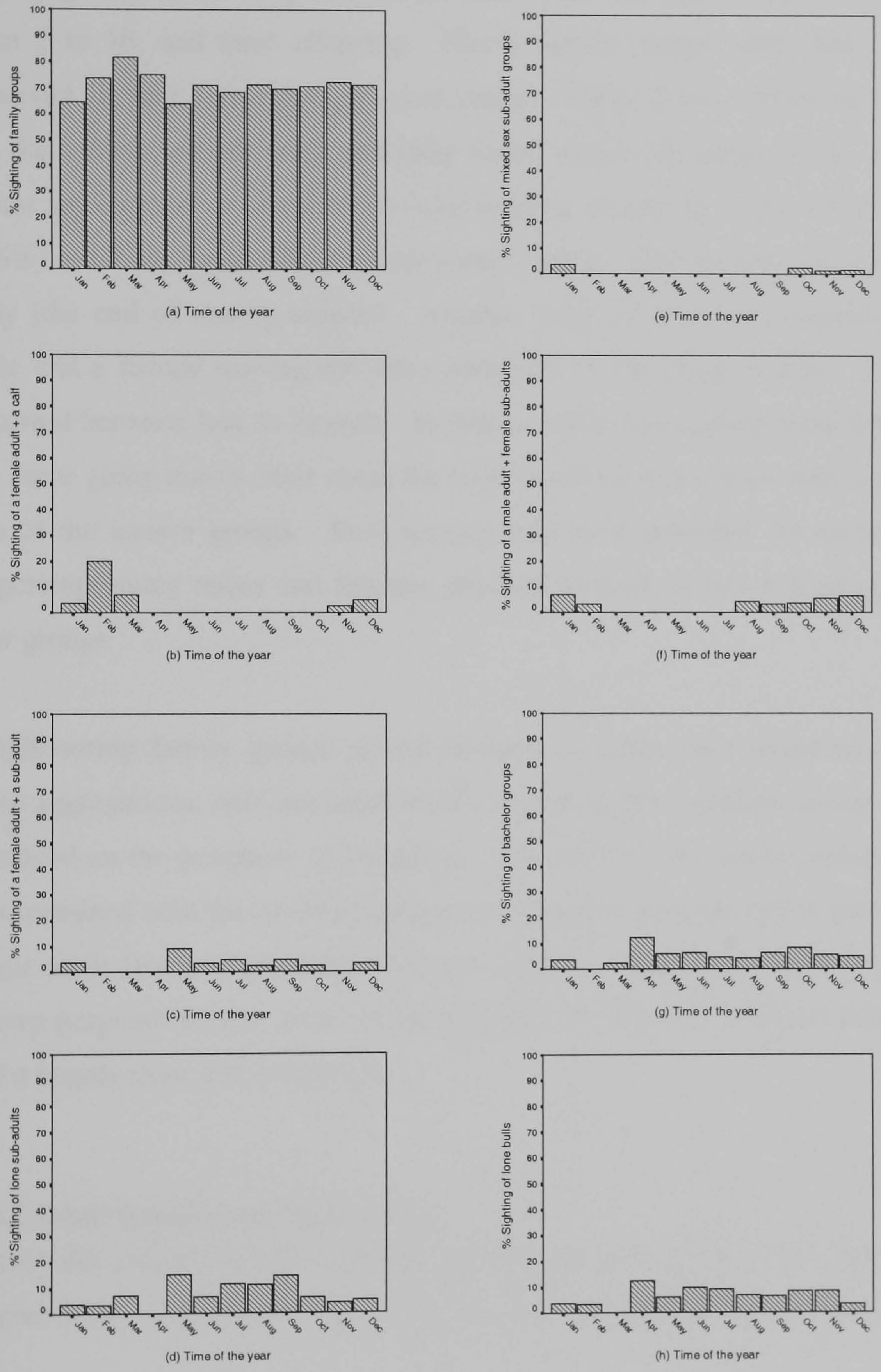


Figure 5.1: Percentage sighting of different hirola group compositions over time during the period of September 1996 and December 2000.

5.2.1 Family groups

70.6% of all sightings of hirola during the study period in Tsavo were of family groups. Family groups were composed of an adult male and adult females ranging in number from 2 to 10, and their offspring. Hirola family groups were quite stable and were observed all year round in their home ranges (Figure 5.1a). When family groups broke up, the splinter groups were generally found within the range of the core area. These minor separations involved either lone females separating from the main family group (4.6%) or a male separating from the female group. Such separations were common after May (the end of mating season). Another form of temporary separation involved the male and a female leaving the other members of the group (1.8%). These separations occurred between July to January. In most cases it was a group male with a female from the same group but in other cases the male involved was a new male and a female from one of the known groups. Such pairing may have provided the nucleus to which the dispersing young males and females attached themselves hence leading to formation of new groups.

Neighbouring family groups joined together on some rare occasions (0.8%). During these aggregations, only one adult male was seen in the combined group. The other male remained on the periphery of the group. Inspection of the males indicated that the male that remained with the combined group was bigger with more robust horns. In rare cases, single adult females also moved between groups. Three such cases were noted when a known pregnant female from VR group joined SAT group, a female from M1 joined B2 and a female from MK joined DK.

5.2.2 Adult females and their calves

During the calving period, isolated females and their calves were seen quite regularly (Figure 5.1b). These observations were during the months of November to March.

5.2.3 Single females and a yearling

During certain periods, adult females were observed in company of their young or sub-adult offspring. These sighting were generally within the range of the group that the female belonged to. The female and her offspring would later rejoin the group, most often in the same day. This phenomenon was most common between May and October (Figure 5.1c) and it coincided with the approach of the calving season.

5.2.4 Lone sub-adults

Remarkably, most young hirola dispersed away from their natal groups in the first year of life. The dispersing individuals ranged in age from about 6 months olds (mainly males) to yearling age (especially for females). At the initial dispersal stage, the dispersed sub-adults young were often seen alone or in company of Grant's gazelle, zebra or oryx. Observations of lone sub-adults comprised 7.7% of the total observations made on hirola in Tsavo; they were common between May and October, with a peak in September (Figure 5.1d). As a result of this behaviour, most of the offspring from the previous year were absent from their natal group during the following calving season.

5.2.5 Mixed sex sub-adult groups

Some of the dispersing lone sub-adult hirola eventually formed temporary groupings of mixed sex sub-adults. These groups were seen between October and January (Figure 5.1e), and constituted 0.9% of the total observations.

5.2.6 Male adult + female sub-adult groups

Groups of an adult male with subadult females were observed between August and February. They appeared to draw their female members from lone sub-adult or mixed sex sub-adult groups. The adult male was a mature or just maturing lone male (section 5.1.8). The formation of such groups coincided with the onset of calving and the eventual dispersal of yearling hirola (Figure 5.1f). During the entire study period, 18 (3.3%) such groups formed. Only one of these groups persisted and eventually formed the SAT group. The groups that disintegrated were of an adult and sub-adult females. The association of an adult male with subadult females may have been a mechanism leading to the formation of new family groups and may have been enhanced by the presence of an adult female.

5.2.7 Bachelor groups

Sighting of bachelor groups (5.4% of total observations) was common between April and December (Figure 5.1g). Field observations indicated that bachelor groups formed as a result of lone adult males joining lone sub-adult males or male members of the mixed sex sub-adult groups.

The smallest group observed was 2 (April 1997) while the maximum observed was 12 (late November 1999). In Tsavo, it appears that all the small bachelor groups eventually joined up into one large group. This large group was observed only in the Satao Camp area, and was composed of young males from nearly all hirola groups. Known young males from the A3, VR, DH, and M2 groups were eventually observed joining up at Satao. The ages of the males in bachelor groups ranged from 6 months to fully mature males.

All of the bachelor groups observed over the study period were temporary and soon broke up. The disintegration of the main bachelor group appeared to to occur after December each year. Members broke up in stages leaving groups of 2 to 3 individual and a number of lone males. Fewer records of lone males after the disintegration may be an indication that such animals either moved to other areas or fell victim to predation. In Garissa, only one bachelor group of 25 individuals was sighted in August 2000 on the banks of the Tana River in the Tana Primate National Reserve out of all the sightings made there during the study.

5.2.8 Lone adult males

Lone adult males were observed on the hirola range throughout most of the year (Figure 5.1h). They were commonly found in areas close to known family groups and often in patches of suitable forage that the group was not utilising. Sightings of mature males was most frequent between April and November (the non-mating period). Observation of lone mature males comprised 6.3 % of total hirola sightings. These were either males temporarily away from their female groups, lone mature males or maturing males from bachelor groups.

5.3 Reproductive behaviour

5.3.1 Herding by male

Hirola family groups appeared to be at least partly under the control and directions of the adult male. Males appeared to initiate most activities. The male was the most alert individual and spent more time watching the surrounding area than females in the group. During grazing, the male generally led the group to green, short, grass patches, (often found on shallow depressions of dry or drying waterholes). As the group grazed he often took up an observation position, sometimes using raised ground or ant-hills, before he led the group to another grazing patch.

At resting times the male led the group to appropriate shade, and appeared to have priority of access to the best shade. At the end of rest periods he often initiated group movement by going to every lying female, nosing at her rump and sometimes prodding her with his fore foot to make her stand. Once every member of the group was standing he would set off and all would follow him. Males also herded females from the back of the group and head-tossed towards females to move them on if they fell behind. Rare cases of conflict occurred with some mature females walking away in another direction. During such occurrences, the male intercepted the females and herded them in the direction taken by the rest of the group.

The group male sometimes defended the group from other animals such as Coke's hartebeest, zebra and Grant's gazelles, chasing them away from a grazing patch or from hirola calves. He also defended weaker females within his group from attack by dominant females.

5.3.2 Male hirola mating strategy

Only three changes of group males were observed during the study. In the first instance, the VR male was observed limping and it appeared that he had a dislocated the left hind leg. He stayed with the group as the leader for one year in this state. Unfortunately he did not seem to recover and eventually started losing weight. Because of this, he could not effectively lead the group and on many occasions was observed trailing behind the group as it moved. I then found him mating a female. He made four consecutive successful mounts and thereafter was barely able to stand. Four days later I found him alone and the group had been taken over by a male that about three weeks earlier had isolated from a bachelor group. The other two observed exchanges may have been as a result of predation of the resident male or a take over. The incoming males had previously been observed first in bachelor groups and later as solitary males.

There appear to be very little direct contact between hirola males. Only one observation was made in 1996 when a lone male accompanied by one female came into contact with a family group. The lone male was violently chased away for about one kilometre, and the female joined the family group. No scars, torn ears or broken horns have been observed in hirola males indicating little physical contact.

Lone hirola males used certain grazing patches within the ranges of family groups accompanied by another male. Observations on four identifiable males indicated high mobility over large sections of the hirola range (Figure 5.2). This suggests that lone males without females were not territorial and perhaps the patchy rainfall conditions in Tsavo may make it unprofitable to defend a fixed area.

5.3.3 Parturition and associated behaviour

The peak calving season was at the end of October and beginning of November. Most calving occurred within a period of about two weeks. However, some isolated calving occurred as early August and as late as March, but such cases were rare.

A total of seven births were observed during the entire study period (Table 5.2). Females that were about to calve could be recognised as early as a week before parturition. The coats of such females became slightly rougher than others, resulting in a pale coloured impression. They spent most of their time resting and always trailed behind the other members during group movements. Sometimes they could be left as far as a kilometre behind in open areas. Other features of the body included a sunken abdomen that gave the impression of an emaciated animal with a bloated stomach.

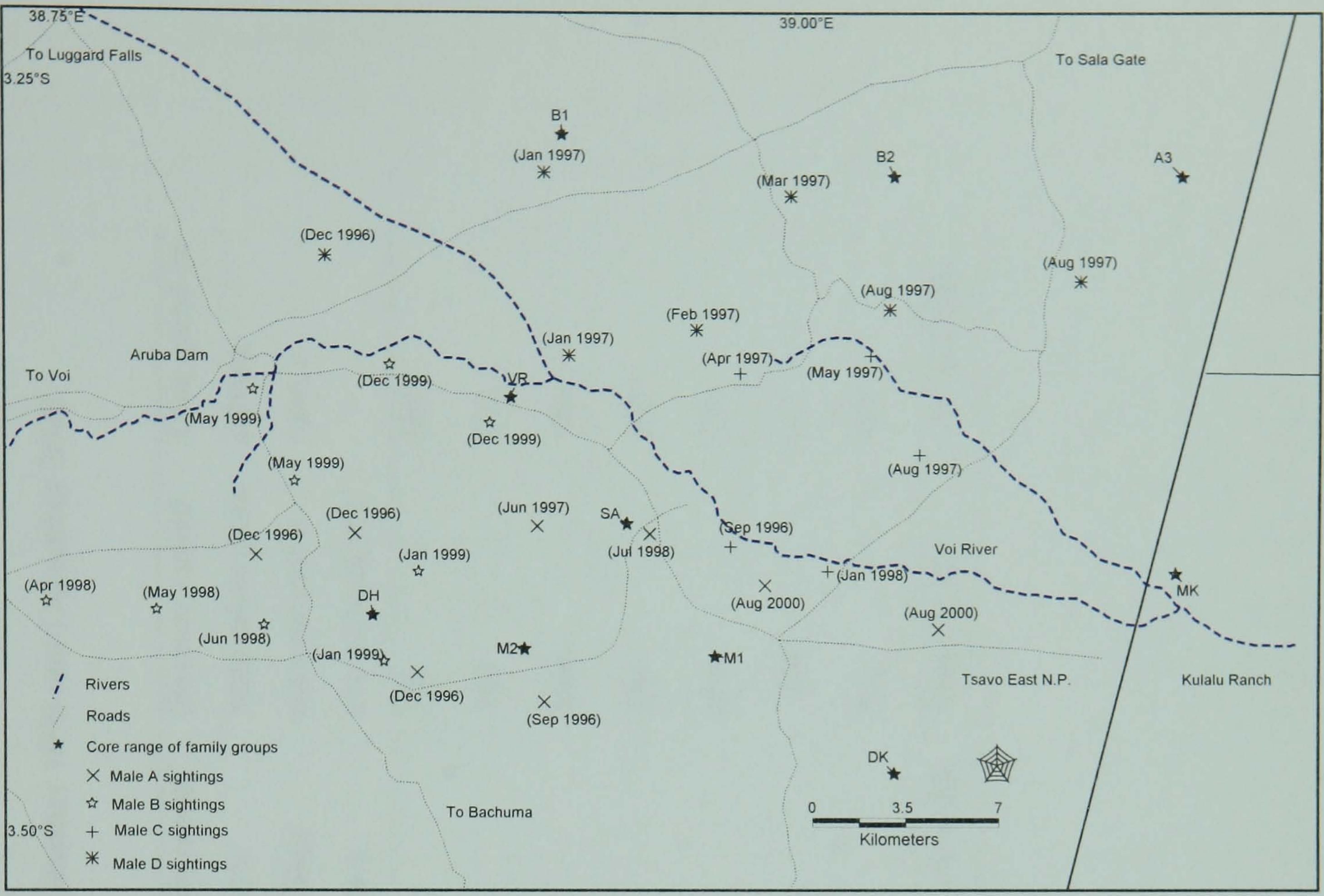


Figure 5.2: Sightings of known male adult lone hirola in relation to core position of family groups in Tsavo between September 1996 and December 2000.

The earliest observed onset of labour was 1115 hrs while the latest was 1415hrs, with an average onset time of about 1240 hrs. Calving took place within the group. Labour ranged from between 1 and 2 hours, with a mean of about 1.4 hours (Table 5.2). At the start of labour, the female became restless and urinated frequently. Urination attracted the attention of the male who tested her urine and displayed flehmen. He often attempted to mount her and on some instances he was successful. (The male behaviour of mounting females under stress was also observed when a female from SAT group was sedated during a hirola collaring exercise in February 1999. In between darting and complete sedation, the group male continually mounted this semi-conscious female, and even continued nosing her as she finally lay down. He did not seem to get disturbed by the darting team that by that time was approaching the site). This created excitement among group members and some females also nosed the female and ran around for short distances.

Table 5.2: Calving periods of hirola in Tsavo East National Park between September 1996 and December 2000.

Name of ♀	Group	Labour onset (Hrs)	Delivery (Hrs)	Sex of calf	Calf walking (Hrs)	Time spend on labour (min.)	Time spend before walking (min.)	Distance moved from calving site after the calf is able to walk (m)	Time spend on calving (min.)
HUB	DH	1215	1320	♀	1355	65	35	500	100
370	SAT	1340	1450	♂	1530	70	40	700	110
399	DH	1115	1245	♂	1325	90	40	1000	130
RMC	VR	1130	1230	♀	1315	60	45	300	105
396	M2	1415	1530	♀	1605	75	35	800	110
LET	DH	1250	1430	♀	1505	100	35	1200	135
342	M1	1220	1420	♂	1500	120	40	400	160
Mean						82.8±22 SD	38.6±3.8 SD	700±326 SD	121.4±21SD

Within 15 - 30 minutes the excitement would cease. At this point the protruding fore feet of the calf were generally visible. At this stage the female was extremely restless, lying down, standing up, moving in circles, nibbling on grass, licking her vulva while standing, sucking her teats while lying, lying in an arched back position, and occasionally making whistling sounds.

In the final stage, the female spent most of her time lying down with the back arched. Progressively the head of the calf would appear and the female would be observed lying and standing more often and turning around more frequently. She also sucked on her own teats more and more, perhaps to open them up for the coming calf. Out of seven births I observed 4 females dropped their calves while standing. The other three expelled their calves while lying on the ground.

The final moments of calving was silent, the rest of the group appearing unconcerned. The female then embarked on licking the calf, starting with the muzzle area, then moving to the umbilical cord and behind the tail before cleaning the other parts of the body. The calf was able to walk well and suckle between 35 to 45 minutes after birth. The placenta was expelled after about the same time period and was eaten by the female.

Once the calf was able to move, and follow the mother, she sometimes started to walk off very alert and whistling. This appeared to stimulate the male to nose her and herd her and the calf in a particular direction that the rest of the group then followed. In most cases if not disturbed the group would move about 500 m away and continue grazing. A strange behaviour was observed in M2 group: an hour after the female had calved and the group had moved 300 meters from calving area, both the male and the female that had produced the calf started running in straight lines in all directions traversing the general calving place. The other group members stood alert watching. This behaviour lasted for 26 minutes. The female (ID 396) had a late calving which ended at about 1605. Overall, the total time spent on calving (from the onset of labour to the time when the calf was able to walk and follow the group) ranged between 1.67 hours and 2.67 hours (Table 5.2).

5.3.4 Young animals in natal groups

All female hirola stayed within the natal group with their newborn calves in the hours immediately after birth. However, some females then separated from the group and stayed isolated with the calf. This behaviour constituted 10.3% of all females observed with calves (10 females out a total of 97 that were known to have calved during the study period). The longest observed isolation was 5 weeks, though this female was always within a kilometre of the natal group. Other isolations were temporary, taking just a few hours (over midday) before the female and calf reunited with group in the evening. Two instances were recorded when a female hirola and her calf were killed by lions, while in isolation (Chapter IV, section **4.2.1**). Within the group, hirola calves associated freely with other members of the group. There were some instances when a calf belonging to a different female would attempt to suckle a lactating female but would be repulsed by a horn threat. Calves within a group tended to stay close to each other while older members of the group grazed.

5.3.5 Dispersal from natal groups

Field observations indicated that both male and female yearlings separated from their natal group before the next calving season. Young males separated as early as 6 months of age while females dispersed at 9 months of age and over. I observed the development stages of a male and female hirola from birth (Figure 5.3). Young males that separated either i) joined groups of Grant's gazelle, ii) formed temporary mixed groups with other dispersing females, or iii) joined bachelor groups with much older males. At over 32 months of age they were mature enough to form a family group or replace a group male.

Females appeared to stay longer in family groups. During separations, they either i) stayed alone or among Grant's gazelle, ii) joined young males and formed temporary yearling groups (of up to 6 in number), iii) joined lone adult males where they matured and formed new groups, and, iv) those that did not disperse separated occasionally from their natal groups, but stayed within reach of the group. Observations indicated that the young hirola were often driven out of the family groups by their parents. Group males showed aggression towards young males when they were as young as 6 months of age. Usually such aggression appeared to be unprovoked. Once I observed a young male

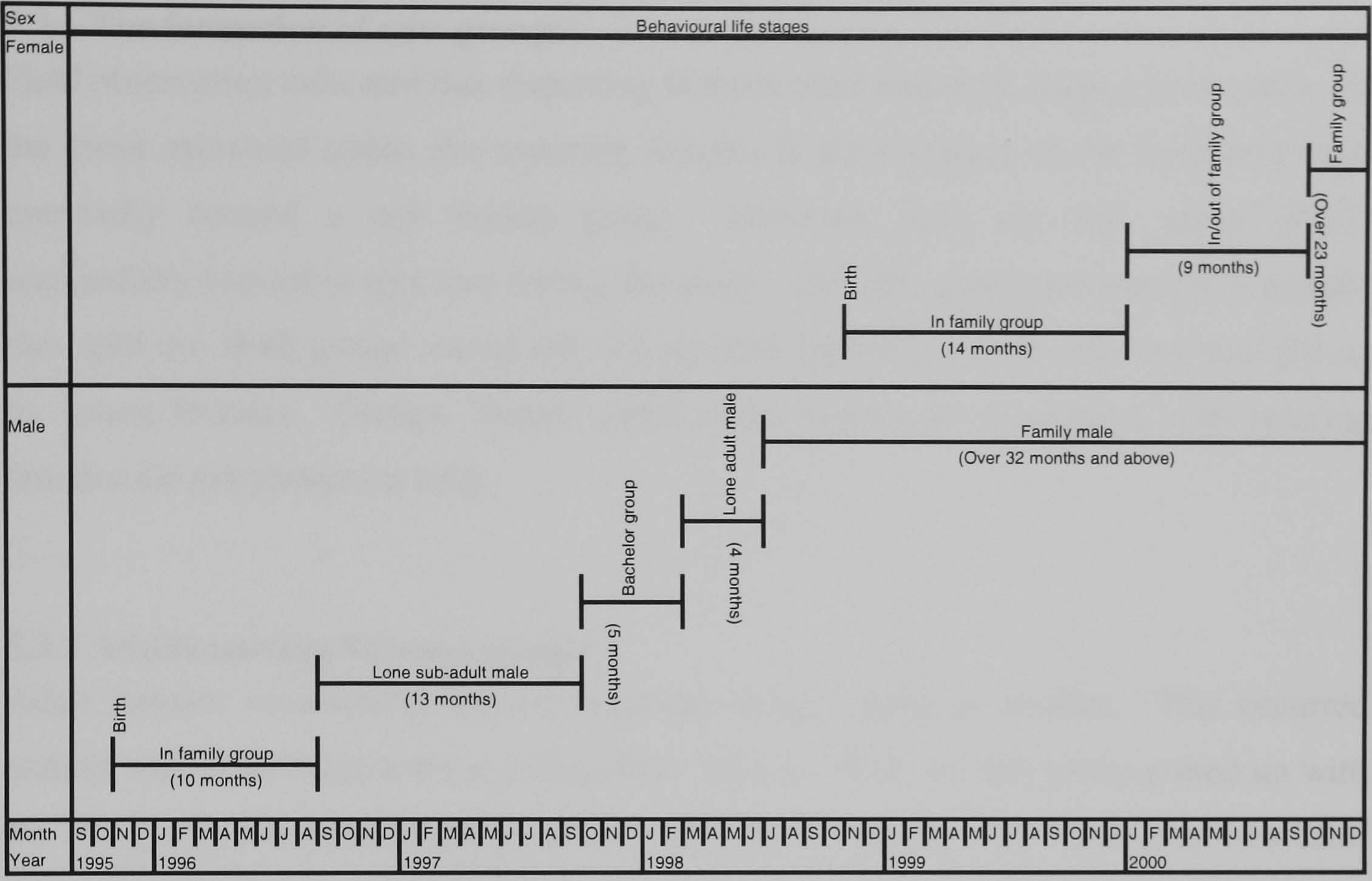


Figure 5.3: Ageing and dispersal behaviour of a known male and female hirola calf between November1995 and December 2000. The information included here dates from September 1995, when I started surveying for and monitoring hirola groups in Tsavo East National Park, before my PhD. study period. The female monitored was from DH group and rejoined the same group later, while the male was originally from M2 group.

attempt to nose a female. On this occasion, the female chased him around, prompting the group male to join in the chase. The male chased the young male away from the group's grazing area until they both disappeared into the bush. He later reappeared without the young male and the latter was never seen with the natal groups again. On other occasions, the group male was seen chasing away young males from the natal groups without any obvious cause. Similar events including frequent chases and aggressive displays by adult females and sometimes the group male also led to young females being driven away. As a result of these actions, isolated young females were sometimes seen within 50m of a natal group. Maturing females returned to family groups at about 2 years of age (Figure 5.3). At this age they were still subjected to harassment by family group females, but by this time, the group male would defend them while attempting to mate with them. Young adult males attempting to return were chased away by the group male.

5.3.6 The formation of new groups

Field observation indicated that dispersing females often ended up joining a lone male. If the group remained stable, the maturing females in the company of the male may have eventually formed a new family group. However, only one new group (SAT) successfully formed in this way during the study. Another group persisted for 6 months then split up. Both groups started off with an adult female and male and were then joined by young females. Groups formed when males formed an association with yearling females did not persist for long.

5.3.7 Adults moving between groups

Adult females occasionally moved from one family group to another. This occurred mainly when two neighbouring groups met. In July 1997, the DH group joined up with the M2 group and lived together for between 3 and 4 weeks. On separation, two adult females and a young female from the M2 group left with the DH group. During the period when the groups were together, only one adult male was present. I searched for the missing M2 group male and found him alone in a section of his group range. The meeting had taken place on the border between the two groups but a little more into the M2 group range. A similar joining together occurred between the DH and VR groups and this time the DH group lost one female to VR when the groups separated.

Adult females moved from one group to another. Three such cases were noted: a known pregnant female from VR group joined the SAT group; a female from the M1 group joined the B2 group; and another female from the MK group joined the DK group. One radio-collared female moved from the DH to the VR group where she spent 2.5 years before leaving again to join the SAT group.

5.4 Daily activity patterns

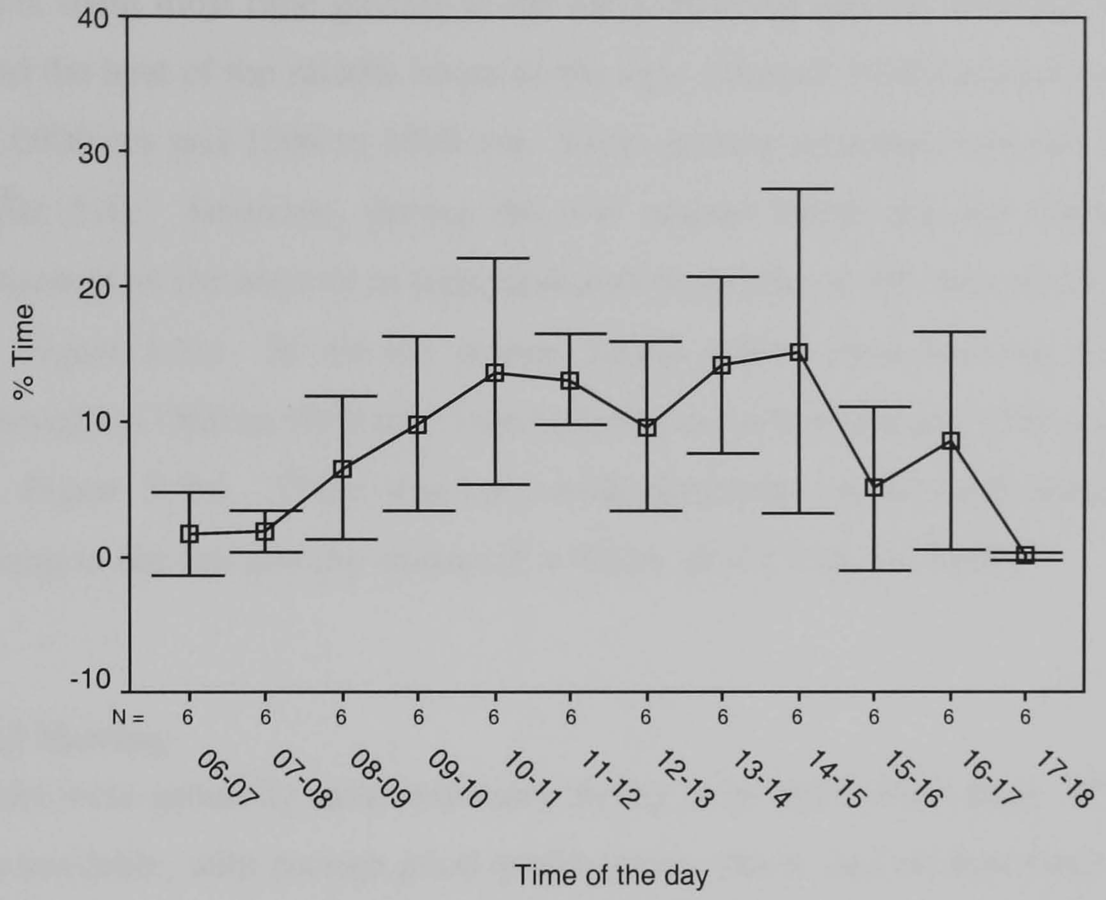
5.4.1 Resting

Hirola appeared to be greatly affected by diurnal temperature changes, seeking shelter and resting when it became hot (Table 5.3). Generally, hirola rested most between 1300 and 1400 and least between 0600 and 0700 hrs (Table 5.3). In the wet season, peak resting occurred between 1300 and 1400 hrs and the least resting occurred between 0600 and 0700 hrs (Table 5.3, Figure 5.4a). During the dry season peak resting occurred between 1600-1700 hrs and least resting was observed between 0600 and 0800 (Figure 5.4b). However, a comparison of the total amount of time spend resting between the wet and dry season indicated no statistical difference (F = 0.063, df = 1,108, P > 0.05). Similarly, all groups spent equal proportions of time resting in the wet season (F = 1.549, df = 5,48, P > 0.05), and dry season (F = 1.285, df = 5,50, P >0.05).

Table 5.3: Diurnal resting patterns of hirola in Tsavo East N.P. Student-Newman-Keul's Test (SNK) shows the periods when resting occurred in order of declining magnitude. Means with the same letters are not significantly different from the other. Numbers in brackets indicate the number of hirola groups in which resting activity was recorded within the relevant time block for wet, dry and all seasons combined. Each group was observed for at least 7 days per season.

Time of the day	Overall % time spent resting	Overall % time spent resting in the wet season	Overall % time spent resting in the dry season
0600-0700	1.9 c (6)	1.7 b (6)	2.1 b (6)
0700-0800	1.5 c (6)	1.9 ab (6)	1.0 b (6)
0800-0900	3.7 ab (6)	6.5 a (6)	0.9 ab (6)
0900-1000	10.9 a (6)	9.9 a (6)	11.9 a (6)
1000-1100	13.2 a (6)	13.7 a (6)	12.6 a (6)
1100-1200	10.1 a (6)	13.2 a (6)	7.1 a (6)
1200-1300	9.4 a (6)	9.7 a (6)	9.1 a (6)
1300-1400	16.3 a (6)	14.2 a (6)	18.5 a (6)
1400-1500	12.7 a (6)	15.2 a (6)	10.1 a (6)
1500-1600	7.3 ab (6)	5.1 ab (6)	9.5 a (6)
1600-1700	11.2 ab (6)	8.6 ab (6)	13.8 a (6)
1700-1800	3.3 bc (6)	-	3.3 ab (6)
F	7.188	3.641	5.424
Df	11, 97	10,42	11,44
P	<0.001	<0.001	<0.001

(a) Wet season resting



(b) Dry season resting

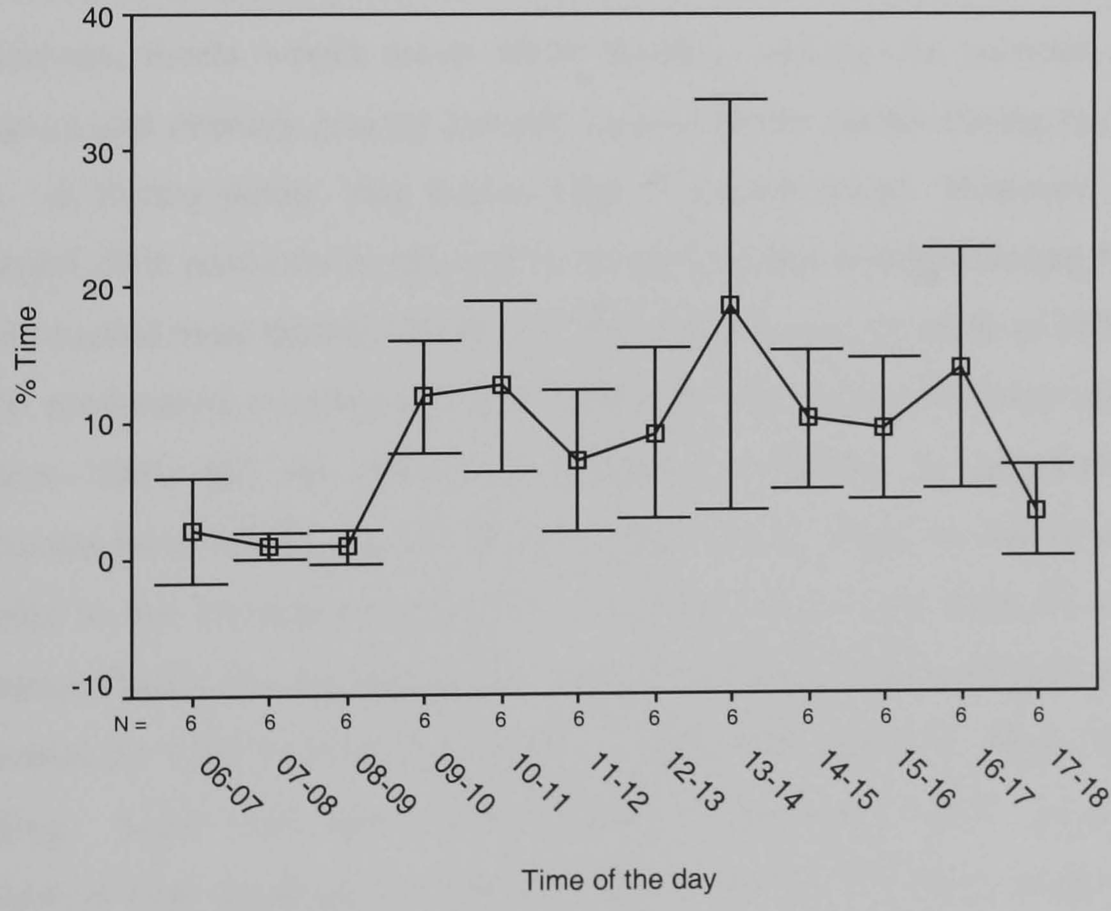


Figure 5.4: Average wet (a) and dry (b) season diurnal resting patterns (mean ± 2SE) of hirola groups in Tsavo East National Park. Data collected between September 1996 and December 2000.

5.4.2 Grazing

Hirola spent most time grazing in the early morning and late evening hours, probably to avoid the heat of the middle hours of the day. Overall, hirola grazed most between 0700 and 0900 hrs and 1500 to 1800 hrs. Least grazing occurred between 1300 and 1400hrs (Table 5.4). However, during the wet season hirola did not show any significant differences in the amount of time allocated to grazing at different times of the day (Table 5.4, Figure 5.5a). In the dry season, hirola grazed most between 0700 and 0900 hrs followed by 1500 to 1800 hrs. Least grazing occurred between 1400 and 1500 hrs (Table 5.4, Figure 5.5b). There was no overall difference in the total amount of time spent grazing in the wet and dry season ($F = 0.034$, $df = 1,124$, $P > 0.05$).

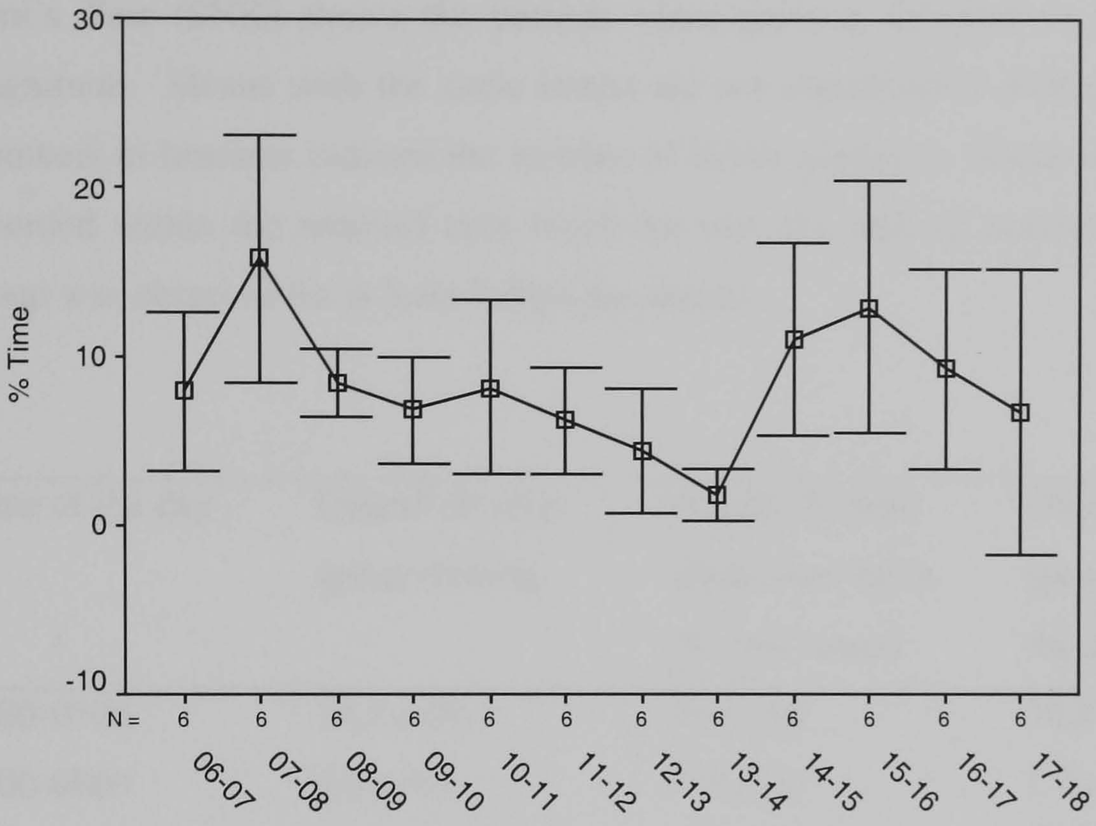
5.4.3 Moving

Hirola were generally quite sedentary during most observation days. When good grazing was available, with enough good quality grass, shade, and no disturbance from predators, tour vehicles, big herds of other grazers or biting flies, hirola would spend the entire day (or more) in or near a particular food patch. However, in the absence of good grazing conditions, hirola would move while feeding, looking for suitable areas during the morning and evening grazing periods, and for better shelter during the hot hours of the day. At resting points, they moved little if in good shade. However, some individuals changed their positions as the area covered by shade changed during the day. Overall, hirola moved most between 0700 and 0900 hrs followed by 1600 to 1700 hrs (Table 5.5). Least movements occurred between 1300 and 1400 when they were resting. In the wet season, hirola did not show any significant variations in movement in relation to particular hours of the day (Table 5.5, Figure 5.6a). Food resources are expected to be limited in the dry season, and thus a foraging animal may need to move considerable distances during the feeding hours. Most movements occurred between 1700 and 1800 followed by 0700 to 0900 (Table 5.5, Figure 5.6b), periods when they were actively feeding. Least movement occurred between 1400 and 1500. A comparison of the amount of time spent on movement between wet and dry season indicated no statistical differences ($F = 0.361$, $df = 1,107$, $P > 0.05$).

Table 5.4: Diurnal grazing patterns of hirola in Tsavo East N.P. Student-Newman-Keul's Test (SNK) shows the periods when grazing occurred in order of declining magnitude. Means with the same letters are not significantly different from the other. Numbers in brackets indicate the number of hirola groups in which grazing activity was recorded within the relevant time block for wet, dry and all seasons combined. Each group was observed for at least 7 days per season.

Time of the day	Overall % time spent grazing	Overall % time spent grazing in the wet season	Overall % time spent grazing in the dry season
0600-0700	7.9 ab (6)	8.0 a (6)	7.8 ab (6)
0700-0800	13.5 a (6)	15.8 a (6)	11.2 a (6)
0800-0900	13.5 a (6)	8.4 a (6)	17.9 a (6)
0900-1000	8.7 ab (6)	6.9 a (6)	10.5 ab (6)
1000-1100	5.3 ab (6)	8.2 a (6)	2.4 bc (6)
1100-1200	6.2 ab (6)	6.3 a (6)	6.2 ab (6)
1200-1300	6.1 ab (6)	4.5 a (6)	7.7 ab (6)
1300-1400	2.1 b (6)	1.9 a (6)	2.2 bc (6)
1400-1500	6.0 ab (6)	11.0 a (6)	0.9 c (6)
1500-1600	10.0 a (6)	13.0 a (6)	7.1 ab (6)
1600-1700	9.7 ab (6)	9.3 a (6)	10.1 ab (6)
1700-1800	11.4 a (6)	6.7 a (6)	16.0 a (6)
F	3.265	1.685	5.961
Df	11,114	11,52	11,50
P	<0.001	>0.05	<0.001

(a) Wet season grazing



(b) Dry season grazing

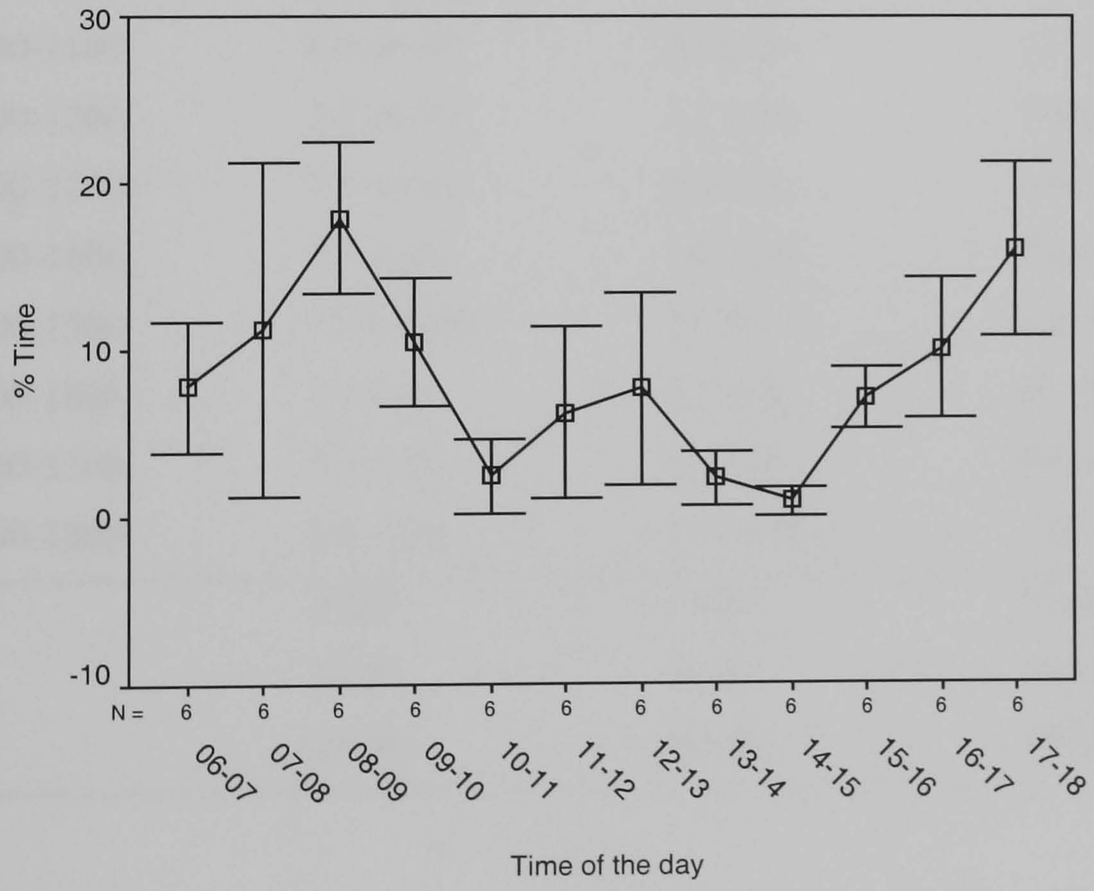
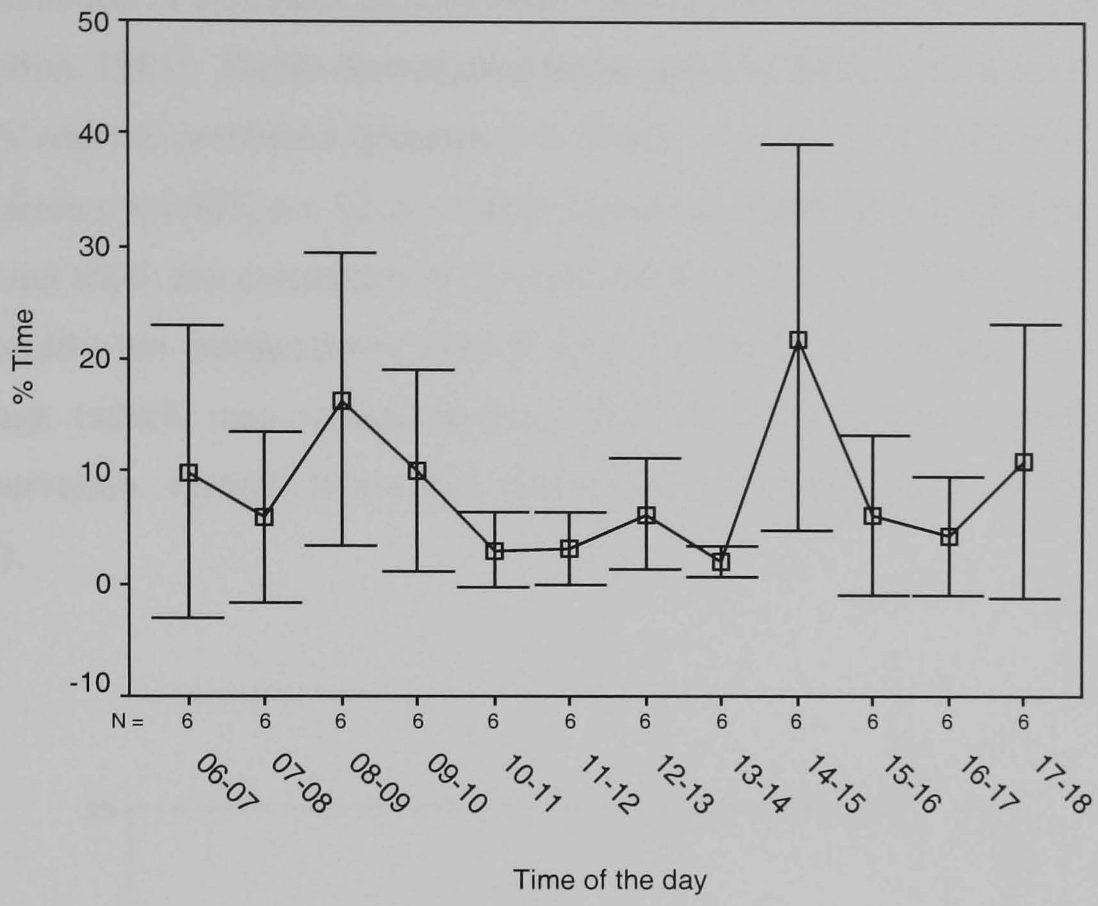


Figure 5.5: Average wet (a) and dry (b) season diurnal grazing patterns (mean ± 2SE) of hirola groups in Tsavo East National Park. Data were collected between September 1996 and December 2000.

Table 5.5: Diurnal movement patterns of hirola in Tsavo East N.P. Student-Newman-Keul's Test (SNK) shows the periods when grazing occurred in order of declining magnitude. Means with the same letters are not significantly different from the other. Numbers in brackets indicate the number of hirola groups in which moving activity was recorded within the relevant time block for wet, dry and all seasons combined. Each group was observed for at least 7 days per season.

Time of the day	Overall % time spend moving	Overall % time spend moving in the wet season	Overall % time spend moving in the dry season
0600-0700	14.3 a (6)	9.9 a (6)	20.8 ab (6)
0700-0800	6.6 a (6)	5.9 a (6)	7.7 a (6)
0800-0900	12.9 a (6)	16.4 a (6)	7.7 a (6)
0900-1000	8.6 ab (6)	10.1 a (6)	6.4 ab (6)
1000-1100	6.4 ab (6)	3.0 a (6)	11.5 bc (6)
1100-1200	3.2 ab (6)	3.1 a (6)	3.6 ab (6)
1200-1300	7.7 ab (6)	6.3 a (6)	9.9 ab (6)
1300-1400	2.3 b (6)	1.9 a (6)	2.9 bc (6)
1400-1500	15.9 ab (6)	21.9 a (6)	6.8 c (6)
1500-1600	7.2 a (6)	6.2 a (6)	8.7 ab (6)
1600-1700	5.2 a (6)	4.3 a (6)	6.0 a (6)
1700-1800	9.6 a (6)	11.1 a (6)	7.5 a (6)
F	3.007	1.685	7.436
Df	11,97	11,52	11,33
P	<0.001	>0.05	<0.001

(a) Wet season movements



(b) Dry season movement

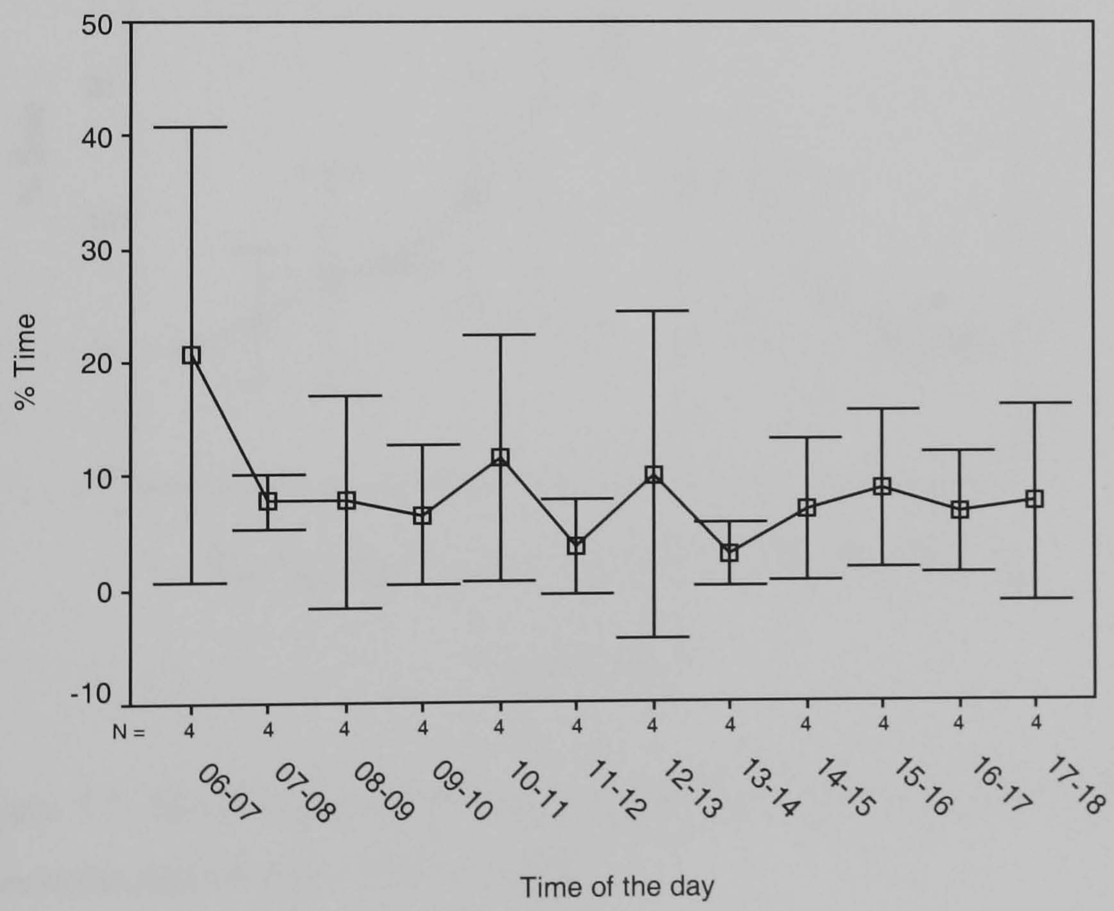


Figure 5.6: Average wet (a) and dry (b) season diurnal movement patterns (mean ± 2SE) of hirola groups in Tsavo East National Park. Data were collected between September 1996 and December 2000.

5.4.4 Ruminating

Rumination in ungulates usually occurs during resting periods (Jarman & Jarman, 1973); (Norton, 1981). Hirola diurnal rumination pattern closely correlated with resting time for both seasons combined (Pearson r = 0.693, n = 12, $p < 0.05$) and in the dry season (Pearson r = 0.635, n = 12, $p < 0.05$). However, rumination frequencies and resting times did not show any correlation in the wet season (Pearson r = 0.261, n = 12, $p > 0.05$). The generally low temperatures (which may encourage less resting) and the better quality forage (which may reduce feeding time) in the wet season could account for this observation. Overall, hirola peak rumination occurred between 1200 and 1300hrs (Figure 5.7).

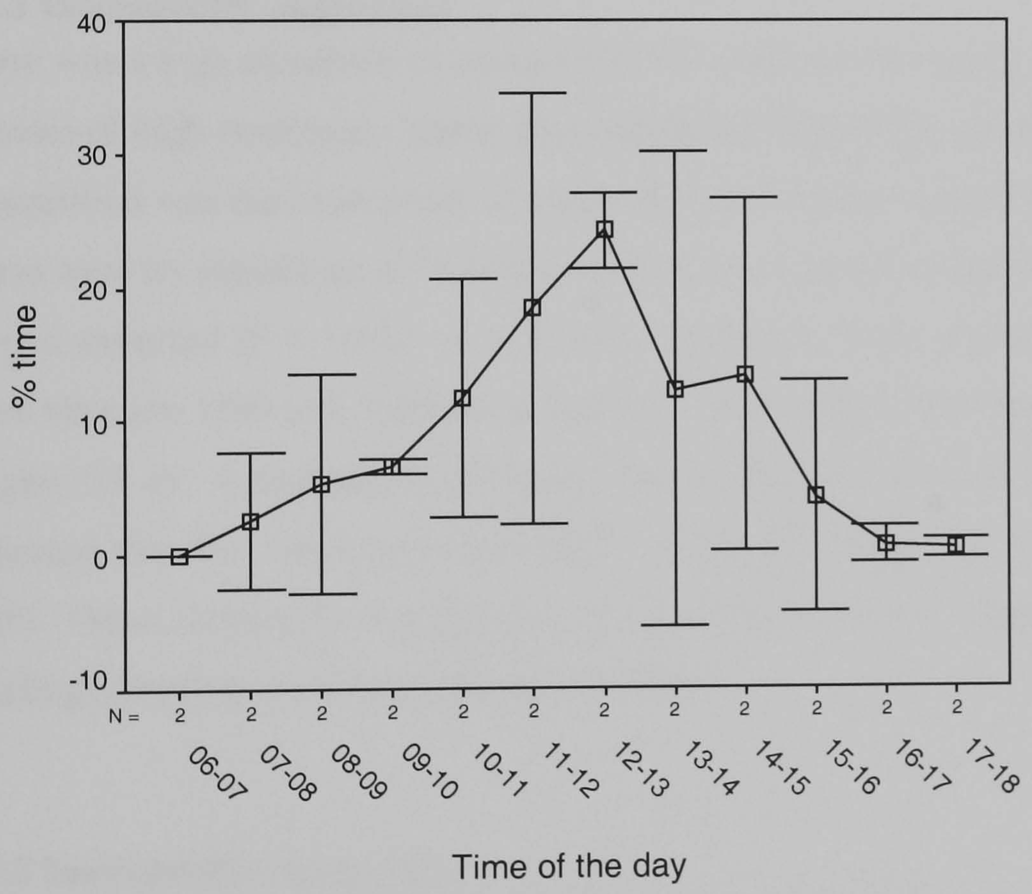


Figure 5.7: Mean dry and wet season ruminating patterns of hirola in Tsavo N.P. Data were collected between 1996 and 2000.

5.4.5 Drinking

Hirola were rarely observed drinking. Out of a total 674 group sightings, hirola were observed drinking water on only 10 occasions (1.5% of total observations). During these observations, hirola drank on 4 occasions between 0930 and 1030 in the morning while on 6 occasions they drank between 1530 and 1630. All these observations were made at the peak of the dry season when it was dry all over the park. Observations of the stomach fat content (Prof. R. Hoffmann pers. comm. 1996) on the individuals that died from the 1996 capture myopathy indicated that hirola can be independent of water for some time. Despite the fact that hirola were rarely seen drinking, 58.2% (392 sightings out a total 674) of their total time was spend grazing on fresh green grasses (mainly *Sporobolus helvolus* and *Echinochloa haploclada*) growing on and around the edges of drying waterholes. Similarly hirola appeared to search for and graze on *Commelina spp.* which are succulent. Hirola may thus obtain much of their water needs from their forage.

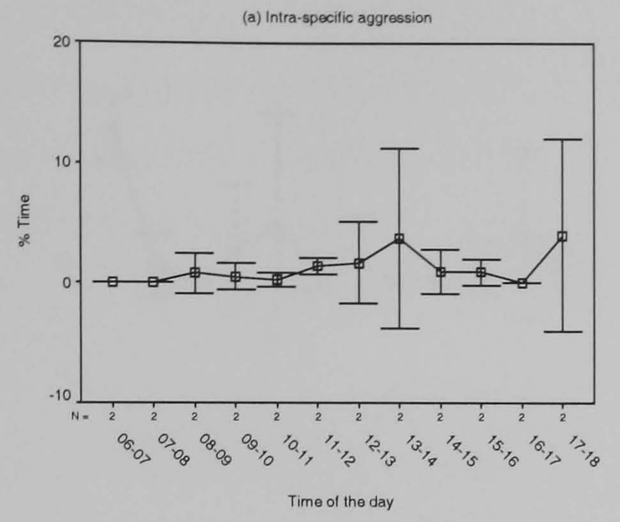
5.5 Social Activity patterns

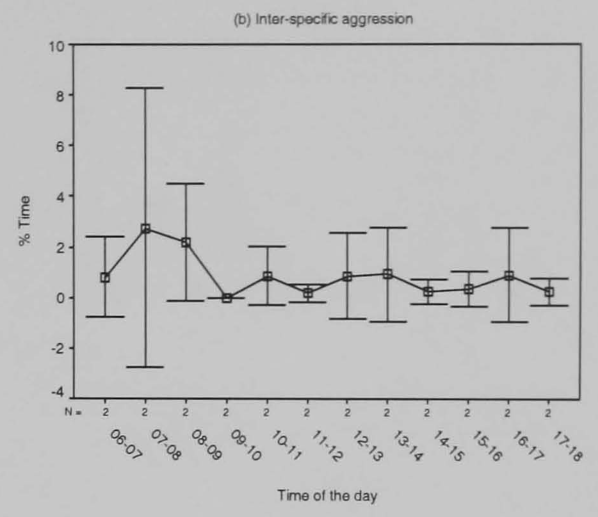
5.5.1 Intraspecific aggression

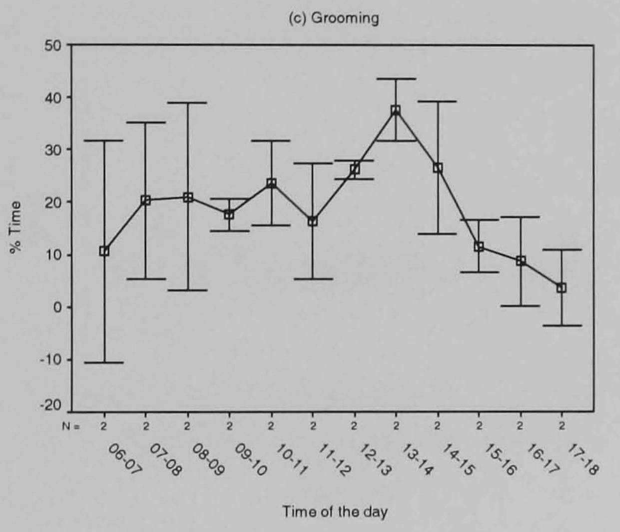
There was a high incidence of competition for shade within hirola groups. The male and females of high dominance status often displaced subordinate members from shade. This competition was the main cause of aggressive interactions among individuals in a group. There were no significant differences between the overall interactions and time of the day as was expected (F = 0.633, df = 11,12). However, these interactions tended to occur more between 1300 and 1400 hrs, a period of intense heat from the sun in the study area (Figure 5.8 a). A comparison of aggressive interactions between the wet and dry season indicated that the competition was higher in the dry season (F = 6.521, df = 1,22, $P < 0.05$). Other incidences of aggression involved the male and sometimes females chasing yearling offspring away from the family group.

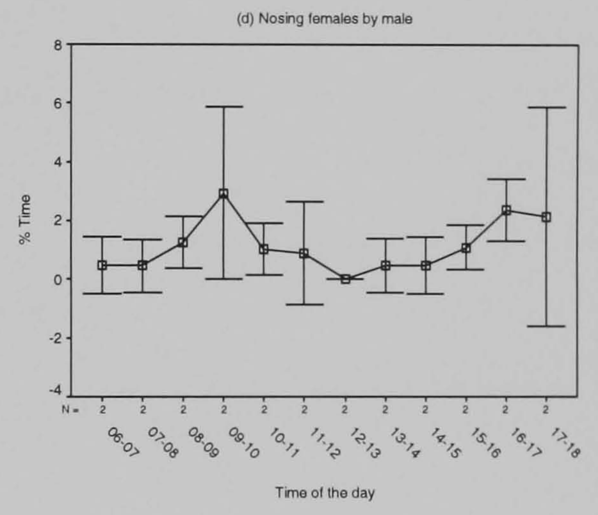
5.5.2 Interspecific aggression

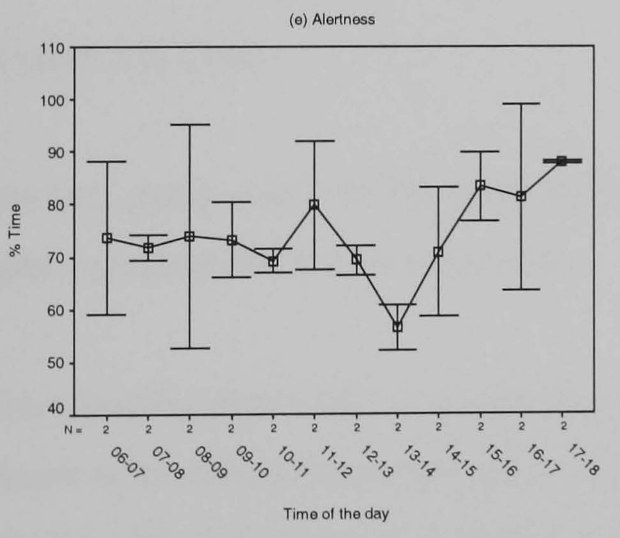
Cases of interspecific aggression involving hirola were rare. However, out of a total of 38 observations made, 25 (65.7%) involved male hirola chasing away Coke's hartebeest (either preventing the hartebeest from joining a hirola group or from using a grazing patch, or when Coke's hartebeest attempted to nose hirola calves), 9 (23.7%) involved hirola males and/or females chasing Grant's gazelle (usually when the Grant's gazelle male nosed hirola calves or caused a 'disturbance' by running around and making grunting sounds), 2 (5.3%) involved hirola males chasing away a male oryx from a











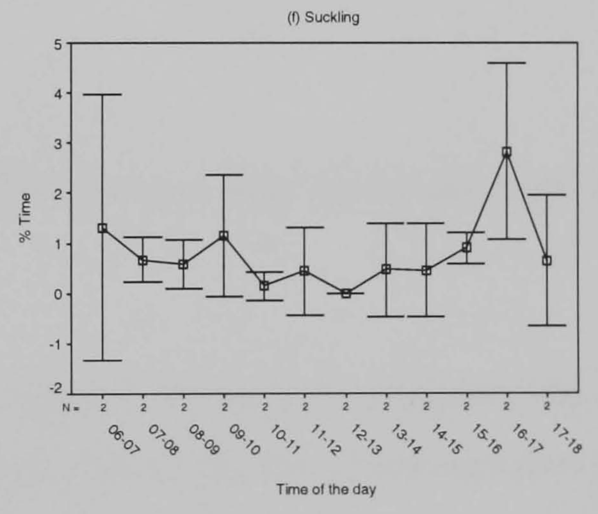


Figure 5.8: Daily social activity patterns (mean season ± SE) for Tsavo hirola groups between September 1996 and December 2000.

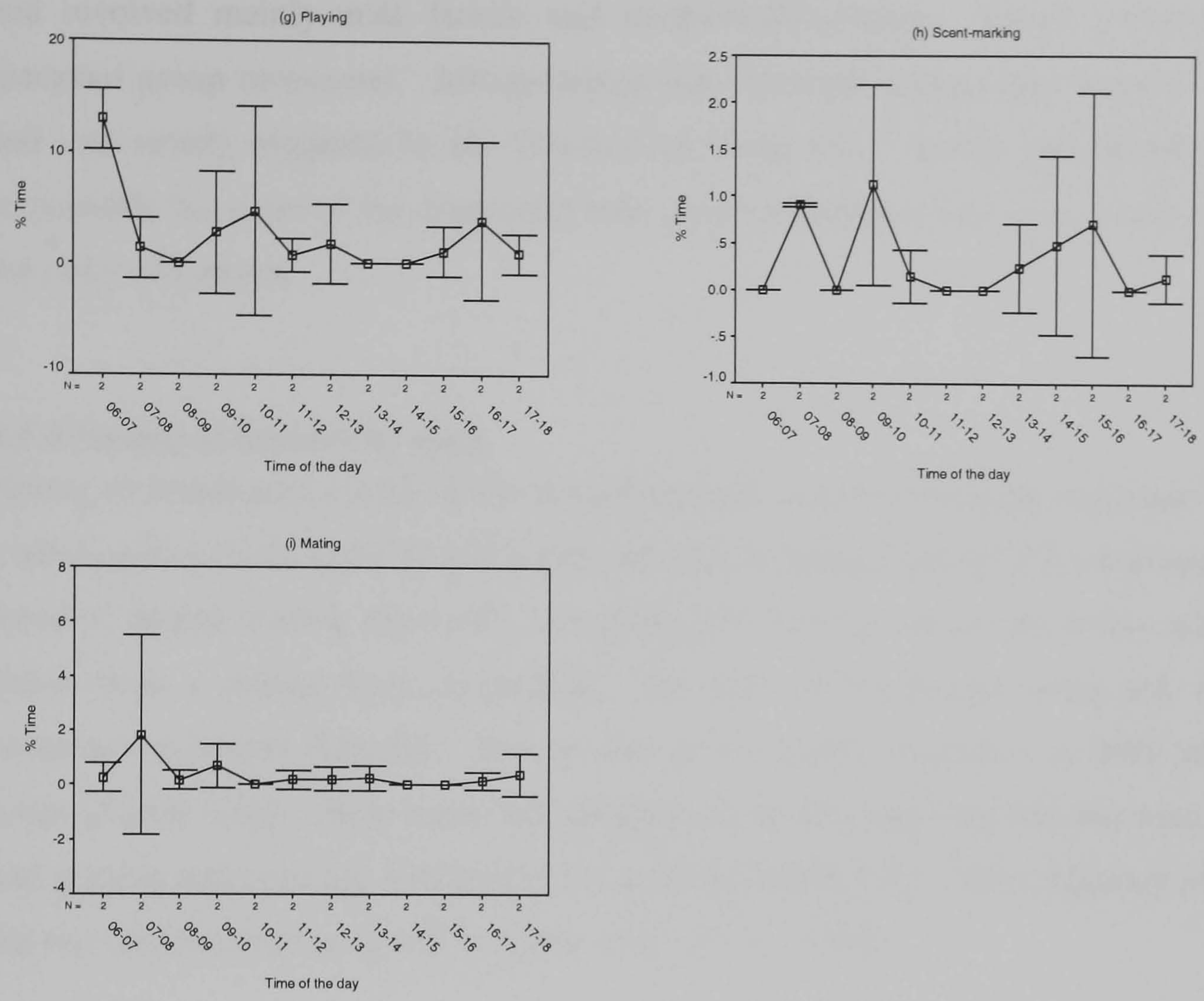


Figure 5.8: Cont.

grazing patch and 2 (5.3%) involved a conflict between male hirola and zebra (all at a green grazing patch by a water hole).

Interspecific aggression was expected to be higher in the early morning and late evening hours when hirola interacted most other species. However, this diurnal variation was not statistically significant (F = 0.653, df = 11,12, p > 0.05) though trends in data indicated a higher occurrence between 0600 and 1000 hrs and leveled off for the rest of the day (Figure 5.8b). The interactions were highest in the morning, a period of intense grazing, because this was when most species were close together after spending the night close together.

5.5.3 Grooming

Grooming among hirola involved all ages and sexes and occurred at most times of day (Figure 5.8c). Social grooming occurred at the peak resting period (1300 to 1400 hrs) and involved mainly male female and mother/calf/subadult. Social grooming often preceded group movement. Self-grooming was common during other times of the day and was mostly triggered by the presence of biting flies. Biting flies appeared to be responsible for some of the observed hirola group movements and were common during the early wet season.

5.5.4 Nosing of females by male

Nosing of females by a male hirola was a key male social and herding technique. Before a hirola group could move to a new site, the male hirola moved around the group nosing females, before leading them off. He displayed the same behaviour when raising the group from a resting place to grazing. He often licked female urine and on some occasions displayed flehmen. Nosing was at its highest frequency at 0900 and 1600 hours (Figure 5.8d). These were cool moments of the day when the females were relaxed and grazing and coincide with periods of mating (Figure 5.8i). The frequency of nosing did not vary between season ($F = 2.884$, $df = 1,15$, $P > 0.05$).

5.5.5 Alertness

In Tsavo where lions and cheetah are common, alertness is vital for the survival of a prey species such as the hirola. Compared to other prey species, hirola appeared to be more sedentary and less vigilant and responsive to danger compared to other species such as Coke's hartebeest. However alertness was a key activity consuming over 70% of their time (Figure 5.8e). The adult male in the group was the most alert, periodically walking around and sometimes standing on old termitaria to observe all directions around a group's grazing position. Hirola were most alert in the late evening hours (1500 to 1800 hrs) and least alert at the peak resting period (1100 to 1400 hrs) (Figure 5.8e). A comparison of alertness between wet and dry season indicated no variation ($F = 2.732$, $df = 1,22$, $P > 0.05$).

5.5.6 Suckling

During the calving season, newly born hirola calves stayed with the family group. However, calves spent most time lying under shade and only moved when the group had to shift from the grazing patch. When the group moved, the mother would nose the lying calf to get it to rise, so that they could move. Sometimes a calf would not respond, forcing the mother to remain far behind the group. Hirola calves were suckled mainly in the morning (0800 to 1000 hrs) and evening hours (1500 to 1700 hrs) (Figure 5.8f).

5.5.7 Playing

Playing among hirola was only common among calves and young animals. Adults rarely engaged in play. Playing occurred mostly early in the morning (0600 to 0700 hrs), with some incidences at the beginning of resting (0900 to 1000) and in the evening (1600 to 1700 hrs) (Figure 5.8g). Rates of playing were similar between seasons (F = 2.864, df = 1,9, P > 0.05).

5.5.8 Scent marking

Scent-marking, though an uncommon behaviour by male hirola, tended to occur mostly in the mid morning (0700 to 0900 hrs) and early evening (1400 to 1600 hrs), just at the end of the resting period ((Figure 5.8h). Hirola males scent marked by kneeling down, slashing through a shrub with their horns, while rubbing the pre-orbital scent glands on vegetation and soil. This was followed by pawing the ground with front legs and defaecating on the spot. Marked sites were usually close to an old termitarium with patchy grass cover. Another form of scent marking involved less vigorous rubbing of the pre-orbital gland on shrub sticks by male hirola. Rates of scent marking between season were similar (F = 2.152, df = 1,7, P > 0.05).

5.5.9 Mating

Mating was seen during March and April. Mating occurred mostly in the morning (0700 to 0900 hrs) (Figure 5.8i) and copulation was swift, short and repeated. Field observations of 40 recorded mating interactions indicated a mean of 5.8 ± 2.8 SD copulations per session. Often, the male would become inactive after mating and temporarily stop leading the group.

5.6 Conclusions

Hirola occured in distinct family groups within specific ranging areas, in which they foraged on patches of suitable grass sward. Hirola family groups were maintained and herded by the group adult male. Family males remained with their groups for long periods and were only replaced by solitary adult males when they were killed by predators or (in one case) when they become too ill to continue. Little physical contact occurred among males. Solitary males may have been waiting for an opportunity to join a family group. Other males may form a new family group by herding lone sub-adult females. Neighbouring hirola family joined together and sometimes exchanged adult females, although this was rare. Overall there was a low rate of exchange of individuals and long tenure by family males.

Hirola females calved during the middle part of the day. At the end of a calving and when the calf was able to walk, the whole group moved from the calving area. The immediate movement away from the calving area may have been an anti-predator behaviour or a normal movements from one grazing patch to another. Calves followed their mothers and stayed within the family group. Occasionally the female and her calf temporarily separated from the main group. Maturing hirola usually moved out of the family group before the onset of the next calving season. Hirola males matured at about 30 months while females matured at about 20 months. Overall, the temporary separation from family groups by females and their young and later the yearling could have possible subjected them to the risk of predation.

Hirola were most active during the early morning and late evening when the weather was cool; they rested during the middle of the day. However some social activities especially intraspecific aggression occurred during resting hours and many of these encounters were caused by competition for shade. Sporadic grazing was observed whenever there were prolonged overcast conditions, or when it rained. These results indicate that temperature has a significant influence on hirola activity patterns and may further affect the group size especially if a group occurs on sites with less suitable shade.

Chapter VI:

The Ungulate Community Structure

6.1 Introduction

Variations in topography, soil conditions, fire regimes, intra- and inter-annual rainfall, as well as the spatial and temporal distribution of surface water, are important in determining the heterogeneity of savanna structure and its scale (Frost et al., 1986). This heterogeneity, particularly when expressed in the diversity of plant communities and habitat types, and in their seasonal availability, is of critical importance for the diversity, distribution, and feeding strategies of the large ungulate community (McNaughton & Georgiadis, 1986; Dunham, 1994; Ben-Shahar, 1995). Irregular water availability in semi-arid savannas affects both the possibilities of drinking and the distribution, quality and quantity of food for large herbivores (McNaughton & Georgiadis, 1986; Skarpe & Bergstrom, 1986). The seasonal availability of resources also dictates whether herbivores are sedentary or whether they are forced to migrate in search of suitable ranges (Crowe, 1995).

Interspecific competition is considered to be a central biotic factor structuring large African herbivore communities (Lamprey, 1963b; Sinclair & Norton-Griffiths, 1982). Competition between two or more species may cause one species to use alternative, less preferred parts of the range. Ungulates are generally believed to minimize interspecific competition through differences in their spatial and temporal patterns of distribution and habitat use (Lamprey, 1963a). However, ungulate communities sometimes show evidence of grazing facilitation, in which the feeding activity of one species improves the food supply available to a second, thus creating useful co-existence (Sinclair & Norton-Griffiths, 1982; de-Boer & Prins, 1990). In grazing species that rely on facilitation from other species, lack of facilitation may precipitate ecological changes such as the progressive growth of bush cover, causing a decline in range condition, especially for grazers such as the hirola (Smith, 1988; Scholes & Walker, 1993; Ludwig et al., 1996).

Foraging in groups is generally interpreted as an anti-predator strategy (Bertram, 1978; Krebs & Davies, 1987), with trade-offs between feeding and vigilance (Illius & Fitzgibbon, 1994); it may also allow quicker and more efficient location of feeding patches (Clark & Mangel, 1984; Valone, 1989). Gregariousness reduces the probability that a prey will be detected and captured by a searching predator (Scheel, 1992). The availability of alternative prey also influences risk and consequently vigilance levels. For example, warthogs, a favoured prey of lions, are less vigilant in the dry season when zebras move into their area (Scheel, 1992). Individuals are more vigilant in cover rich habitats (reedbuck, impala, topi, and wildebeest: (Underwood, 1982; FitzGibbon, 1988; Gosling & Petrie, 1990), reflecting the greater hunting success of stalking predators in these areas (Orsdol, 1984). Hirola are often found in the company of other animals such as topi, (Kingdon, 1982) and such associations could increase the chance of detecting approaching predators and dilute the chance that the hirola will be killed if attacked. According to Bunderson (Bunderson, 1981), Garissa hirola were often associated with beisa oryx, gerenuk and giraffe. Similarly, Dahiye (Dahiye, 1999) observed that hirola associated with Burchell's zebra and Grant's gazelle. However, information is lacking on the annual cycles of these associations with hirola and their benefits to hirola survival.

Predation risk may also affect community structure and the life history strategies of prey species (Rowe & Ludwig, 1991, Kotler et al., 1992). In the Serengeti, lions were observed to prefer wildebeest and zebra during the migration period while specializing on warthog and buffalo when the migrants were scarce (Scheel, 1993). In this chapter, I show how the abundance of prey species varied on a seasonal basis in Tsavo NP and how this might have affected the hirola groups in terms of exposure to predation by lions, cheetah, leopard, and hyaena, particularly in periods when alternative prey were scarce on the hirola range.

6.2 Community structure

6.2.1 Community structure in Tsavo East N.P.

A total of 18 species were observed frequently in the Tsavo study area during the two years of monthly road transects (Figure 6.1, Appendix 1). The results showed that the area was dominated numerically by buffaloes, Grant's gazelle, zebra, elephant and eland (Figure 6.1a). However, elephants and buffaloes contributed the most in terms of biomass (Figure 6.1b).

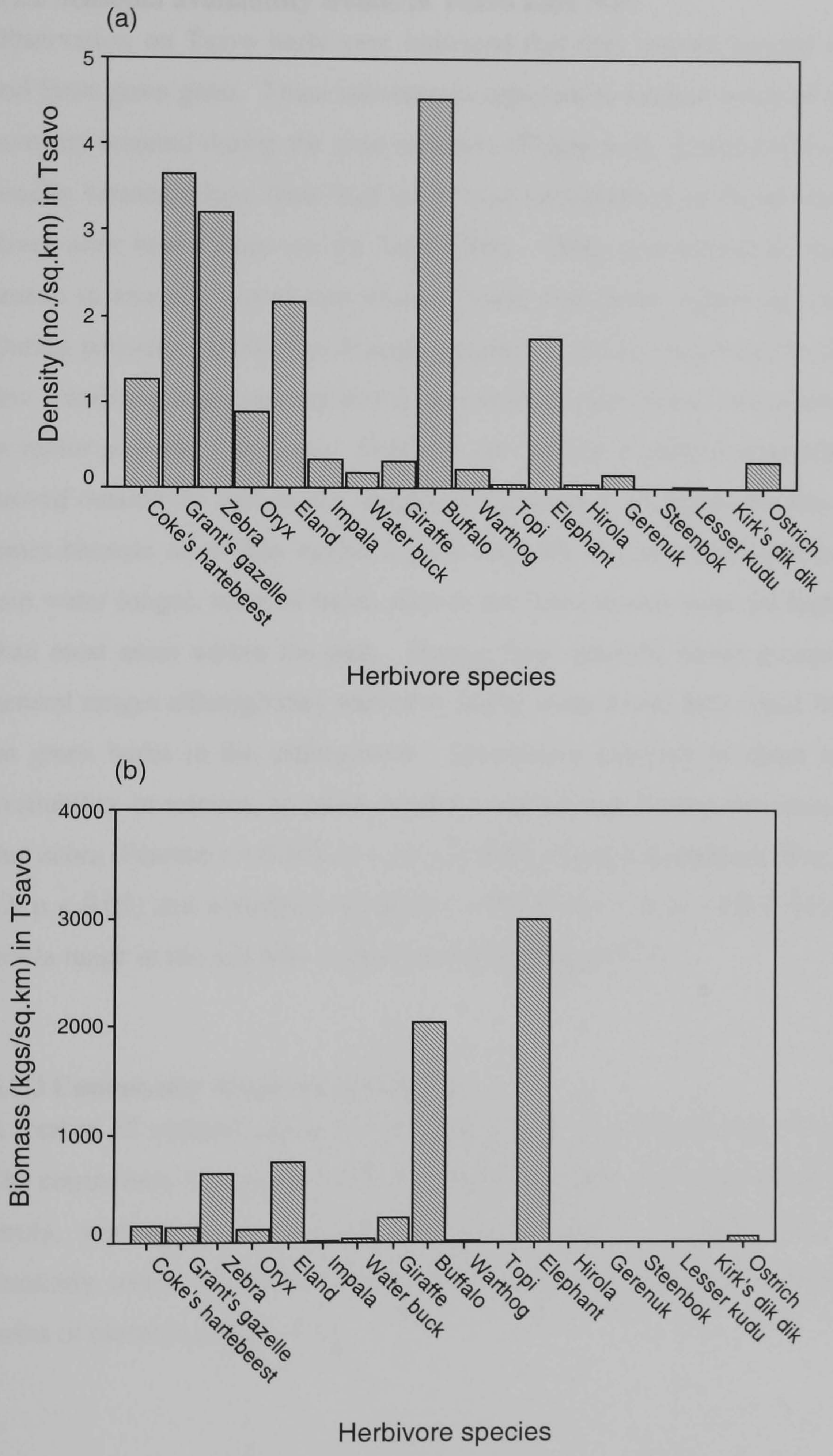


Figure 6.1 Mean density (per km²) and biomass (unit weights were based on data used by Coe (Coe et al., 1976)) of herbivore species observed on Tsavo hirola range between 1998 and 2000.

6.2.2 Seasonal availability trends in Tsavo East N.P.

Observation on Tsavo herbivores indicated that they moved around in search of water and fresh green grass. These movements appeared to explain much of the variation in the numbers counted during the road transects (Figure 6.2). Large herbivore concentrations usually formed where there had been local precipitation or flood waters from the Voi River after heavy rains on the Taita Hills. Other concentrations occurred in the dry season in swampy places that retained water and green vegetation long after the rains. During periods of prolonged drought, animals in these concentrations dispersed, with the few remaining ungulates occurring near drying water holes, and places with wind-mills or motor powered bore holes. However, as vegetation quality deteriorated, most animals moved outside the park to the neighbouring ranches. Ranches became attractive at such times because other than having a good network of piped water and large dams to keep rain water longer, some of them, such as the Taita Ranch received higher annual rainfall than most areas within the park. During these periods, hirola groups maintained their general ranges although they moved to bushy areas where they could find shade and feed on green herbs in the undergrowth. Correlation analyses of mean monthly herbivore availability in relation to mean monthly rainfall data during the study period indicated that zebra (Pearson $r = 0.658$, $n = 12$, $p < 0.05$), Coke's hartebeest (Pearson $r = 0.651$, $n = 12$, $p < 0.05$) and waterbuck (Pearson $r = 0.733$, $n = 12$, $p < 0.01$) occurred more on the hirola range in the wet than in the dry season (Figure 6.2).

6.2.3 Community structure in Garissa

A total of 12 ungulate species were observed on the hirola range in Garissa (Figure 6.3). The community was numerically dominated by cattle, sheep and goats, followed by topi, hirola, warthog, water buck and gerenuk (Figure 6.3a) among the wildlife species. Similarly, cattle, followed by topi, waterbuck, hirola and giraffe contributed the most in terms of biomass (Figure 6.1b).

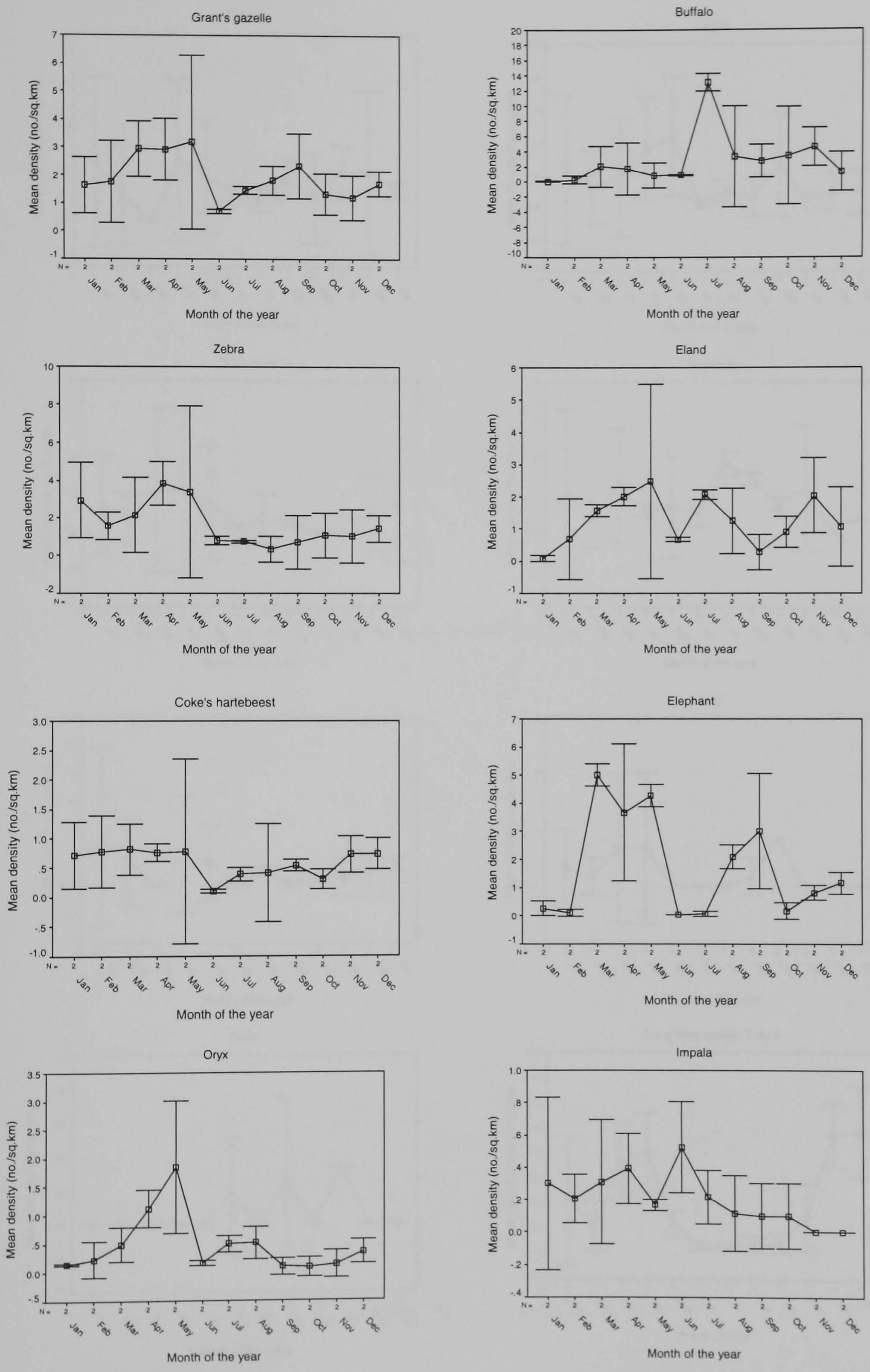
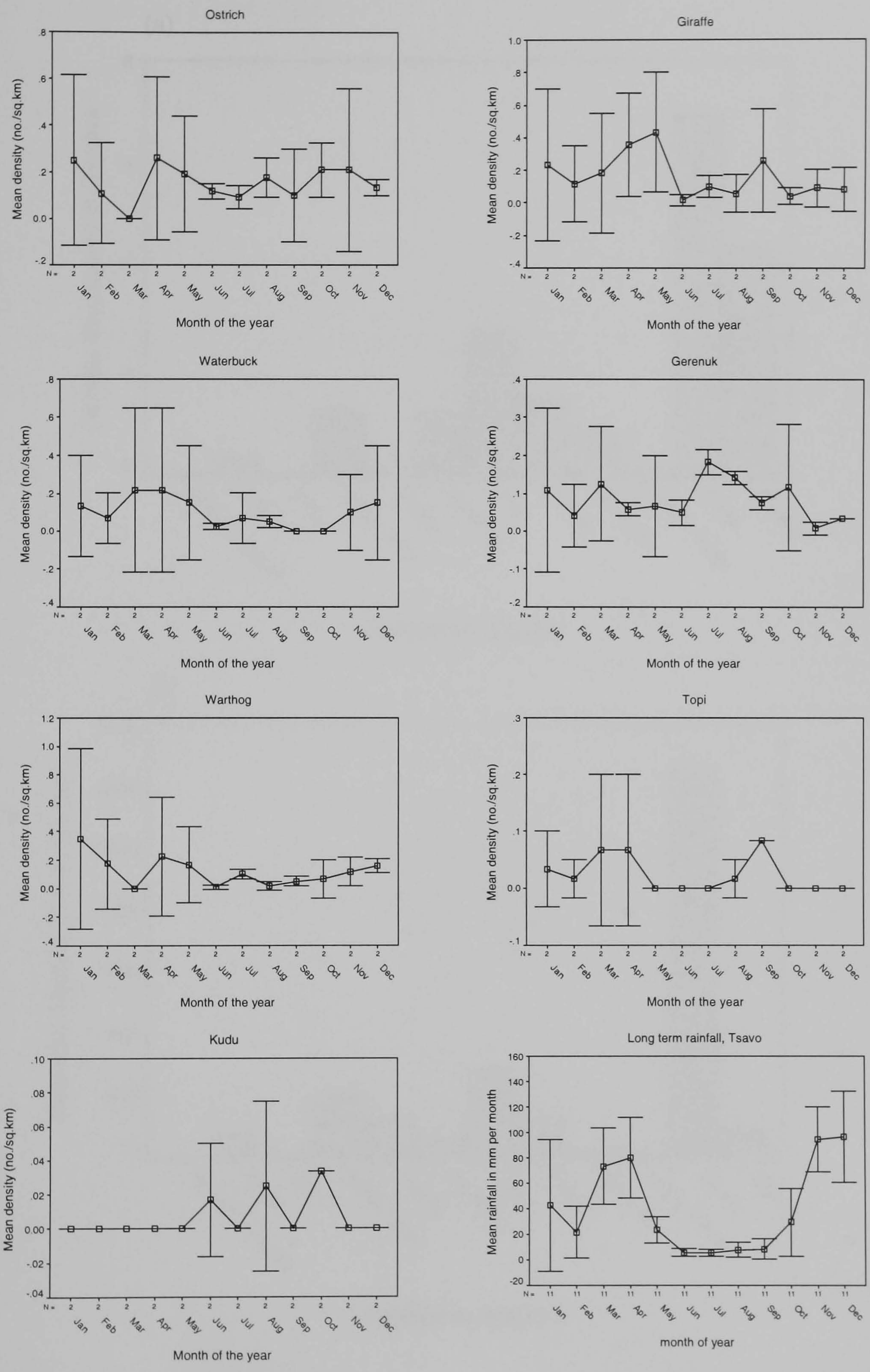


Figure 6.2: Average density (±2SE) of each animal species observed per month in the Tsavo NP study area between 1998 and 2000, and average monthly rainfall.



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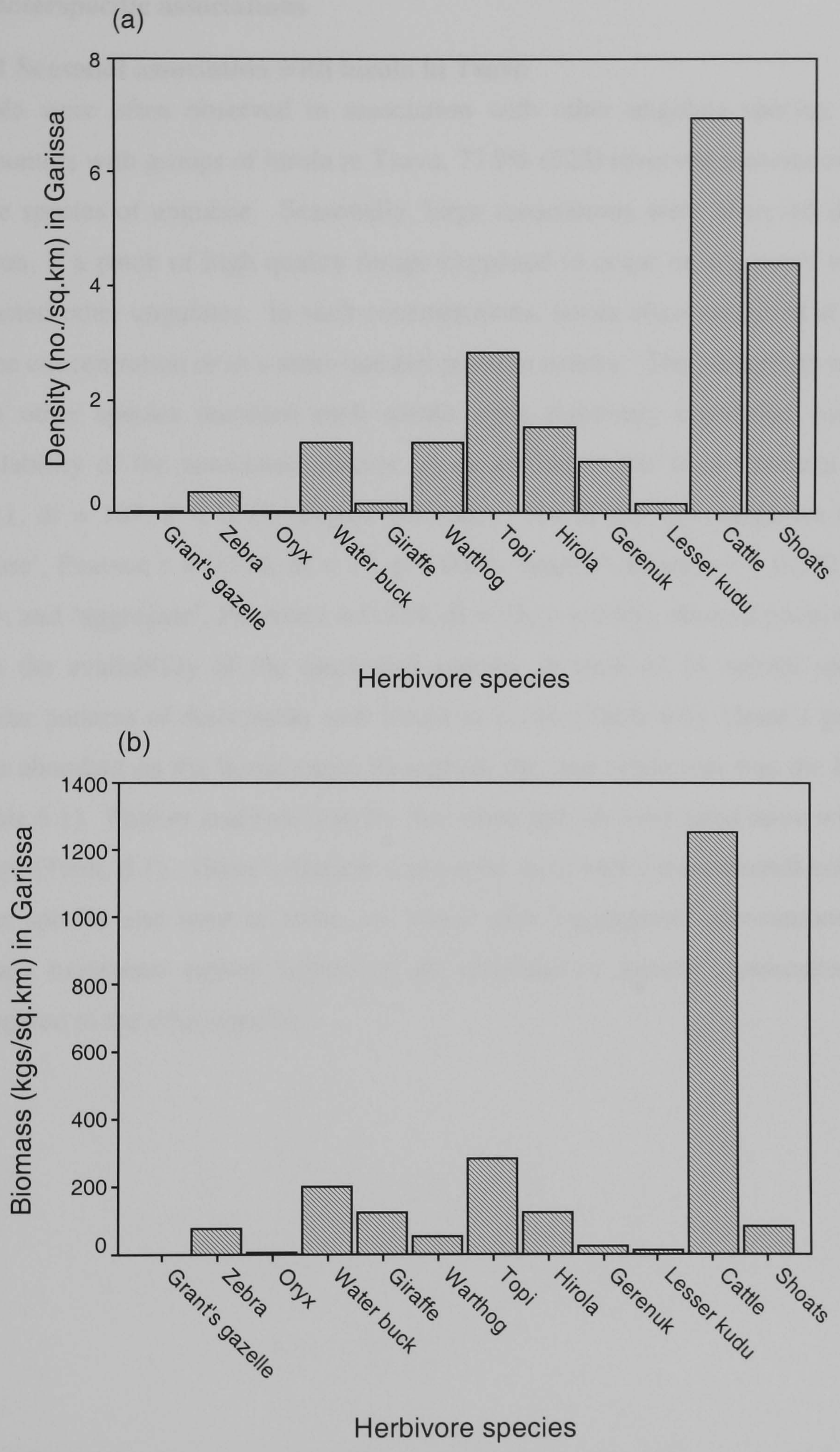


Figure 6.3 Mean density (per km²) and biomass (unit weights based on data used by Coe (Coe et al., 1976)) of herbivore species observed in the Garissa hirola range between 1998 and 2000.

6.3 Interspecific associations

6.3.1 Seasonal association with hirola in Tsavo

Hirola were often observed in association with other ungulate species. Out of 674 encounters with groups of hirola in Tsavo, 77.9% (525) involved associations with one or more species of ungulate. Seasonally, large associations were observed during the wet season, if a patch of high quality forage happened to occur on a group's range and thus attracted other ungulates. In such concentrations, hirola often remained at the periphery of the concentration or in a semi-isolated position nearby. The percentage of associations with other species recorded each month were positively correlated with percentage availability of the associated species, as quantified in the road transects (Pearson $r = 0.511$, $df = 107$, $P < 0.05$) (Figure 6.4 a&b). All of the sub-categories of association ('close', Pearson $r = 0.734$, $df = 77$, $p < 0.05$; 'nearby', Pearson $r = 0.272$, $df = 77$, $p < 0.05$; and 'aggregate', Pearson $r = 0.379$, $df = 53$, $p < 0.05$), showed positive correlations with the availability of the associated species. A total of 14 animal species showed regular patterns of association with hirola in Tsavo (Table 6.1). Grant's gazelle was the most abundant on the hirola range throughout the year while topi was the least abundant (Table 6.1). Further analyses indicate that some species associated more with hirola than others (Table 6.1). Grant's Gazelle associated most with hirola overall compared to the other species and most in terms of 'close' and 'aggregated' associations (Table 6.1). Coke's hartebeest ranked highest as an associate in 'nearby' association with hirola compared to the other species.

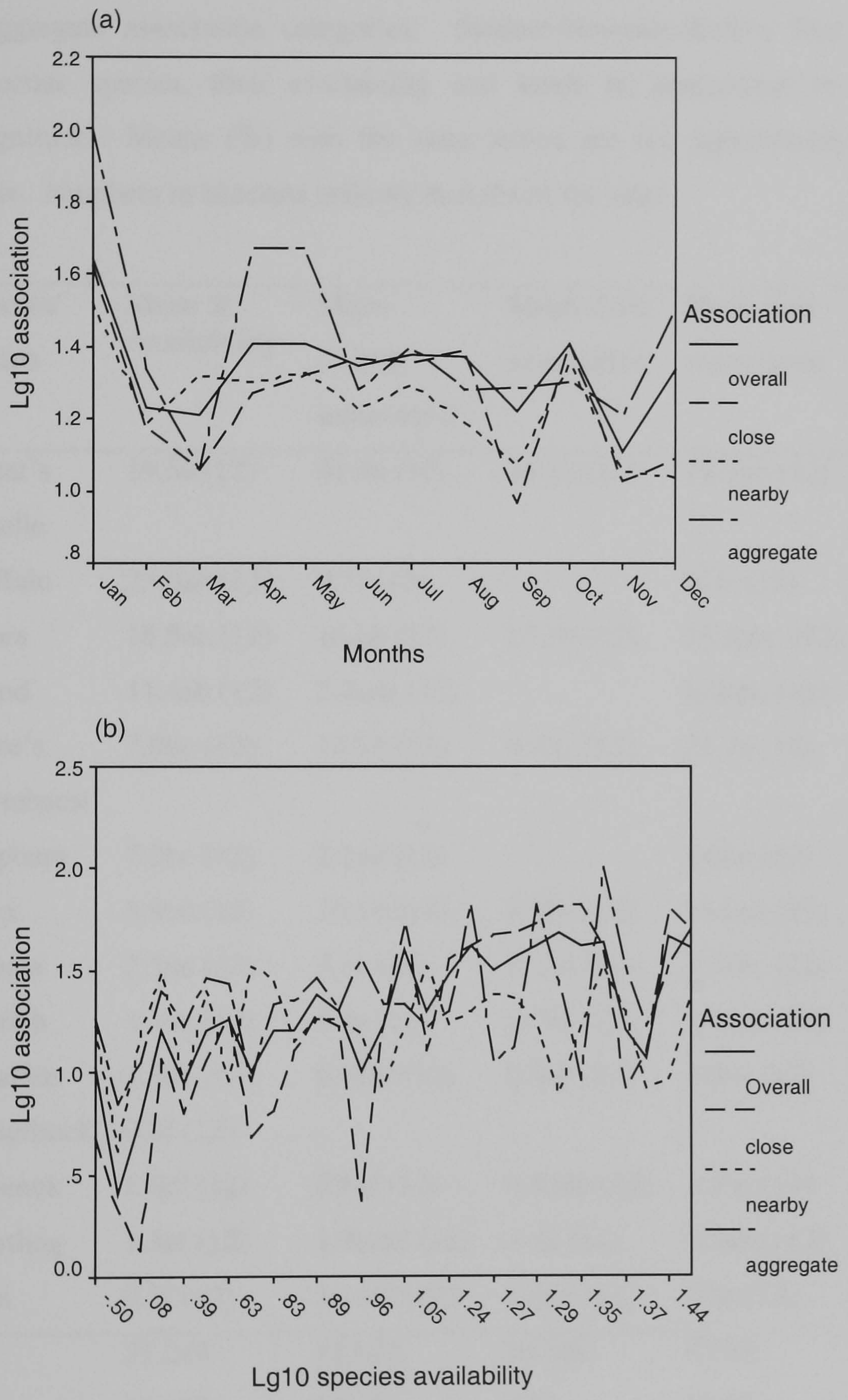


Figure 6.4: Average seasonal variation in the frequency of associations between hirola and other species of ungulates (a) and variation in associations with other ungulates in relation to their availability. Data were collected between June 1998 and May 2000.

Table 6.1: Tsavo hirola associates showing their mean % availability %close, %near and %aggregate association categories. Student-Newman-Keul's Test (SNK) shows the associate species, their availability and kinds of association in order of reducing magnitude. Means (%) with the same letters are not significantly different from the other. Numbers in brackets indicate months of the year.

Species/ Means	Mean % Availability	Mean overall association	Mean close association	Mean near association	Mean aggregate association
Grant's gazelle	19.5a (12)	41.4a (12)	54.1a (12)	18.7ab (12)	36.5a (12)
Buffalo	25.0ab (12)	0.3f (12)	-	0.7c (12)	0.9c (12)
Zebra	16.9ab (12)	16.6b (12)	17.3b (12)	13.8abc (12)	14.1ab (12)
Eland	11.4ab (12)	2.3cde (12)	-	6.0abc (12)	5.6abc (12)
Coke's Hartebeest	7.0bc (12)	13.5b (12)	9.3bc (12)	21.2a (12)	17.7ab(12)
Elephant	7.2bc (12)	2.1cd (12)	-	2.0bc (12)	12.0bc (12)
Oryx	3.9cd (12)	10.1b (12)	8.7bc (12)	18.6ab (12)	-
Impala	2.5de (12)	5.1c (12)	5.1cd (12)	5.5abc (12)	1.4bc (12)
Ostrich	1.8de (12)	3.9c (12)	1.9de (12)	5.0abc (12)	8.7abc (12)
Giraffee	1.5de (12)	0.9def (12)	0.0de (12)	2.8bc (12)	1.2c (12)
Waterbuck	0.8f (12)	-	-	-	-
Gerenuk	1.0ef (12)	0.8ef (12)	0.45de (12)	1.3bc (12)	1.4bc (12)
Warthog	1.3ef (12)	1.9cdef (12)	1.5e (12)	3.3abc (12)	0.6c (12)
Topi	0.2f (12)	1.1def (12)	1.6de (12)	0.9c (12)	-
F	25.249	42.622	34.100	5.178	3.343
df	13,139	12,101	9,73	12,67	7,43
P	< 0.01	<0.01	<0.01	<0.05	<0.05

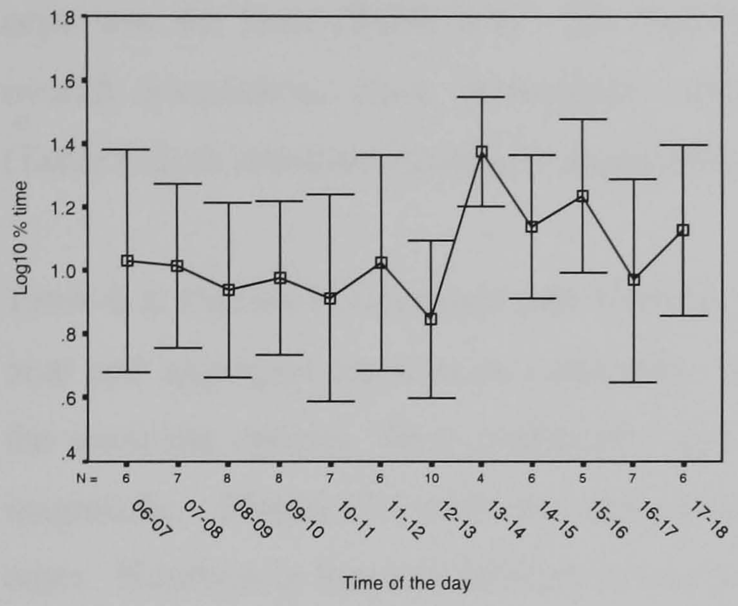
6.3.2 Diurnal variation in interspecific associations with hirola in Tsavo

Hirola associated more with other species in the early morning, during peak resting times and in the late evening. This may have been because hirola groups moved towards open areas for grazing in the morning and evening, places where they were more likely to meet other ungulates (e.g., Grant's gazelle, Coke's hartebeest, topi and zebra, Figure 6.5). On other occasions groups of other ungulates could be seen coming closer to hirola as night approached. An early morning check indicated that the association often persisted through the night. However, despite these observations, statistical analysis of the data obtained indicated no significant variations in the levels of association at different hours of the day for wet season observations ($F = 0.910$, $df = 11,68$, $P > 0.05$, Figure 6.5a), dry season ($F = 0.323$, $df = 11,89$, $P > 0.05$, Figure 6.5b) and all seasons combined ($F = 0.619$, $df = 11,169$, $P > 0.05$). However, a comparison of total association between wet and dry season indicated that hirola associated more during the wet season ($F = 5.874$, $df = 1,179$, $P < 0.05$, Figure 6.5c).

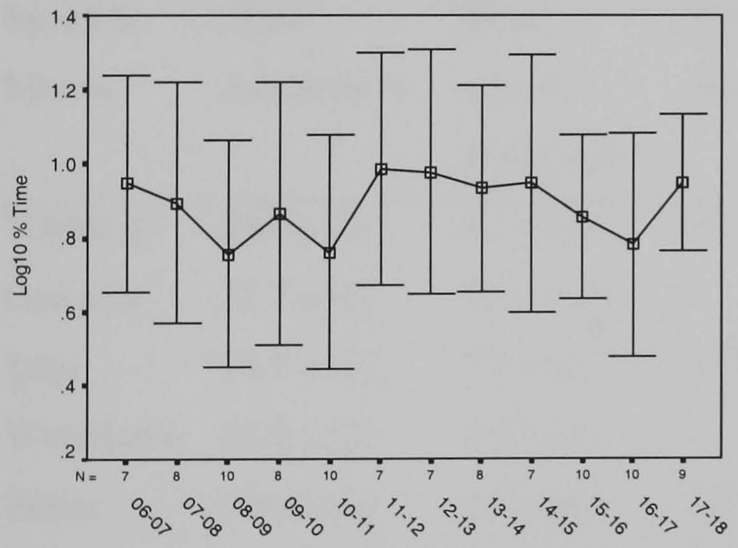
6.3.3 Association with hirola in Garissa

From a total of 122 field hirola encounters in Garissa, 28.6% (35) involved an association with one or more species of ungulate. Transect counts revealed that 12 wildlife species were available for association on the hirola range. Hirola were observed to associate with only 7 of these (Table 6.2). The other species, included the lesser kudu (mostly solitary and in bush habitat), buffaloes (preferring forest and riverine habitats away from hirola and very gregarious) and giraffe (shy as a result of frequent poaching and occupying bush areas with scant grass herb cover that is unsuitable for hirola). Field observations on ungulates also indicated that local migration of topi and buffalo occurred. During the Garissa dry season, they moved southwards to the coastal forest areas, where there was generally some rainfall at this time and thus abundant tall green grass and watering points. In the wet season, as resources became widely dispersed, they moved north into the hirola range. It was not possible to access many areas within the hirola range due to security risks and the difficulty of travelling during the wet season. However, the data collected indicated that hirola interspecific association were not correlated to overall availability of associated species, as they were in Tsavo ('overall' Pearson $r = 0.191$, $df = 12$, $p > 0.05$), 'close' (Pearson $r = 0.335$, $df = 7$, $p > 0.05$), 'nearby' (Pearson $r = 0.005$, $df = 9$, $p > 0.05$), and 'aggregate' associations (Pearson $r = -0.475$, $df = 4$, $p > 0.05$).

(a) Wet season diurnal association



(b) Dry season diurnal association



(c) Wet versus dry seasonal diurnal associations

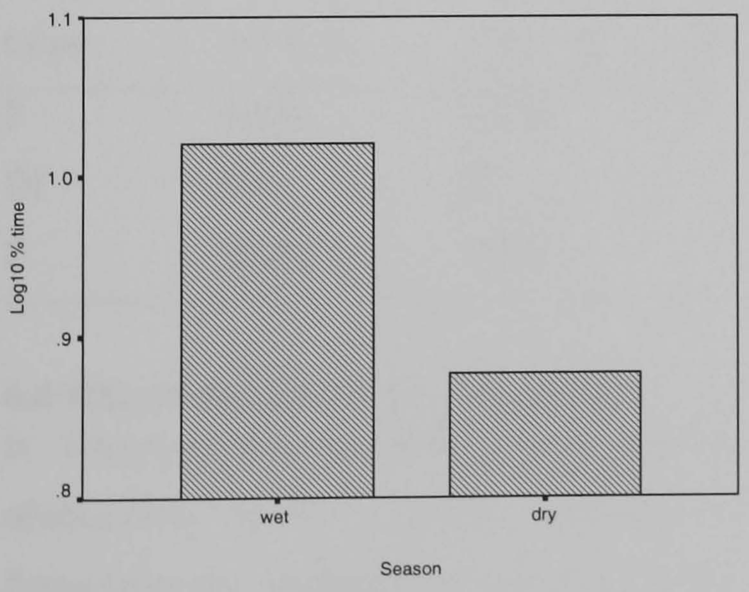


Figure 6.5: Comparison of hirola diurnal levels of association (mean ± SE) between wet and dry season in Tsavo between 1996 and 2000.

However, some species were more abundant on the hirola range than others (Table 6.2). Warthog was the most abundant and thus available for association on the range while oryx was the least (Table 6.2). No significant results were obtained with respect to overall association, close association, nearby association and aggregate association (Table 6.2) in relation to associate availability.

Table 6.2: Garissa hirola associates showing mean percentage availability, overall, close, near and aggregate association categories. Student-Newman-Keul's Test (SNK) shows the associate species, their availability and kinds of association in order of reducing magnitude. Means (%) with the same letters are not significantly different from the other. Numbers in brackets indicate survey period (2).

Species/ Means	Mean Availability	Mean overall association	Mean close association	Mean near association	Mean aggregate association
Warthog	29.0 a (2)	9.3 a (2)	10.0 a (2)	10.0 a (2)	-
Gerenuk	21.7 a (2)	18.6 a (2)	-	28.3 a (2)	30.0 a (2)
Topi	16.5 a (2)	32.3 a (2)	55.0 a (2)	18.3 a (2)	-
Waterbuck	19.8 a (2)	4.8 a (2)	-	8.3 a (2)	10.0 a (2)
Zebra	7.9 ab (2)	4.8 a (2)	5.0 a (2)	8.3 a (2)	-
Ostrich	4.1 ab (2)	16.4 a (2)	10.0 a (2)	26.7 a (2)	10.0 a (2)
Oryx	1.0 b (2)	13.9 a (2)	20.0 a (2)	-	50.0 a (2)
F	4.936	1.498	-	0.201	-
Df	6,7	6,5	-	6,2	-
P	<0.05	>0.05	-	>0.05	-

6.4 Effects of association on vigilance

In Tsavo, hirola associated most frequently with Grant's gazelle. However, daily observation on hirola groups showed that these associations were very variable. Sometimes the foraging movements of hirola took them in an area where Grant's gazelle were present and sometimes the opposite occurred. However, hirola, especially the male were also observed to threaten or chase Grant's gazelle males away, particularly when the gazelle males came too close and nosed hirola calves, a behaviour that occurred on a number of occasions.

In order to test if there might be any anti-predator benefit from the interspecific association between hirola and Grant's gazelle, one hour observation periods (with scan samples collected at five minute intervals) were carried out on hirola alone (45 hours), Grant's gazelle alone, (41 hours) and hirola/Grant's gazelle associations (31 hours) (Table 6.3). These data were collected between 1000hrs and 1600hrs. Early and late hours of the day were avoided because, at these times of active feeding, hirola and Grant's gazelle tended to be found in loose and constantly changing association with other herbivores such as Coke's hartebeest, oryx and zebra. Percentage vigilance per scan hour per group was calculated from the proportion of time animals were observed in a head-up posture (Chapter III, section 3.3.3).

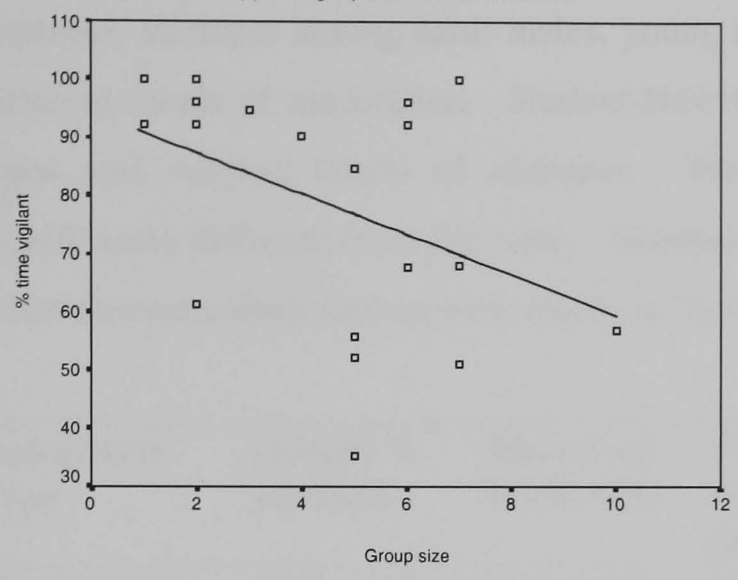
Results indicated that vigilance in both hirola (Pearson $r = -0.37$, $df = 45$, $p < 0.05$) and Grant's gazelle (Pearson $r = -0.05$, $df = 41$, $p < 0.01$) decreased with increase in group size (Figure 6.6a&b). While in isolation, hirola were the most vigilant compared to Grant's gazelle (Figure 6.6c, Table 6.4). However, hirola were least vigilant compared to Grant's gazelle while in association (Figure 6.6c, Table 6.4). There were no significant differences in levels of alertness among adult males, young males, females or young hirola, or of Grant's gazelle with respect to the type of association (Table 6.4); however, female hirola were more alert while in isolation (Table 6.4).

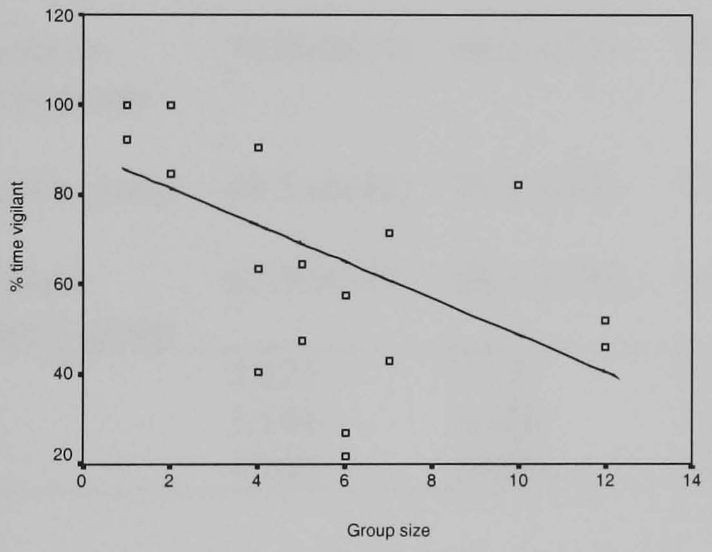
6.5 Conclusions

14 ungulate species occurred commonly in the Tsavo study area, while 7 occurred in Garissa. Large concentrations occurred in Tsavo where green grass and drinking water was locally abundant. Other concentrations were associated with the presence of artificial dams and pumped borehole water. However, water was not the only cause of ungulate concentrations because watering points in areas without food were eventually deserted. In general, large concentrations formed as a response to resource availability, which in turn were influenced by rainfall, a majority of concentrations thus occurred in the wet season. Similarly, in Garissa, large concentrations of herbivores were associated

Table 6.3: Summary of one hour scan sample data taken between 1000hrs and 1600hrs on varying group sizes of hirola alone, Grant's gazelle alone and hirola and Grant's gazelle associations between September 1999 and September 2000 in Tsavo East National Park.

Species	Group size	n	Mean % alert ± SD
Hirola alone	1	4	96.2±4.2
	2	8	87.5±16.3
	3	2	94.8
	4	2	90.4
	5	10	57.3±20.4
	6	9	85.5±13.3
	7	9	73.0±21.5
	10	1	56.9
Total scan hours		45	
Grant's gazelle alone	1	6	96.2±4.2
	2	9	89.7±7.7
	4	6	64.8±22.4
	5	4	56.1±9.8
	6	5	38.2±17.9
	7	5	60.0±15.7
	10	2	82.3
	12	4	49.2±3.4
Total scan hours		41	
Hirola in association with Grant's gazelle	1	1	76.9
	6	17	59.8±23.4
	7	12	65.2±18.9
	8	1	61.3
Total scan hours		31	
Grant's gazelle in association with hirola	1	4	100
	3	8	65.3±15.2
	4	4	90.4
	5	10	64.6±26.8
	9	4	42.7
	10	1	69.2
Total scan hours		31	


(a) Hirola group size in relation to alertness


(b) Grant's gazelle group size in relation to alertness

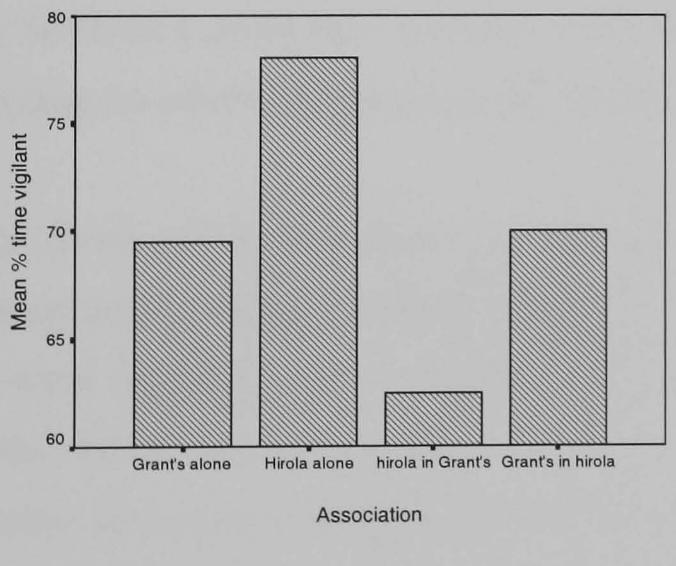

(c) Varying levels of association and vigilance

Figure 6.6: Relationship between group size and alertness for lone hirola groups (a) and Grant's gazelle. A comparison of vigilance on hirola in a group of Grant's gazelle, Grant's gazelle in a group of hirola, and isolated hirola and Grant's gazelle groups (c). Fewer data points on graphs (a) and (b) are as a result of data overlaps (see Table 6.3).

Table 6.4: Tsavo hirola and Grant's gazelle associations showing their mean overall % alertness, alertness among adult males, young males, adult females and young females at different levels of association. Student-Newman-Keul's Test (SNK) shows association types and varying levels of alertness. Means (%) with the same letters are not significantly different from the other. Numbers in brackets indicate the number of hours when alertness observations were made on each type of individual and group.

Association Type	Overall % alertness	Adult male % alertness	Young male % alertness	Adult female % alertness	Young female % alertness
Hirola group	78.0 a (45)	81.1 a(35)	62.5 a (17)	80.7 a(38)	77.8 a(23)
Grants in hirola group	70.0 ab(31)	69.2 a(26)	75.4 a(5)	66.5 a(22)	84.6 a(5)
Grant's group	69.5 ab(41)	73.1 a(39)	55.2 a(7)	66.8 a(15)	55.1 a(9)
Hirola in Grant's group	62.5 b(31)	68.1 a (30)	58.2 a(17)	61.4 a(22)	66.6 a(21)
F	2.825	2.237	0.852	3.381	2.17
Df	3,144	3,126	3,42	3,93	3,54
P	<0.05	>0.05	>0.05	<0.05	>0.05

with the presence of resources on the hirola range during the wet season. The presence of other herbivores could have provided some benefit to hirola through grazing facilitation (including the effects of trampling and grazing), particularly within hirola core areas.

Observations on lion movements and prey selection indicated that they preyed on locally abundant prey (Chapter IV, section **4.2.8**). Data on hirola associations in Tsavo indicated that while buffaloes were abundant herbivore, hirola associated most with Grant's gazelle, whose abundance came close to that of buffaloes. Overall associations rates increased with an increase in the availability of associating species. However, in Garissa, while warthog was the most numerous wild species on the range, hirola were observed to associate most with topi, whose numbers were minimal during the dry season. In Tsavo, hirola association rates were higher during the wet season. Further, hirola were less vigilant while in association with Grant's gazelle. These results indicate that hirola may have derived an anti-predator benefit from this association, especially in the wet season when most association occurred. This also suggests that hirola may have been at higher risk from predation during the dry season when little association occurred and when many of the migratory ungulate species had left the area. However, further research is required to determine the advantages and disadvantages of other associate species to hirola during all hours of the day and if possible, during the night.

Chapter VII:

Ecology of Hirola

7.1 Introduction

The basic question of why members of a particular species are present in some places and absent in others is of enormous practical importance to conservation biologists. Most studies on the geographical ranges of species examine features of the range such as its extent, shape, and overlap with neighbouring species at some point in time. However, these features are influenced by environmental conditions and are subject to change when environmental conditions change (Brown et al., 1996). Populations tend to be larger and less variable at the center of the species' range because the environmental conditions there are more suited to the species (Curnutt et al., 1996). This implies that in cases of extreme environmental perturbations, the final population of a species would be found near the centre of its historical range (Mehlman, 1997). However, human influences (hunting, habitat destruction, and introduced species) affect species distributions (Towns & Daugherty, 1994), with the result that the range that retains the remnant species population (Towns & Daugherty, 1994; Channell & Lomolino, 2000), is not necessarily in the species' optimal habitat. In fact, since people and their livestock often compete for similar resources, the remnant population may often be in sub-optimal habitat. The current hirola distribution both in Tsavo and Garissa may well be a product of these processes.

Antelopes are ground dwelling herbivores, so that the plant communities within their ranges provide not only a major part of their physical environment, including cover and shade for instance, but also supply all their food and, for many species, the majority of their water and mineral intake. Most antelopes are grazers and a majority of them occur within plant communities that support large proportion of grasses (Jarman, 1974). Obviously shade is least abundant in open grasslands or semi arid environments, while cover (visual screening) has a more complex relationship with the vegetation community structure and to the size and behaviour of the antelope species (Jarman, 1974). Hirola may have to compromise between occupying the best grazing areas and the need for shade and, possibly, cover against predation.

Variation in topography, soil conditions, fire regimes, intra- and inter-annual variation in rainfall, as well as spatial and temporal variation in the distribution of surface water, is important in determining the heterogeneity of savanna structure and its function on different scales (Frost et al., 1986). This heterogeneity, expressed most importantly in the diversity and distribution of plant communities and habitat types, is of utmost importance for the distribution and habitat utilization of large forbivores (McNaughton & Georgiadis, 1986; Dunham, 1994; Ben-Shahar, 1995).

Irregular water availability in semi-arid savannas affects both the possibilities of drinking and the distribution, quantity and quality of food for large forbivores (Skarpe & Bergstrom, 1986; McNaughton & Georgiadis, 1986). In semi-arid savannas of southern and eastern Africa, many, but not all, species of forbivores undertake long distance movements in response to water and food availability (Crowe, 1995). On the other hand, many species have a degree of water independence and can survive for long periods or even indefinitely on water contained in their food plants; some graze preferentially at times when dew forms on their forage.

Food quality and quantity are always temporally and spatially variable in semi-arid environments. These variations are usually caused by soil types and rainfall amounts and seasonality (East, 1984; Ben-Shahar & Coe, 1992; Fritz & Duncan, 1994). Scattered and often erratic showers create spatial variation in food which forces grazers such as hirola to make local shifts in search of quality pasture. The search for resources within an area often determines the home range of a species. Hence, relatively small home ranges among members of a species in a particular habitat may indicate that the habitat is of high quality. Furthermore, climatic factors will affect the nutritive value of forage: increasing temperature and light intensity stimulate stem development and lignification and reduce the stem and leaf digestibility of tropical grasses. The nutritive value decreases by 1% per unit if the temperature increases by 1°C ('tMannetje, 1984). When protein content falls below 6% the microbial process does not work well enough to digest food in the rumen and intake is reduced (Mentis & Duke, 1976). Therefore, the retention rate increases and the animal is not able to maintain its weight and body condition. In most savanna grasslands (*Themeda triandra* grassland), grass protein ranges between 3-6%, while the protein content of most shrubs and forbs, leguminous and non-leguminous plants, which contribute about 3% of the total sward, ranges between 10-20% (McKay, 1971).

Predation risk influences an array of behaviours in individual animals, including foraging, vigilance, patch use, diet and habitat selection, reproductive behaviour, and parental care (Lima & Dill, 1990). Habitat structure can influence vigilance behaviour through its effect on early predator detection. Detecting a terrestrial predator is dependent on visibility (Lamprey, 1963a; Pulliam & Caraco, 1984), and animals have been observed to display less vigilance when further from obstructing cover (Elgar, 1989; Lazarus & Symonds, 1992) and when they are near a refuge (Elgar, 1989). In the case of hirola, which inhabit grasslands with scattered bushes, grass heights may affect their vigilance and the risk of predation. This chapter aims to quantify hirola home ranges and the resources and other characteristics of these ranges, to provide a basis for comparing reproductive success and survival.

7.2 The area occupied by hirola in Tsavo National Park

Hirola occupied and used only a part of the Tsavo East National Park, south of the Galana River. In 1963, hirola translocated to Tsavo were released at Ndara plains and Irima Hill (Monthly Game Reports, Tsavo East National Park, December 1963, Figure 7.1). The current distribution (Figure 7.1) indicates that hirola moved away fromthese sites to settle at their present location. Hirola appear to have selected a region of relatively less rainfall compared to other surrounding sites (Figure 7.1). The Irima area is at a higher elevation (600m asl) than the current range which has an elevation of 150 to 300m asl. Both the Irima and Ndara areas are characterised by black cotton soils that are usually waterlogged in the wet season, in contrast to the red sandy soils of the current hirola range. In addition, the flat plains at Irima and Ndara are often flooded during the rain seasons by flood waters from Mbololo and Maungu hills respectively. The combination of periodic flooding and black cotton produces an open plains habitat with uniform stands of tall grasses. The gently sloping parts of Irima and Ndara bear thick *Combretum/Commiphora* bushes. In contrast, the area currently occupied by hirola supports shorter grass species or more variable height with scattered trees and bushes.

7.3 Tsavo hirola group home ranges

A majority of the hirola population in Tsavo were in the area around Satao Camp (Figure 7.1). Observations of family group ranges also showed that there was very high overlap the ranges in this area (Figure 7.2). On average, hirola home ranges measured 81.5 ± 38.4 km^2 and varied between 26.0 and 164.7 km^2 (Table 7.1). The large variation in size could reflect variability in habitat quality and possibly disturbance from predation. Further observations indicated that some ranges overlapped completely with the ranges of a number of other groups. However, no ranges overlapped completely with only one other range. The M1 group had the largest home range and the highest overlap frequency with other groups. The B1 group showed no overlap, although it shared a common boundary with group B2 (Table 7.2). Despite the high degree of overlap, it was relatively rare for hirola groups to meet. They usually occupied parts of the range out of sight of their neighbours.

Within each home range there were particular small areas (called 'core areas) that hirola used most intensively. Some groups remained almost permanently on these core areas while others moved periodically to other core areas. An analysis of group ranges revealed that these core areas varied from 1 to 6 per group (Table 7.1). The Voi River group (VR) had the highest (6) number of core areas while Balguda 1 (B1) and Mukwaju 1 (M1) had only one. Core areas were typically on raised grounds with red soils. They generally had a short grass sword and were characterized by scattered bushes interspersed with open grass patches. Anecdotal observations indicated that hirola groups moved to those cores areas that had the most short green grass (following rain showers), and that they avoided sites with large herds of buffaloes or elephants, or that contained predators, especially cheetahs or lions. Core areas averaged 3.4 ± 1.3 km^2 in size. Group ranges tended to overlap in high quality core areas and on the rare occassions when groups merged for a while, they tended to do so at such places.

7.4 Rainfall and transient waterholes

Out of a total 674 group sightings, hirola were observed drinking water on only 10 occasions (1.5% of total observations). The current distribution of the population (Figure 7.1) shows that they occupy an area that receives on average less rainfall than surrounding areas (i.e., about 400 mm). The area occupied by the population was low in altitude (between 320 and 420m a.s.l.), and within this area they occur on both elevated

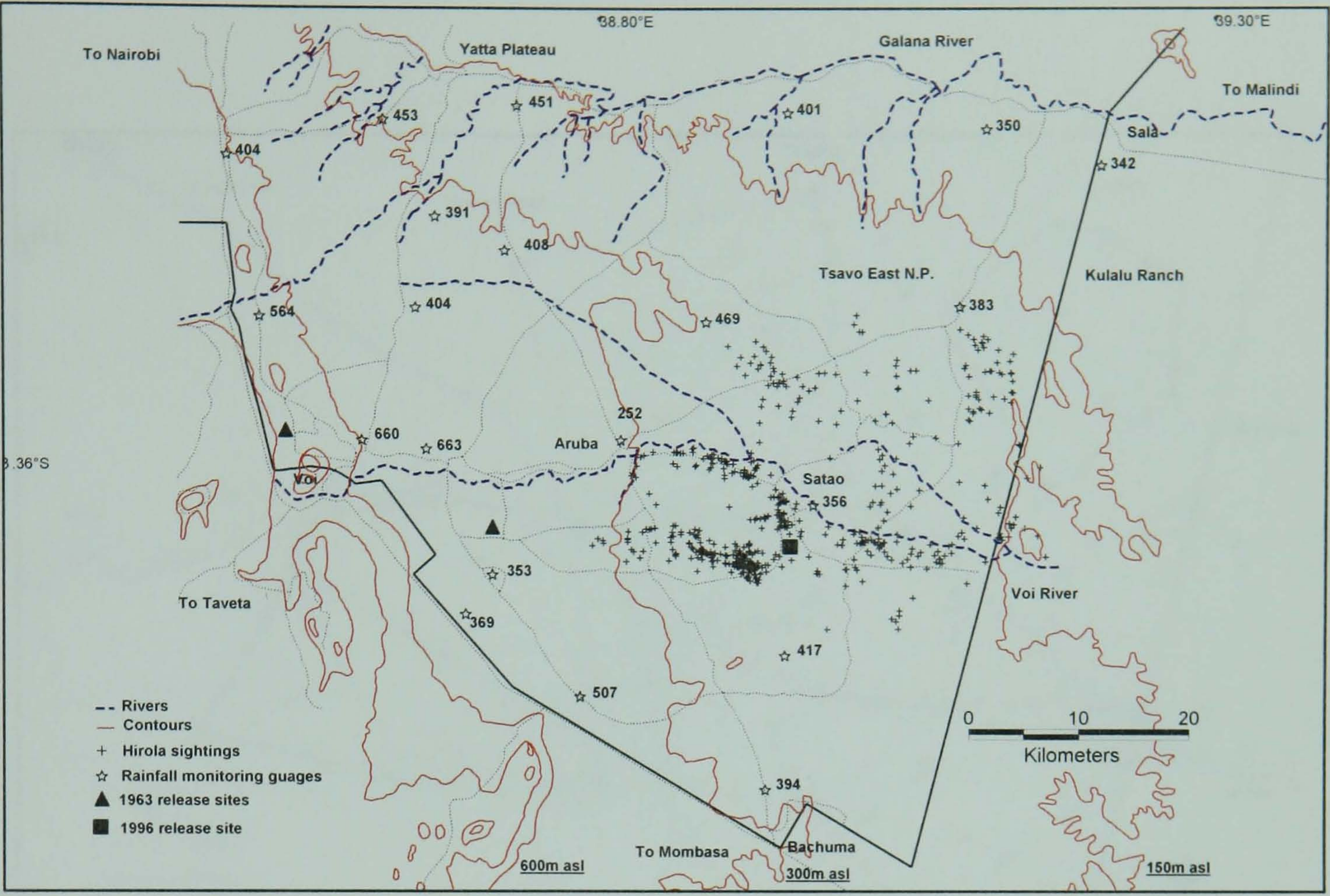


Figure 7.1: Map of Tsavo East National Park, south of Galana River Showing all sightings of hirola groups between September 1996 and December 2000. The map also includes the release sites for the 1963 and 1996 introductions, annual rainfall, and altitude.

areas with red soils and lower areas with black cotton soils. These areas were interspersed with flood plains that contained a number of shallow seasonal water holes (Figures 7.3 & 7.4). Despite the fact that hirola were very rarely seen drinking, 58.2% of their total time (392 sightings out a total 674) was spend grazing on fresh green grass growing on and around drying waterholes. I mapped nearly all the waterholes on the range occupied by hirola. The results showed a positive correlation between the number of waterholes per hirola home ranges and home range size (Pearson $r = 0.776$, $n = 9$, $p < 0.05$). Further, the degree of overlap with neighbouring group ranges was positively correlated with the number of waterholes (Pearson $r = 0.651$, $n = 9$, $p < 0.05$, Figure 7.3).

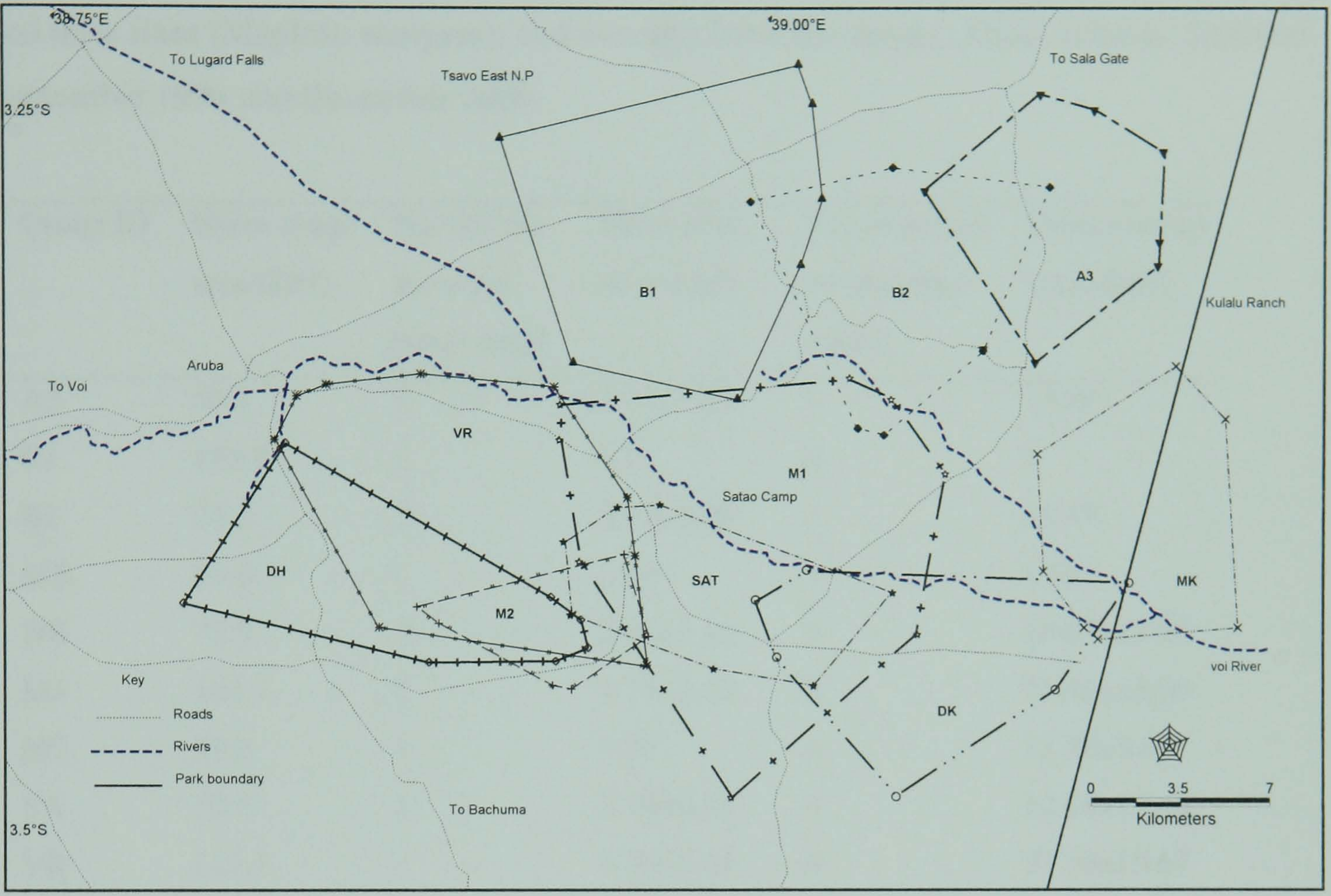


Figure 7.2: Map of Tsavo East National Park, south of the Galana River showing boundaries of the hirola group home ranges. Data were collected between September 1996 and December 2000.

Table 7.1: Tsavo hirola group home range sizes (Ranges V output); number of core areas and their sizes (MapInfo analyses); and overlaps between ranges. Data collected between September 1996 and December 2000.

Group ID	Home range area (km^2)	No. of core areas per home range	Mean core area (km^2)	No. of groups overlapping with it	Mean overlap areas (km^2)
A3	64.3	2	2.31±1.64	1	13.49
B1	110.8	1	3.51	0	0
B2	71.5	2	3.13±0.06	1	13.49
MK	63.6	1	1.40	1	1.28
DK	74.9	3	2.89±1.12	3	10.62±13.08
M1	164.7	5	3.79±1.20	6	31.41±13.06
M2	26.0	1	6.39	4	17.52±8.87
SA	55.9	2	3.49±0.26	4	12.68±13.45
VR	111.4	6	3.74±1.54	4	27.50±19.67
DH	69.59	4	3.70±0.61	3	20.99±8.48
Mean	81.5±38.4		3.43±1.28		

Table 7.2: Percentage overlap between the Tsavo hirola group home ranges. Overlaps were estimated using "Ranges V". Data were collected between September 1996 and December 2000.

Groups	M1	M2	MK	A3	B2	B1	VR	DK	DH	SAT
M1	-	2.9	-	-	2.1	0.2	7.3	14.6	-	31.9
M2	18.3	-	-	-	-	-	64.3	-	49.5	28.5
MK	-	-	-	-	-	-	-	5.4	-	-
A3	-	-	-	-	26.1	-	-	-	-	-
B2	4.6	-	-	23.5	-	7.7	-	-	-	-
B1	0.2	-	-	-	5.1	-	-	-	-	-
VR	10.9	13.5	-	-	-	-	-	-	33.7	7.1
DK	31.8	-	4.6	-	-	-	-	-	-	18.7
DH	-	18.0	-	-	-	-	52.4	-	-	0.1
SAT	94.1	13.4	-	-	-	-	14.0	24.8	0.1	-

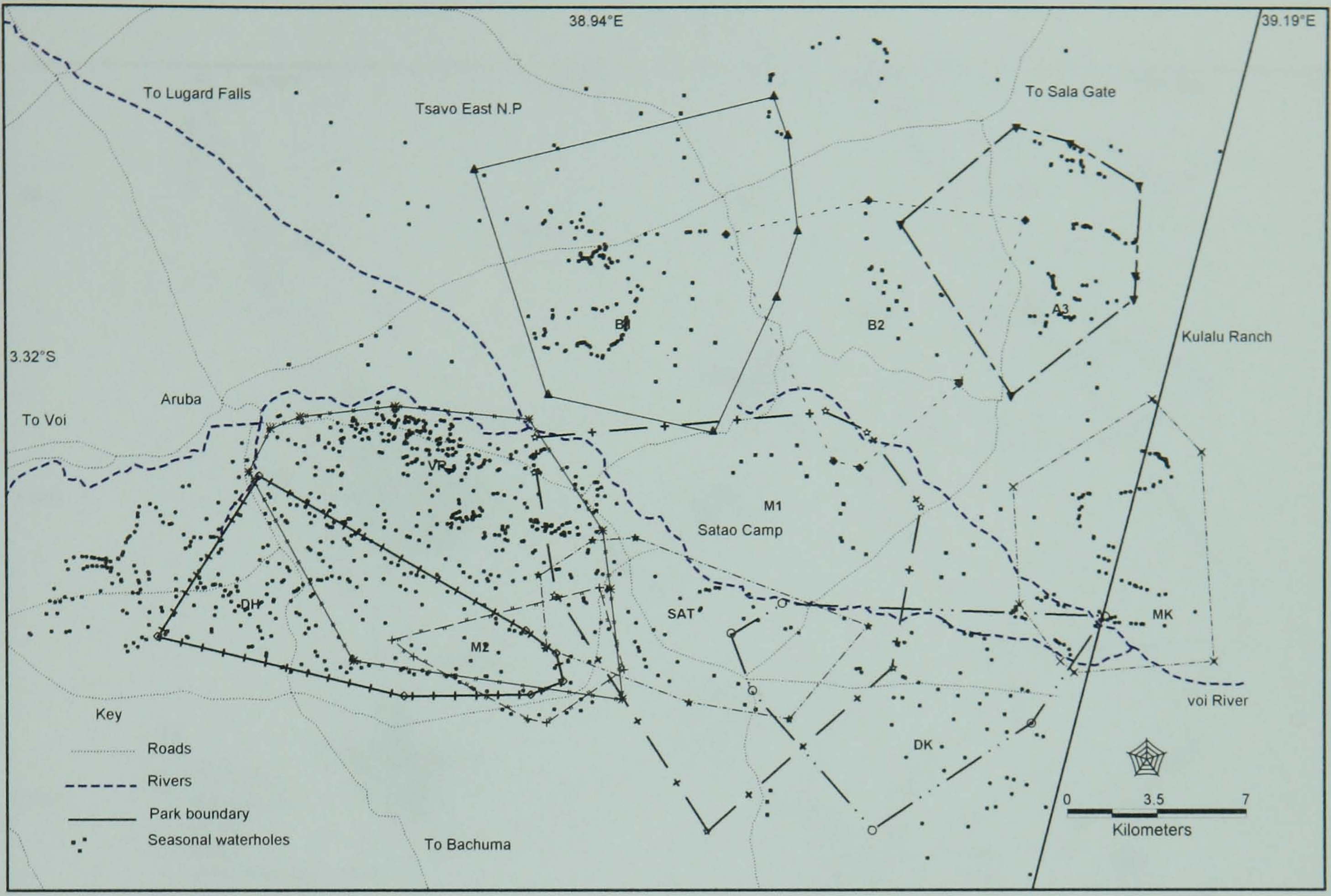


Figure 7.3: A map of Tsavo East National Park, showing overlap between hirola home ranges in relation to the availability of transient waterholes. Data collected between September 1996 and December 2000.

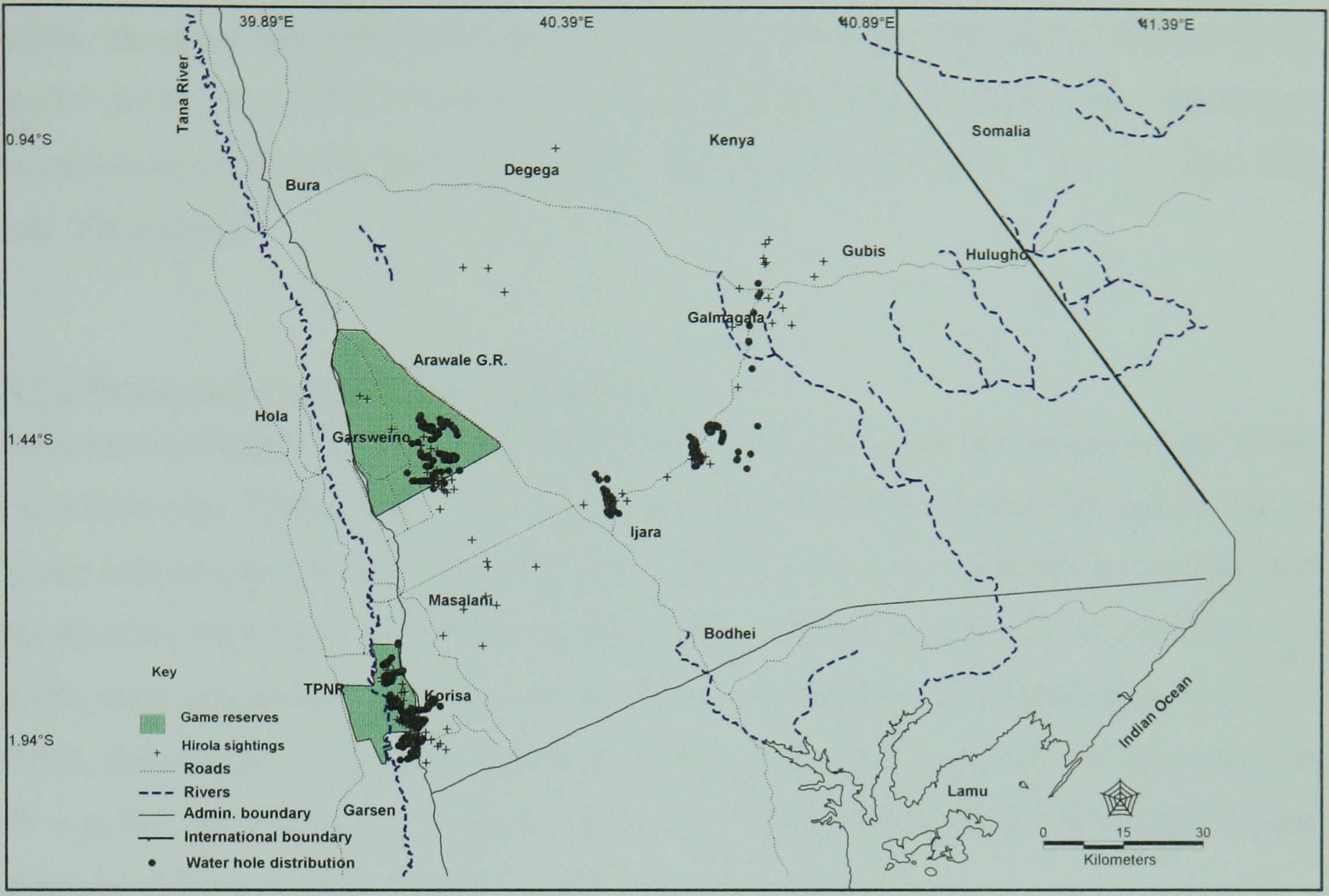


Figure 7.4: A map of Garissa east of the Tana River, showing hirola distribution in relation to the availability of transient waterholes between September 1996 and December 2000.

7.5 Vegetation community structure

7.5.1 Tsavo trees and shrubs

Data were collected on trees and shrubs, their densities and their structure, in the wet and dry season ranges of each hirola group (Table 7.3). There was no significant variation between seasonal ranges in the total number of trees and shrubs ($F = 0.001$, $df = 1,16$, $p > 0.05$), or of trees and shrubs taller than 1.8 m with crown diameter (CD) less than 5 m ($F = 0.287$, $df = 1,16$, $p > 0.05$), trees and shrubs shorter than 1.8 m with crown diameter (CD) less than 5 m ($F = 0.006$, $df = 1,16$, $p > 0.05$), or trees and shrubs shorter than 1.8 m high with CD more than 5 m ($F = 0.770$, $df = 1,3$, $p > 0.05$).

Overall comparison of group ranges indicate that there was no variation in total counts of trees and shrubs ($F = 1.249$, $df = 8,9$, $p > 0.05$), trees and shrubs taller than 1.8 m with crown diameter (CD) more than 5 m ($F = 0.164$, df = 8,3, $p > 0.05$) and trees and shrubs shorter than 1.8 m with crown diameter (CD) less than 5 m ($F = 1.174$, df = 8,9, $p > 0.05$). However, trees and shrubs taller than 1.8 m with crown diameter (CD) less than 5 m ($F = 5.142$, df = 1,10, $p < 0.05$) varied between group ranges (Figure 7.5). The largest numbers occurred in the MK group range, followed by those of B1, B2, A3, DH, M2, DK, VR and M1.

7.5.2 Tsavo and Garissa trees and shrubs

Data were collected on trees and shrubs densities in the wet and dry season ranges of the two hirola sites (Table 7.4). There was no variation between wet and dry season ranges in the total number of trees and shrubs ($F = 0.178$, df = 1,6, $p > 0.05$), or of trees and shrubs taller than 1.8 m with crown diameter (CD) less than 5 m ($F = 0.216$, df = 1,6, $p > 0.05$), trees and shrubs taller than 1.8 m with crown diameter (CD) more than 5 m ($F = 0.073$, df = 1,6, $p > 0.05$), trees and shrubs shorter than 1.8 m high with CD less than 5 m ($F = 0.731$, df = 1,6, $p > 0.05$) and trees and shrubs shorter than 1.8 m with crown diameter (CD) more than 5 m ($F = 0.183$, df = 1,6, $p > 0.05$).

Table 7.3: A comparison of Tsavo hirola group ranges showing the densities of trees and shrubs of various height and canopy size categories in the wet and dry season grazing ranges. Data was acquired from 30, 20m x 20m sample plots per group range per season and were collected between September 1996 and December 2000.

Group ID's	No./km^2 of all trees/shrubs		No./km^2 of tress/shrubs>1.8m, CD<5m		No./km^2 of trees/shrubs>1.8m, CD>5m		No./km^2 of trees/shrubs<18m, CD<5m		No./km^2 of trees/shrubs<1.8m, CD>5m	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
M1	22000	39000	1167	5000	0	1500	20833	32500	0	0
M2	22083	12083	3667	3333	333	333	18083	8417	0	0
MK	59000	43500	23250	11333	83	250	35667	31917	0	0
A3	95000	35167	9333	4250	0	667	85500	30250	167	0
B2	25000	79333	6000	10417	0	1500	19000	66667	0	750
B1	46166	31750	12000	9917	0	1667	34083	20167	83	0
VR	40583	21667	3667	1833	333	833	36583	18833	0	167
DK	25750	45833	2083	3917	0	1583	23667	40250	0	83
DH	37500	27667	6250	4417	0	1250	31250	22000	0	0

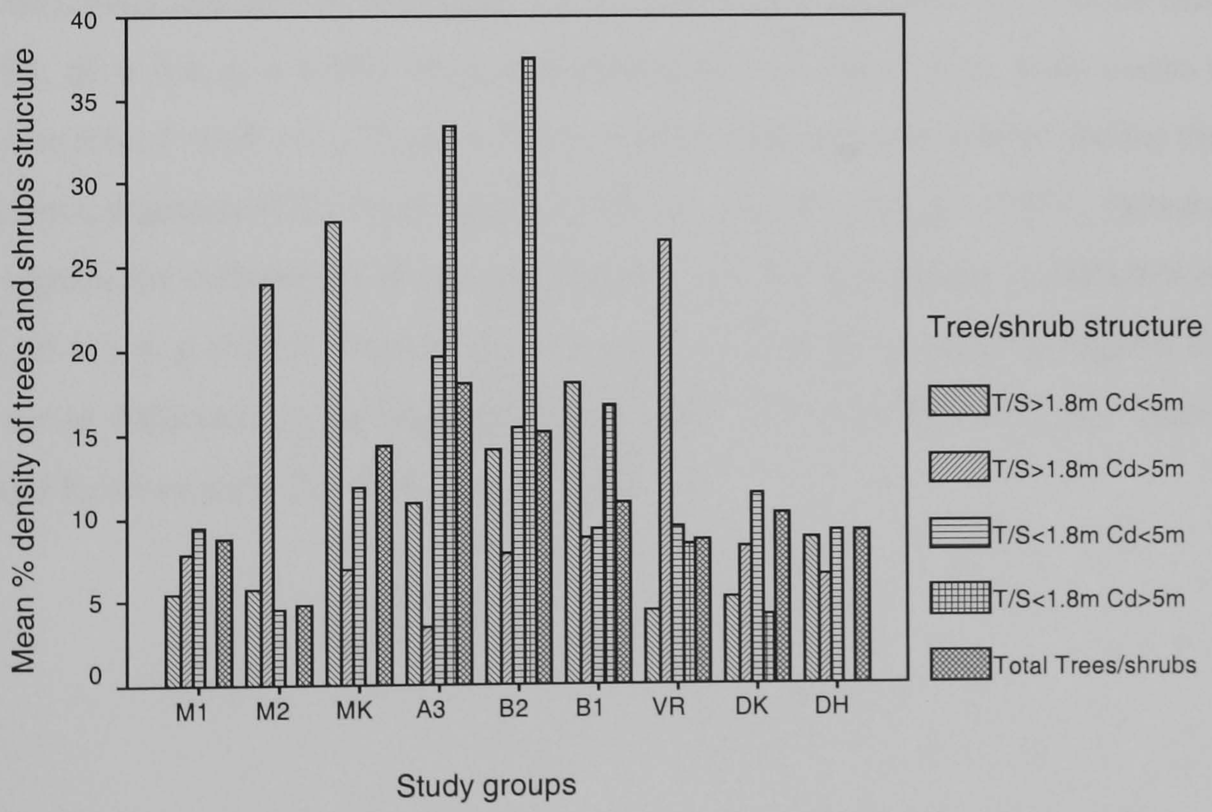


Figure 7.5: Mean % densities of trees and shrubs of defined height categories and canopy dimensions among Tsavo hirola group ranges. Data were collected between September 1996 and December 2000.

Table 7.4: A comparison of Tsavo and Garissa hirola group ranges showing the densities of trees and shrubs of defined height categories and canopy dimensions. Data were from 30, 20m x 20m sample plots per group range per season in Tsavo and 30 plots per site per season in Garissa and were collected between September 1996 and December 2000.

Sites	No./km^2 of all trees/shrubs		No./km^2 of tress/shrubs>1.8m, CD<5m		No./km^2 of trees/shrubs>1.8m, CD>5m		No./km^2 of trees/shrubs<18m, CD<5m		No./km^2 of trees/shrubs<1.8m, CD>5m	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Tana Primate N.R.	20625	14634	2625	792.7	11250	25854	813	122	35313	41402
Arawale G.R.	11250	58000	3000	6250	172625	28500	2250	250	189125	93000
Galmagala	19750	18188	1625	2625	34125	33000	438	875	55938	54688
Tsavo East N.P.	7491	6046	83	1065	33852	30111	28	111	41454	37333

Overall comparison of study sites indicate that there were no variation in density of trees and shrubs taller than 1.8 m with crown diameter (CD) less than 5 m ($F = 1.871$, df = 3,4, $p > 0.05$), trees and shrubs taller than 1.8 m with crown diameter (CD) more than 5 m ($F = 2.784$, df = 3,4, $p > 0.05$), trees and shrubs shorter than 1.8 m with crown diameter (CD) less than 5 m ($F = 1.172$, df = 3,4, $p > 0.05$) and trees and shrubs shorter than 1.8 m with crown diameter (CD) more than 5 m ($F = 2.113$, df = 3,4, $p > 0.05$). However, there were significant differences in the total density of trees and shrubs at different sites ($F = 9.652$, df = 3,4, $p < 0.05$, Figure 7.6): Arawale Game Reserve had the highest amount of bush cover followed by Galmagala; Tsavo East National Park and the Tana Primate National Reserve were the most open (Figure 7.6).

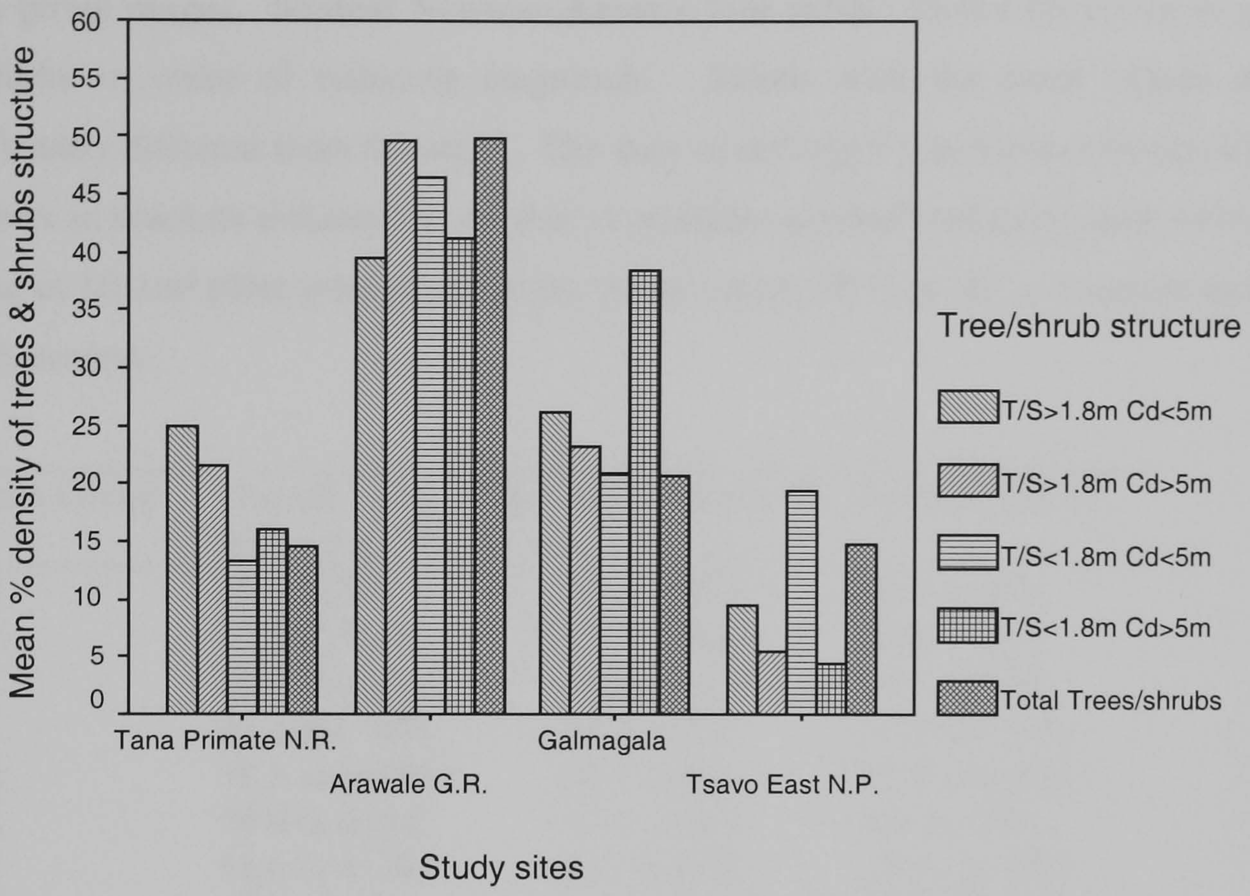


Figure 7.6: A comparison between the Tsavo and Garissa hirola ranges of mean % densities of trees and shrubs of defined height categories and canopy dimensions. Data were collected between September 1996 and December 2000.

7.5.3 Tsavo grass and forbforb cover

A comparison of the data collected from Tsavo group ranges showed that they were similar with respect to grass % cover. However, significant variations occurred between group ranges in terms of combined grass and forb % cover (the herb layer) age and forb % cover (Table 7.5, Figure 7.7). Group M2's range had the highest combined grass and forb % cover and forb layer % cover compared to the other groups.

7.5.4 Comparison of Tsavo and Garissa grass and forb cover

The Garissa hirola range was in a typical pastoral area with a high density of livestock and so it was not surprising that the herb layer cover was noticeably lower than in Tsavo.The data collected confirmed this impression (Table 7.6, Figure 7.8). Within Garissa, the Arawale Game Reserve had the highest grass and forb. Observations in Galmagala suggested that high densities of livestock were responsible for the low grass

Table 7.5: A comparison of the mean % cover of grasses and forbs between the Tsavo hirola group ranges. Student Newman-Keuls's Test (SNK) shows the cover of grasses and forbs in order of reducing magnitude. Means with the same letters are not significantly different from the other. The data were Log10 transformed before analysis. Numbers in brackets indicate the number of quadrats in which measurements were made. A total of 60 1m² plots were sampled per group range, 30 in in the wet season and 30 in the dry season.

Hirola Group	Overall grass & forb cover (%)	Grass cover (%)	Forb cover (%)
M2	74.2 a (60)	56.8 a (60)	17.3 a (60)
M1	70.5 ab (60)	50.1 a (60)	20.4 a (60)
B2	65.7 ab (60)	45.6 a (60)	20.1 ab (60)
A3	62.2 abc (60)	49.3 a (60)	12.9 abc (60)
VR	58.5 abcd (60)	46.5 a (60)	12.0 abc (60)
DK	59.0 bcd (60)	52.4 a (60)	6.6 bc (60)
B1	54.6 bcd (60)	43.7 a (60)	10.9 abc (60)
MK	49.6 cd (60)	38.9 a (60)	10.7 abc (60)
DH	47.1 d (60)	41.8 a (60)	5.3 c (60)
F- Value	5.687	1.793	3.743
d.f.	8,524	8,490	8,281
P	<0.001	>0.05	<0.05

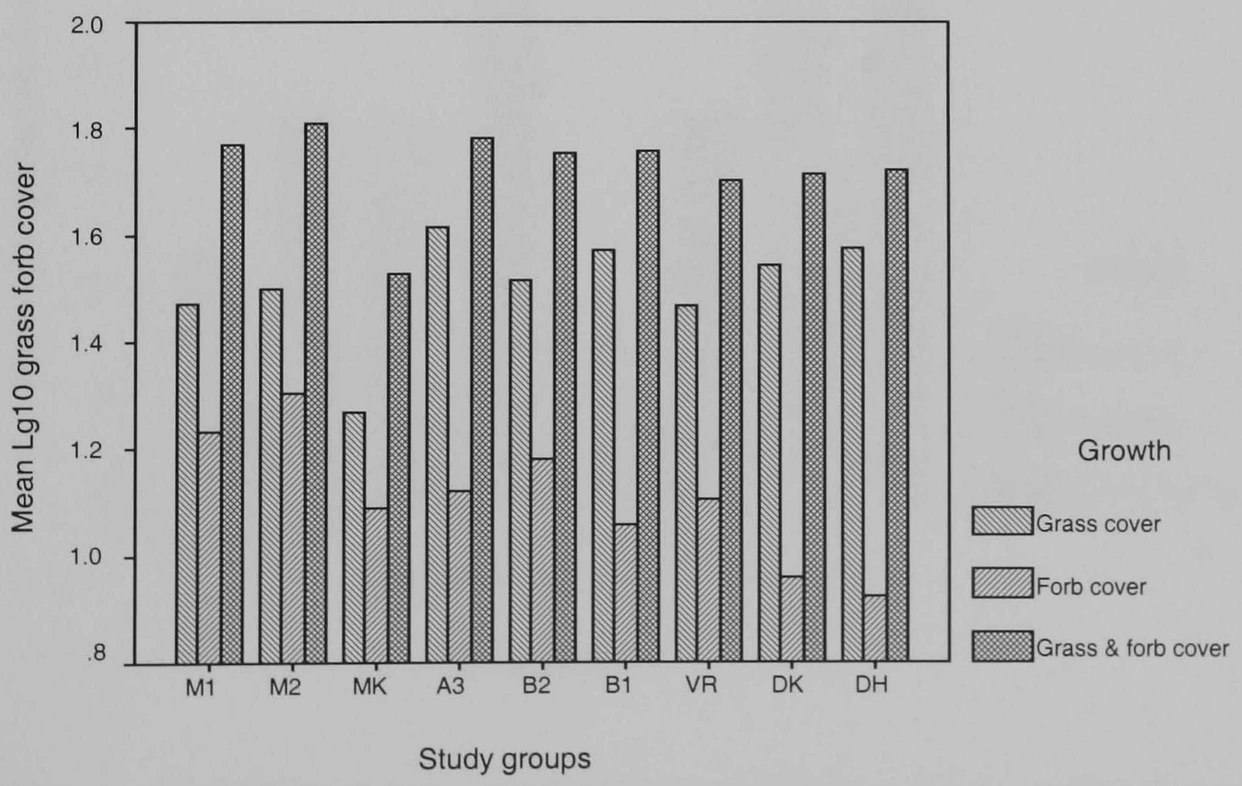


Figure 7.7: Variation in the % cover of grasses and forbs among the Tsavo hirola group ranges. Data collected between September 1996 and December 2000.

Table 7.6: A comparison of the Tsavo and Garissa hirola ranges showing mean % cover of grasses and forbs. Student Newman-Keuls's Test (SNK) shows grass and forb % cover in order of reducing magnitude. Means with the same letters are not significantly different from the other. The data were Log10 transformed before analysis. Numbers in brackets indicate the number of quadrats in which measurements were made. A total of 540 1m² plots were sampled in Tsavo and 60 plots were sampled per group range in the Garissa hirola sites.

Site	Overall grass and forb cover (%)	Grass cover (%)	Forb cover (%)
Tsavo East N.P.	60.1 a (540)	47.2 a (540)	12.9 a (540)
Arawale G.R	36.7 b (60)	27.0 b (60)	9.7 b (60)
Galmagala	22.1 c (60)	14.0 c (60)	8.1 b (60)
Tana P.N.R.	23.6 c (60)	15.6 c (60)	8.0 b (60)
F - Value	78.594	89.371	27.379
d.f.	3, 707	3, 662	3, 440
P	<0.001	<0.001	<0.001

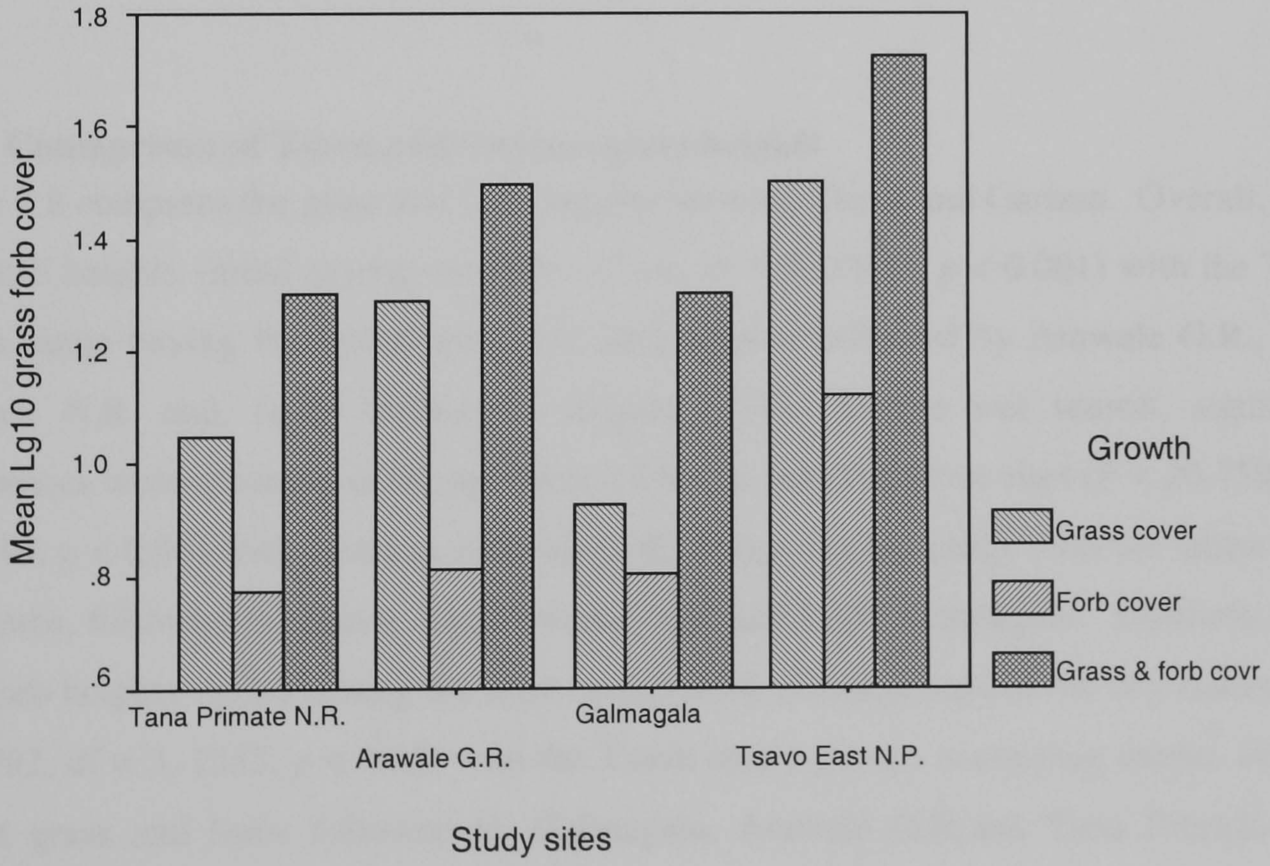


Figure 7.8: A comparison of grass and forb % cover between Tsavo and the three parts of the Garissa hirola range. Data were collected between September 1996 and December 2000.

and forb cover. Hirola ranges within the TPNR were sometimes used by livestock, but high numbers of other grazers including buffalo, topi and hippo, and frequent floods caused by swelling of the River Tana in the wet season could also have contributed to the low grass and forb ground cover. Surprisingly enough, high numbers of hirola were sighted in TPNR and Galmagala areas.

7.5.5 Tsavo grass heights

Table 7.7 shows grass and forb measurements within the different hirola group ranges in Tsavo. Data on grass and forb heights collected from the Tsavo hirola group ranges indicated that hirola used areas with shorter grasses in the wet season (23.9±22.9 cm SD) and areas with taller grass in the dry season (37.5±19.1 cm SD). A comparison of mean grass and forb heights among group ranges showed significant variation between groups in terms of overall height ($F = 48.715$, df = 8, 2309, $p < 0.001$), wet season heights ($F = 86.276$, 8, 1241, $p < 0.05$), and dry season heights ($F = 3.891$, 8, 1059, $p < 0.05$). Overall, group M2 occupied the range with the tallest grass and forb layer, while group B1 occupied the range with the shortest (Figure 7.9).

7.5.6 Comaprison of Tsavo and Garissa grass heights

Table 7.8 compares the grass and forb heights between Tsavo and Garissa. Overall, grass and forb heights varied among sites ($F = 117.6$, df = 3, 3367), $p < 0.001$) with the Tsavo hirola range having the tallest grass and forb heights followed by Arawale G.R., Tana Primate N.R. and, lastly Galmagala (Figure 7.10). In the wet season, significant differences were recorded in the incidence of hirola between these sites ($F = 20.759$, df = 3, 1810, $p < 0.05$) with hirola in Arawale G.R. occupying the range with the tallest grass and forbs, followed by Tsavo, Tana Primate N.R. and lastly Galmagala. Similarly, grass and forb heights varied among the sites occupied by hirola groups in the dry season ($F = 256.692$, df = 3, 1553, $p < 0.05$) with the Tsavo hirola groups occupying ranges with the tallest grass and forbs followed by Galmagala, Arawale G.R.and Tana Primate N.R. (Figure 7.10).

Table 7.7: A comparison of the height of grasses and forbs in the Tsavo hirola group ranges for both wet and dry seasons.

		Overall grass & forb height (cms)			Grass height (cms)			Forb height (cms)		
Groups	Data	Overall	Wet	Dry	Overall	Wet	Dry	Overall	Wet	Dry
M1	N	236.0	110.0	126.0	231.0	108.0	123.0	5.0	71.0	90.0
	Mean	**41.7**	**44.1**	**39.6**	**41.9**	**44.3**	**39.8**	**33.4**	**33.5**	**33.3**
	SD	21.0	23.9	18.0	21.1	23.9	18.1	17.9	31.8	11.5
M2	N	215.0	94.0	121.0	206.0	88.0	118.0	9.0	111.0	116.0
	Mean	**49.0**	**58.1**	**41.9**	**49.1**	**58.6**	**42.0**	**47.3**	**51.3**	**39.3**
	SD	22.1	23.5	18.1	22.1	23.9	17.7	22.7	17.0	34.6
MK	N	314.0	201.0	113.0	214.0	102.0	112.0	100.0	99.0	-
	Mean	**23.5**	**16.0**	**37.0**	**26.3**	**14.2**	**37.3**	**17.7**	**17.8**	**-**
	SD	23.8	22.5	19.9	20.4	12.9	19.8	29.1	29.2	-
A3	N	286.0	162.0	124.0	196.0	72.0	124.0	90.0	90.0	-
	Mean	**25.4**	**13.7**	**40.7**	**33.2**	**20.3**	**40.7**	**8.5**	**8.5**	**-**
	SD	20.4	9.4	20.9	20.0	8.9	20.9	5.8	5.8	-
B2	N	234.0	126.0	108.0	214.0	107.0	107.0	20.0	46.0	-
	Mean	**32.5**	**31.5**	**33.6**	**33.3**	**32.8**	**33.8**	**23.8**	**23.9**	**-**
	SD	20.7	20.0	21.5	21.1	20.7	21.5	13.0	13.4	-
B1	N	209.0	117.0	92.0	150.0	63.0	87.0	59.0	54.0	5.0
	Mean	**19.4**	**9.6**	**31.8**	**23.8**	**12.6**	**31.8**	**8.3**	**6.1**	**32.0**
	SD	17.3	8.3	17.8	16.7	7.8	16.7	13.6	7.5	34.2
VR	N	251.0	125.0	126.0	215.0	92.0	123.0	36.0	33.0	3.0
	Mean	**31.6**	**23.6**	**39.6**	**35.6**	**29.9**	**39.8**	**8.2**	**5.9**	**33.3**
	SD	19.4	17.3	18.0	17.8	15.7	18.1	9.2	4.5	11.5
DK	N	298.0	171.0	127.0	196.0	76.0	120.0	102.0	95.0	7.0
	Mean	**23.9**	**13.8**	**37.4**	**31.5**	**22.1**	**37.5**	**9.2**	**7.2**	**36.6**
	SD	20.8	14.0	20.8	20.4	15.3	21.1	11.6	8.2	16.8
DH	N	275.0	144.0	131.0	214.0	101.0	113.0	61.0	80.0	18.0
	Mean	**29.9**	**26.3**	**33.8**	**33.3**	**32.3**	**34.2**	**17.9**	**12.3**	**31.2**
	SD	18.6	21.0	14.7	18.0	21.1	14.7	15.6	12.5	14.5

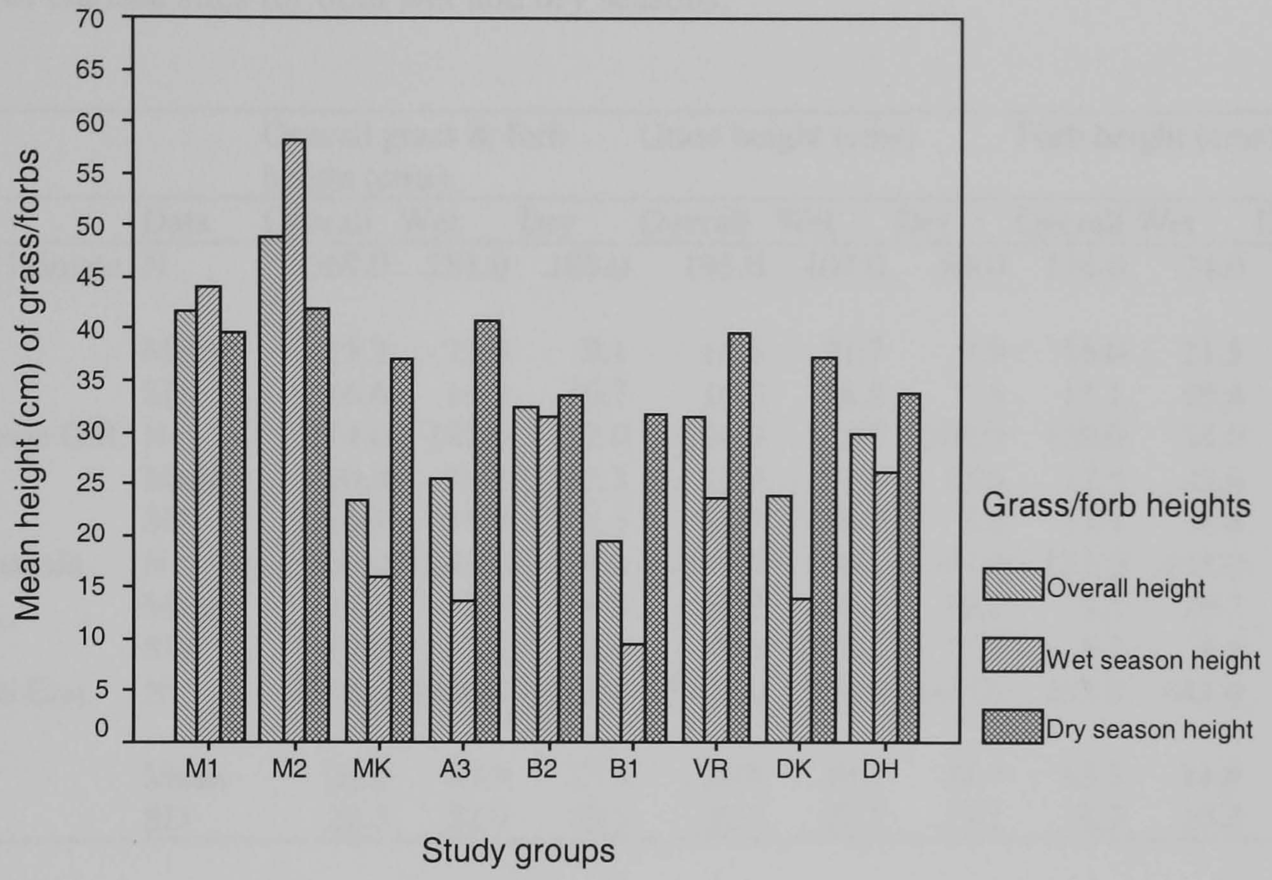


Figure 7.9: Seasonal differences in the mean heights (cm) of grasses and forbs among the Tsavo hirola group ranges. Data collected between September 1996 and December 2000.

Table 7.8: A comparison of mean grass and forb heights between Tsavo and the three sites in Garissa sites for both wet and dry seasons.

		Overall grass & forb height (cms)			Grass height (cms)			Forb height (cms)		
Sites	Data	Overall	Wet	Dry	Overall	Wet	Dry	Overall	Wet	Dry
Tana Primate N.R.	N	369.0	181.0	188.0	195.0	107.0	88.0	174.0	74.0	100.0
	Mean	15.3	21.6	9.1	15.5	21.7	7.9	15.0	21.5	10.2
	SD	16.6	19.2	10.7	16.3	18.8	7.4	17.1	19.8	12.9
Arawale G.R.	N	314.0	142.0	172.0	196.0	88.0	108.0	118.0	54.0	64.0
	Mean	20.5	29.2	13.3	22.3	33.0	13.6	17.5	23.0	12.8
	SD	16.1	18.8	8.3	17.3	19.3	8.6	13.4	16.4	7.7
Galmagala	N	370.0	241.0	129.0	197.0	100.0	97.0	173.0	141.0	32.0
	Mean	14.1	13.7	14.8	18.0	17.9	18.2	9.5	10.7	4.5
	SD	12.2	12.1	12.4	13.7	15.1	12.2	8.2	8.2	6.0
Tsavo East N.P.	N	2318.0	1250.0	1068.0	1836.0	809.0	1027.0	482.0	441.0	41.0
	Mean	30.2	23.9	37.5	34.6	30.7	37.7	13.3	11.6	32.4
	SD	22.3	22.9	19.1	21.1	22.7	19.1	18.3	17.3	18.6

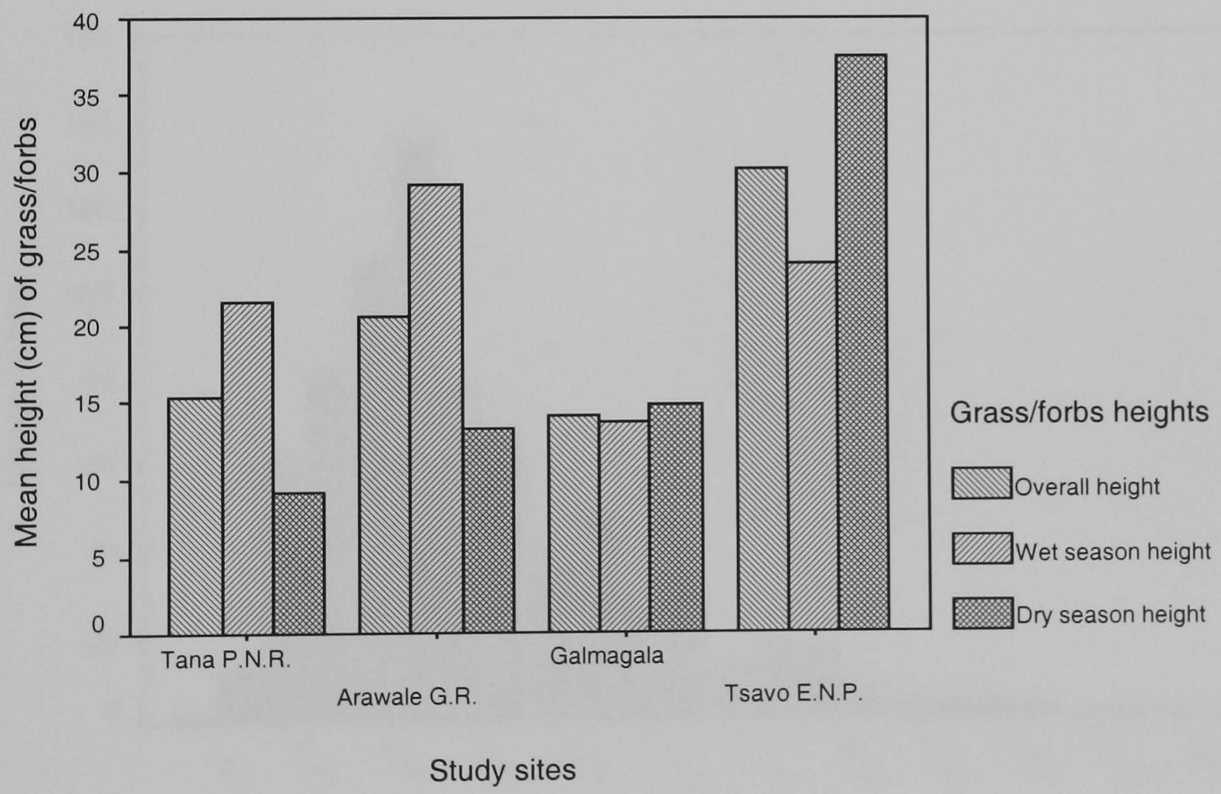


Figure 7.10: The mean heights of grass and forbs in Tsavo and the three sites in Garissa in wet and dry seasons. Data collected between September 1996 and December 2000.

7.6 Hirola feeding ecology

7.6.1 Tsavo grazing heights

Hirola bite heights were within a narrow vertical range (Figure 7.11), usually between 5 and 7cm. However, some bites were found as low as 1cm and as high as 32 cm. Mean bite height was 7.4 ± 3.93 SD. Mean bite height in the wet season was 7.8 ± 4.32 SD (n = 392) in the dry season, 7.09 ± 3.46 SD (n =390). Hirola preferred grazing on sites with relatively short and green grass. In the wet season, hirola moved away from places with tall lush grass to areas that were relatively dry with green sprouting grass. When the grass in such areas became tall they moved again to short grass areas elsewhere. Spatial variation in the availability in this type of microhabitat was common due to Tsavo's patchy rainfall pattern. In the dry season, hirola preferred bushier areas which provided shade and greener grass and forbs growing underneath the shrub canopy. Observations indicated that hirola generally fed on entire plants (leaf, stem, inflorence combined).

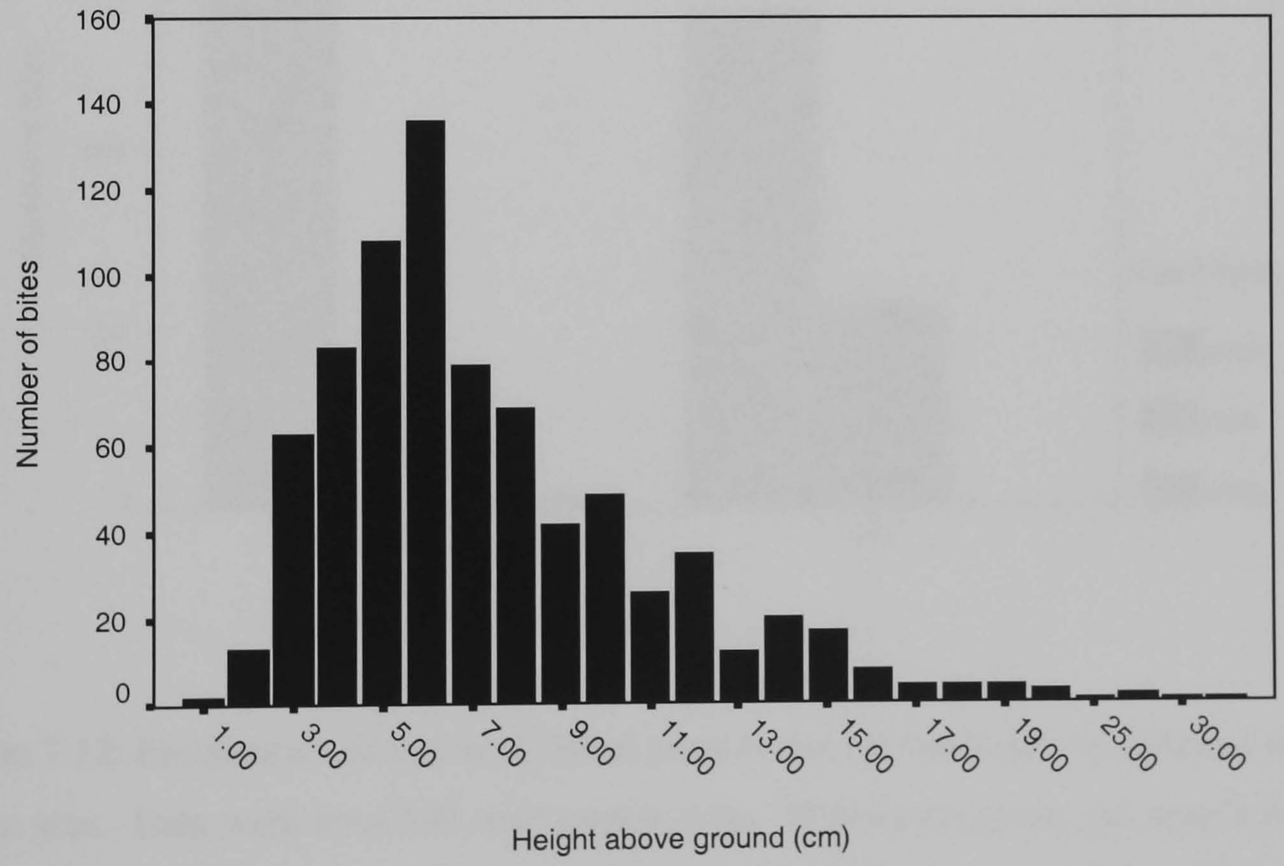


Figure 7.11: The frequency distribution of feeding bite heights by hirola in Tsavo. The data were from 540, 1m² sample plots, 30 plots per hirola family group per season from 9 hirola groups in Tsavo East, and were collected between September 1996 and December 2000.

7.6.2 Hirola food plants

Overall, hirola were observed to feed on a total of 56 plant species in Tsavo. Of these, 29 were grasses, 16 forbs and one a sedge. Grasses comprised 74.9 %, forbs 24.2% and sedges 0.9% of the diet (Figure 7.12). During the wet season, grass comprised 78.3% of the diet, forbs 19.9% and sedge 1.8%, while during the dry season, grass comprised 71.5% and forbs 28.5%. For the 56 food species, their density within the study area had been determined to enable calculation of electivity index, which measures preference for food plant relative to their density in the habitat (Table 7.9). The high degree of variation suggests that food plant choice is not simply based on random encounter rates with individuals of different species.

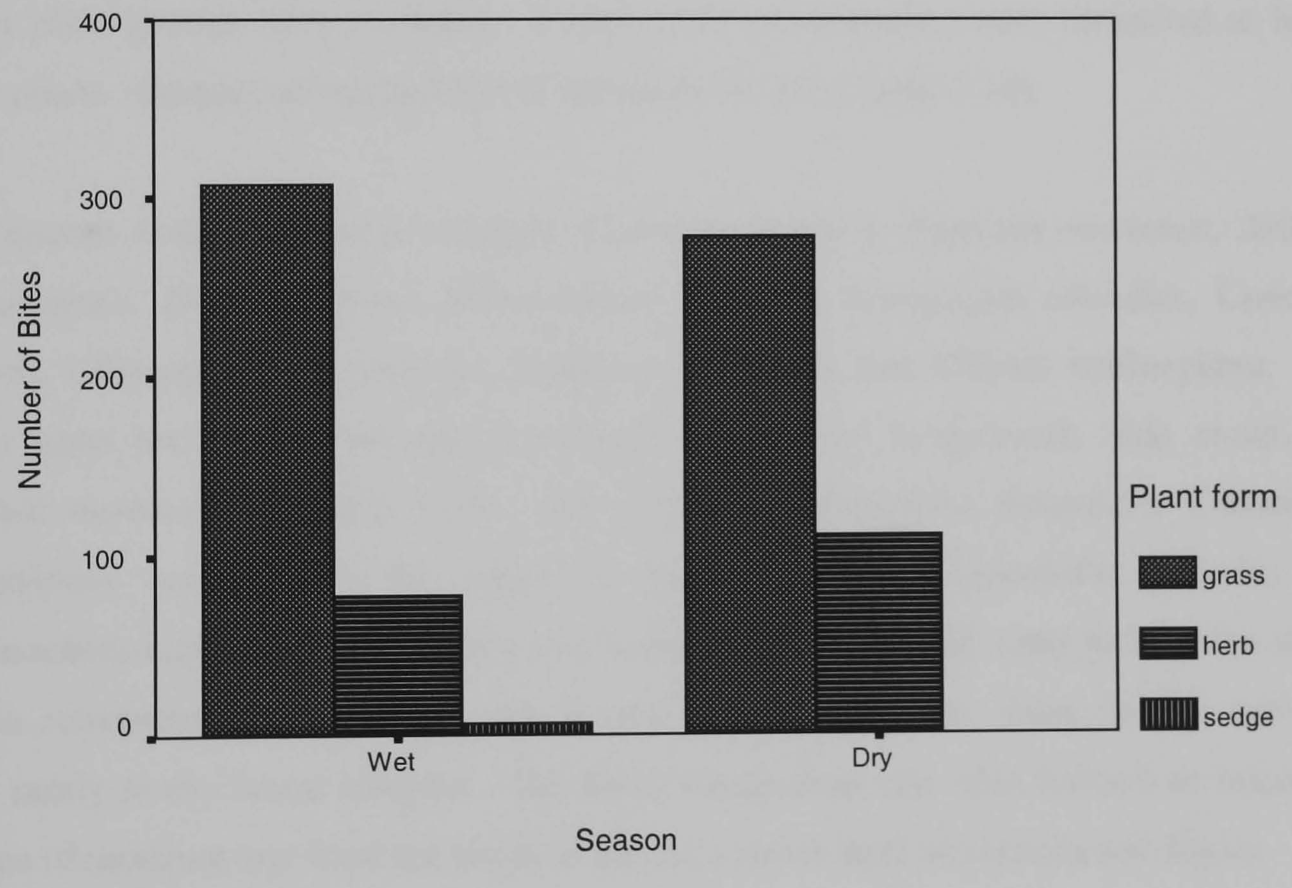


Figure 7.12: Frequencies of use of different plant forms by hirola during different season of the year. Data were from 540, 1m² sample plots, 30 plots per group per season from 9 hirola groups in Tsavo East and were collected between September 1996 and December 2000

The grasses eaten in Tsavo included, *Echinochloa haploclada, Panicum maximum, Sporobolus fimbriatus, Digitaria rivae, Digitaria milanjiana, Paspalum scrobiculatrum,* *Cyperus sp, Cynodon dactylon, Chloris pygnothrix, Tetra bidentatus, Sporobolus helvolus, Heteropon contortus*, and *Panicum infestum. The forbs eaten* included *Lannea triphilla, Commelina benghalensis, Commelina forskalaei, Cassia mimosoides, Portulaca oleracea, Sida ovata, Cleome hirta, Indigofera arrecta, Tephrosia pumila, Indigofera volkensii*, and *Heliotropium steudneri* (Table 7.9). *Panicum maximum* and, *Commelina bengalensis/forskalaei* occurred at the edges of bushes whereas *Echinochloa haploclada* and *Sporobolus helvolus* occurred in or at the edges of drying waterholes, sites that hirola grazed most.

Data on preferred food plants for the Garissa hirola population was acquired from faecal analysis. Due to the difficulty in identifying plant tissue using this procedure and the likelyhood that certain plant material have varying digestibility and degradation rates, fewer plant species were recorded. A total of 27 plant species were identified as hirola food plants. Grasses comprised 85.2% and forbs 14.8% (Table 7.10).

The grasses eaten in Garissa included: *Cynodon dactylon, Panicum maximum, Aristida adscensionis, Digitaria rivae, Bothriochloa radicans, Tetrapogon tennellus, Cenchrus ciliaris, Chrysopogon plumulosus, Panicum coloratum*, and *Chloris roxburgiana. The forbs eaten* included *Commelina forskalaei, Commelina bengalensis, Sida ovata, and Ipomea mombasana* (Table 7.10). As in Tsavo, *Commelina forskalaei, Commelina bengalensis* occurred on the edges of bushes whereas *Sporobolus helvolus* and *Echinochloa haploclada* occurred on the flood plains and around water holes, sites where hirola concentrations formed for dry season grazing; however, these species occurred only rarely in the faecal samples. The forbs *Commelina spp.* also formed an important source of moisture and food for hirola in the dry season, both in Garissa and Tsavo.

Table 7.9: Tsavo grasses and forbs occurring within the hirola range showing food plants selected and their preference level (Electivity indices) for overall use and for each season. "N" denotes a plant that was not eaten, "E" indicates a plant that was eaten. Availability data was calculated from total % cover per species (540, 1m² sample plots, 30 plots per group per season from 9 hirola groups) while data on use was calculated from total bites per species (540, 1m² sample plots, 30 plots per group per season from 9 groups).

Species	E/N	Overall %	Overall %	Ei Overall	Ei wet season	Ei dry season
Grassess		availablility	use	use	use	use
Echinochloa haploclada	E.	0.03	1.53	0.96	0.86	1
Panicum maximum	E.	0.33	6.14	0.9	0.92	0.86
Sporobolus fimbriatus	E.	0.08	1.02	0.85	-1	0.9
Digitaria rivae	E.	0.06	0.38	0.75	0.38	1
Digitaria milanjiana	E.	0.03	0.13	0.64	.	0.66
Paspalum vaginatum	E.	0.11	0.51	0.64	.	-1
Cyperus distans	E.	0.19	0.9	0.64	0.68	-1
Cynodon dactylon	E.	0.03	0.13	0.64	.	1
Chloris pygnothrix	E.	0.41	1.79	0.62	0.55	-1
Tetrapogon bidentatus	E.	1.44	5.63	0.59	0.5	0.66
Sporobolus helvolus	E.	0.75	2.81	0.58	0.77	0.41
Heteropogon contortus	E.	0.33	0.9	0.46	0.82	-1
Panicum infestum	E.	0.33	0.9	0.46	1	.
Digitaria macroblephara	E.	1.02	2.43	0.41	0.29	0.59
Panicum coloratum	E.	0.06	0.13	0.4	-1	-1
Schmidtia bulbosa	E.	1.05	2.17	0.35	0.57	-0.06
Eragrostis caespitosa	E.	3.98	8.18	0.35	0.13	0.42
Cenchrus ciliaris	E.	2.62	5.24	0.33	0.29	0.4
Brachiaria leersioides	E.	5.03	8.44	0.25	0.16	0.33
Bothriochloa radicans	E.	1.6	2.56	0.23	0.21	0.25
Chloris roxburghiana	E.	5.03	6.39	0.12	0.19	0.03
Brachiaria deflexa	E.	3.42	4.22	0.1	0.15	0.09
Eragrostis cilianensis	E.	0.11	0.13	0.07	-1	0.24
Chrysopogon aucheri	E.	0.86	0.9	0.02	0.01	0.03
Leptochloa obtusiflora	E.	0.14	0.13	-0.04	-0.06	.
Tetrapogon tenellus	E.	4	3.58	-0.06	0.25	-0.5
Latipes senegalensis	E.	6.74	5.88	-0.07	0.07	-0.25
Enteropogon macrostachyus	E.	0.19	0.13	-0.2	-1	0.24
Chloris barbata	E.	3.4	2.05	-0.25	-0.07	-0.34
Aristida adscensionis	E.	8.04	3.07	-0.45	-0.28	-0.6
Brachiaria eruciformis	N.	0.11	0	-1	.	.
Brachiaria serrifolia	N.	0.28	0	-1	-1	-1
Cymbopogon pospischilii	N.	0.17	0	-1	-1	.
Dactyloctenium aegyptium	N.	0.06	0	-1	-1	-1
Eragrostis horizontalis	N.	0.19	0	-1	-1	-1
Eragrostis superba	N.	0.66	0	-1	-1	-1

Tragus berteronianus	N.	0.03	0	-1	.	-1
Forbs						
Lannea triphilla	E.	0.03	0.26	0.81	0.64	1
Commelina benghalensis	E.	0.75	1.79	0.41	0.08	0.69
Commelina forskalaei	E.	3.34	7.67	0.39	0.25	0.49
Cassia mimosoides	E.	0.41	0.77	0.3	-0.22	0.93
Portulaca oleracea	E.	0.36	0.64	0.28	-1	-1
Sida ovata	E.	0.28	0.38	0.16	0.05	0.42
Cleome hirta	E.	2.51	2.05	-0.1	-0.19	-0.02
Indigofera arrecta	E.	0.55	0.38	-0.18	-1	-1
Tephrosia pumila	E.	3.65	1.92	-0.31	-0.72	0.08
Indigofera volkensii	E.	1.22	0.51	-0.41	-0.77	0.03
Heliotropium steudneri	E.	3.73	1.28	-0.49	-0.51	-0.47
Digera mucronata	E.	2.32	0.77	-0.5	-0.58	-0.4
Pupalia lappacea	E.	3.89	1.28	-0.51	-0.49	-0.51
Phyllansus maderaspatensis	E.	2.98	0.77	-0.59	-0.74	-0.43
Ipomea mombasana	E.	2.54	0.64	-0.6	-0.54	-0.66
Hibiscus micranthus	E.	1.02	0.26	-0.6	-0.64	-0.55
Abutilon fruticosum	N.	0.44	0	-1	-1	-1
Acalipha fruticosa	N.	0.11	0	-1	-1	-1
Achyranthes aspera	N.	0.06	0	-1	-1	-1
Aloe deserti	N.	0.11	0	-1	-1	.
Amaranthus aschersonianus	N.	0.19	0	-1	-1	-1
Amaranthus graecizans	N.	0.06	0	-1	-1	.
Asparagus falcatus	N.	0.28	0	-1	-1	-1
Bacium sp.	N.	0.17	0	-1	-1	-1
Baleria ramulosa	N.	0.41	0	-1	-1	.
Blepharis linarifolia	N.	1.93	0	-1	-1	-1
Commelina albescens	N.	0.03	0	-1	-1	.
Commicarpus stellatus	N.	0.03	0	-1	.	.
Coccinia grandis	N.	0.03	0	-1	.	.
Kalanchoe sp.	N.	0.03	0	-1	-1	.
Crotalaria agatiflora	N.	0.03	0	-1	-1	.
Croton dichogamus	N.	0.03	0	-1	.	.
Ecbolium revolutum	N.	0.03	0	-1	.	.
Euphorbia cuneata	N.	0.06	0	-1	-1	.
Euphorbia polyantha	N.	0.03	0	-1	.	-1
Euphorbia spinescens	N.	0.08	0	-1	-1	.
Evolvulus alsinoides	N.	0.11	0	-1	-1	-1
Grewia nematopus	N.	0.03	0	-1	.	.
Gizekia pharnaceoides	N.	0.41	0	-1	-1	.
Blepharis fruticulosa	N.	0.86	0	-1	-1	-1
Hibiscus palmatus	N.	0.11	0	-1	-1	-1
Indigofera spinosa	N.	0.52	0	-1	-1	-1
Justicia flava	N.	0.3	0	-1	-1	-1
Justicia heterocarpa	N.	0.25	0	-1	-1	-1
Lannea alata	N.	0.03	0	-1	-1	.
Leucas nubica	N.	0.03	0	-1	.	-1
Losinia sp.	N.	0.06	0	-1	-1	.

Melhania taylori	N.	0.41	0	-1	-1	-1
Monechma debile	N.	0.33	0	-1	-1	-1
Notonia sp.	N.	0.14	0	-1	-1	.
Ochna inermis	N.	0.03	0	-1	.	-1
Ocimum americanum	N.	0.36	0	-1	-1	-1
Polygala sphenoptera	N.	0.03	0	-1	.	-1
Salvadora persica	N.	0.03	0	-1	.	-1
Scilla kirkii	N.	0.08	0	-1	.	-1
Sericocomopsis pallida	N.	0.03	0	-1	.	-1
Sesbania sericea	N.	0.19	0	-1	-1	-1
Solanun incanum	N.	1.46	0	-1	-1	-1
Solanun teitense	N.	0.83	0	-1	-1	.
Sonchus sp.	N.	0.11	0	-1	-1	.
Stylosanthes fruticosa	N.	0.03	0	-1	.	-1
Talinum caffrum	N.	0.25	0	-1	.	-1
Talinum portulacifolium	N.	0.22	0	-1	-1	-1
Tephrosia noctiflora	N.	4.89	0	-1	-1	-1
Tephrosia subtriflora	N.	0.06	0	-1	-1	.
Tragia arabica	N.	0.14	0	-1	-1	-1
Tragia subsessilis	N.	0.03	0	-1	.	-1
Tribulus terrestris	N.	0.47	0	-1	-1	-1
Vernonia cinerea	N.	0.28	0	-1	-1	.
Vernonia hildebrandtii	N.	0.19	0	-1	-1	-1
Waltheria indica	N.	0.11	0	-1	.	-1
Santhevieria intermedia	N.	0.03	0	-1	.	-1

Table 7.10: Garissa grasses and forbs occurring within the hirola range showing the plant species eaten and their preference level (Electivity indices) overall and in each season. "N" denotes a plant that was not eaten and "E" one that was not eaten. Availability was calculated from the total % cover per species (180, 1m² sample plots, 30 plots per range per season from 3 sites) while data on use were calculated from microscopic analysis of the areas of plant tissues under X400 magnification (30 faeces samples per site per season from 3 sites).

Species	E/N	Overall % availability	Overall % use	Ei overall use	Ei wet season use	Ei dry season use
Grassess						
Cynodon dactylon	E	0.18	7.57	0.95	0.94	0.96
Panicum maximum	E	0.28	8.45	0.94	0.96	0.92
Aristida adscensionis	E	0.09	2.49	0.93	0.91	1
Digitaria rivae	E	0.09	1.93	0.91	1	0.68
Bothriochloa radicans	E	0.82	7.86	0.81	0.82	0.79
Tetrapogon tennellus	E	0.62	3.28	0.68	0.67	1
Cenchrus ciliaris	E	0.53	2.45	0.64	0.61	1
Chrysopogon plumulosus	E	0.47	2.17	0.64	1	0.45
Panicum coloratum	E	0.27	1.19	0.63	0.04	1
Chloris roxburgiana	E	2.77	9.47	0.55	0.68	0.43
Eragrostis caespitosa	E	0.72	2.46	0.55	0.37	0.75
Echinochloa haploclada	E	2.61	8.81	0.54	0.7	0.49
Brachiaria deflexa	E	0.44	1.14	0.44	0.4	1
Eragrostis cilianensis	E	2.22	5.18	0.4	-0.09	1
Sporobolus helvolus	E	6.52	11.74	0.29	0.36	0.22
Chloris barbata	E	4.47	7.97	0.28	0.75	-0.13
Digitaria milanjiana	E	1.32	2.3	0.27	1	-0.44
Enteropogon macrostachyus	E	3.19	1.33	-0.41	0.27	-0.49
Dactyloctenium aegyptium	E	1.19	0.43	-0.47	-0.77	-0.23
Brachiaria leersioides	E	5.73	2.01	-0.48	-0.45	-0.53
Chloris rivae	E	5.08	1.11	-0.64	-0.69	0.03
Cymbopogon pospischilii	E	3.92	0.18	-0.91	-0.91	-1
Cyperus rotundus	E	1.96	0.08	-0.93	-1	-0.92
Cyperus esculentus	N	0.62	0	-1	-1	.
Hereropogon contortus	N	0.8	0	-1	-1	.
Paspalum commersonii	N	0.62	0	-1	-1	.
Setaria holstii	N	0.18	0	-1	-1	.
Tragus heptaneuron	N	1.26	0	-1	-1	-1
Cyberus bulbosus	N	1.32	0	-1	.	-1
Enteropogon somalensis	N	1.5	0	-1	.	-1
Kyllinga erecta	N	0.66	0	-1	.	-1
Oropetium thomaeum	N	0.94	0	-1	.	-1
Forbs						
Commelina forskalaei	E	3.98	4.72	0.08	-0.33	0.46

Commelina bengalensis	E	3.16	3.09	-0.01	-0.36	0.05
Sida ovata	E	0.82	0.49	-0.25	-1	0.13
Ipomea mombasana	E	0.18	0.1	-0.29	-0.29	.
Abutilon fruticosum	N	1.47	0	-1	-1	-1
Abutilon racemosa	N	0.55	0	-1	-1	-1
Achyrances aspera	N	0.74	0	-1	-1	-1
Asparagus fulcatus	N	0.18	0	-1	-1	.
Asystacia sp.	N	0.18	0	-1	-1	-1
Barleria ramulosa	N	4.31	0	-1	-1	-1
Blepharis maderaspatensis	N	1.97	0	-1	-1	-1
Cassia mimosoides	N	0.28	0	-1	-1	-1
Crassula schimperi	N	2.47	0	-1	-1	-1
Digera mucronata	N	2.51	0	-1	-1	-1
Evolvulus alsinoides	N	0.89	0	-1	-1	.
Euphorbia hirta	N	0.53	0	-1	-1	.
Grabbea velutina	N	0.73	0	-1	-1	-1
Heliotropium steudneri	N	0.83	0	-1	-1	-1
Hibiscus micranthus	N	0.27	0	-1	-1	.
Indigofera arrecta	N	3.93	0	-1	-1	-1
Indigofera volkensii	N	1.29	0	-1	-1	-1
Justicia flava	N	1.16	0	-1	-1	.
Libia caviodora	N	0.27	0	-1	-1	.
Monchema debile	N	0.71	0	-1	-1	.
Ocimum americanum	N	3.29	0	-1	-1	-1
Phylanthus maderaspatensis	N	0.89	0	-1	-1	.
Portulaca oleracea	N	0.27	0	-1	-1	.
Pupalia lapacea	N	1.38	0	-1	-1	-1
Solanum incanum	N	0.75	0	-1	-1	-1
Tephrosia pumila	N	2.08	0	-1	-1	-1
Aerva lanata	N	0.19	0	-1	.	-1
Aspilia mossabicensis	N	0.09	0	-1	.	-1
Bacium sp.	N	0.66	0	-1	.	-1
Barleria eranthemoides	N	0.47	0	-1	.	-1
Barleria prionitis	N	0.38	0	-1	.	-1
Cadaba farinosa	N	0.19	0	-1	.	-1
Aloe deserti	N	0.09	0	-1	.	-1

7.7 Nutrient analyses

7.7.1 Vegetation samples

Analyses of four macronutrients from samples of Tsavo food plants indicated that there was no variation between seasons with regard to amounts of phosphorus and calcium. However, results on nitrogen and potassium indicated significantly higher concentrations in the wet season than in the dry season (Table 7.11).

A comparison of macronutrients content between Tsavo and Garissa food plants during the wet season revealed that there was no variation in nitrogen and potassium content. However, there were differences with respect to the content of phosphorus, with Tsavo having higher amounts than Garissa (Table 7.12).

Table 7.11: Variation of macronutrients between wet and dry season samples of Tsavo hirola food plants collected between September 1996 and December 2000.

Nutrient type	Season	Mean ± SD	Df	F	P
% Nitrogen	Wet	1.67±0.45	1,46	35.379	<0.001
	Dry	1.00±0.32			
% Phosphorus	Wet	0.19±0.09	1,46	1.414	>0.05
	Dry	0.17±0.07			
% Potassium	Wet	1.56±1.06	1,46	9.173	<0.01
	Dry	0.79±0.64			
% Calcium	Wet	0.43±0.16	1,46	3.491	>0.05
	Dry	0.36±0.11			

Table 7.12: Variation of wet season macronutrients between Tsavo and Garissa hirola food plants between September 1996 and December 2000.

Nutrient type	Site	Mean ± SD	Df	F	P
% Nitrogen	Tsavo	1.67±0.45	1,40	1.289	>0.05
	Garissa	1.84±0.48			
% Phosphorus	Tsavo	0.19±0.09	1,40	22.737	<0.001
	Garissa	0.08±0.03			
% Potassium	Tsavo	1.56±1.06	1,40	0.599	>0.05
	Garissa	1.33±0.80			
% Calcium	Tsavo	0.43±0.16	-	-	-
	Garissa	-			

7.7.2 Faecal samples

Analyses of fresh hirola faecal samples in Tsavo indicated that potassium contents did not vary between seasons. However nitrogen, phosphorus and calcium contents were higher in the dry than the wet season (Table 7.13). Similar analyses on hirola faeces from Garissa showed that all nutrients measured except phosphorus varied with season. Higher amounts of nitrogen, calcium, and potassium were recorded in the dry season (Table 7.14).

Table 7.13: Variation of macronutrients between wet and dry season samples of Tsavo hirola faecal material collected between September 1996 and December 2000.

Nutrient type	Season	Mean ± SD	Df	F	P
% Nitrogen	Wet	1.37±0.23	1,34	22.191	<0.001
	Dry	1.68±0.25			
% Phosphorus	Wet	0.45±0.10	1,34	4.848	<0.05
	Dry	0.37±0.12			
% Potassium	Wet	0.30±0.11	1,34	1.899	>0.05
	Dry	0.25±0.14			
% Calcium	Wet	1.29±1.17	1,34	7.448	<0.05
	Dry	2.54±1.60			

Table 7.14: Variation of macronutrients between wet and dry season samples of Garissa hirola faecal material collected between September 1996 and December 2000.

Nutrient type	Season	Mean ± SD	Df	F	P
% Nitrogen	Wet	1.22±0.20	1,35	7.147	<0.05
	Dry	1.51±0.37			
% Phosphorus	Wet	0.61±0.18	1,35	2.347	>0.05
	Dry	0.73±0.24			
% Potassium	Wet	0.18±0.11	1,35	7.607	<0.01
	Dry	0.30±0.12			
% Calcium	Wet	0.86±0.26	1,35	14.780	<0.001
	Dry	2.08±1.17			

Comparisons of the nutrient content of hirola faeces between Tsavo and Garissa indicated that calcium did not vary between the two sites. However, Tsavo had higher concentrations of nitrogen, phosphorus and potassium Garissa (Table 7.15). Nitrogen, potassium and calcium were similar in the two areas during the dry season, but there proved to be higher concentrations of phosphorus at Garissa than in Tsavo (Table 7.15).

Table 7.15: Seasonal comparison of Tsavo and Garissa hirola faecal macronutrients. Samples collected between September 1996 and December 2000.

Season	Nutrient type	Site	Mean ± SD	df	F	P
Wet	% Nitrogen	Tsavo	1.37±0.13	1,31	6.357	<0.05
		Garissa	1.22±0.20			
	% Phosphorus	Tsavo	0.45±0.12	1,31	10.942	<0.01
		Garissa	0.61±0.18			
	% Potassium	Tsavo	0.30±0.11	1,31	9.140	<0.01
		Garissa	0.19±0.11			
	% Calcium	Tsavo	1.29±1.12	1,31	1.997	>0.05
		Garissa	0.86±0.23			
Dry	% Nitrogen	Tsavo	1.68±0.25	1,38	2.454	>0.05
		Garissa	1.51±0.37			
	% Phosphorus	Tsavo	0.36±0.12	1,38	31.867	<0.001
		Garissa	0.73±0.24			
	% Potassium	Tsavo	0.25±0.14	1,38	1.514	>0.05
		Garissa	0.30±0.12			
	% Calcium	Tsavo	2.54±1.60	1,38	1.079	>0.05
		Garissa	2.08±1.17			

7.7.3 Food plant selection in relation to nutrient contents

The data obtained suggested that, hirola fed on plant material that was low in calcium during the wet season (Table 7.16). Nitrogen, phosphorus and potassium had no additional effects on selectivity. However, during the dry season, hirola fed on plants that were low in nitrogen (Table 7.16). Phosphorus, potassium and calcium concentrations had no additional effects. These analyses suggest that hirola could have suffered from a shortage of calcium in the wet season and nitrogen in the dry season.

7.6 Use of shade

The semi-arid environments in which the hirola lives are always very hot during the day, irrespective of the season. The hirola's smooth shiny coat could reflect some of the sun rays and thus be an adaptation to such environmental conditions. Hirola generally sought shaded positions when the sun became hot. This could take place as early as 0700 on hot days. Hirola seemed to prefer a cluster of isolated shrubs or trees in which to seek shade. Such places may have been preferred because the animals could watch their surroundings for predators while inside the shade.

Table 7.16: Backward multiple regression analyses (model 1) of electivity indices and nutrient contents of hirola food with respect to season.

Wet season	Variable	Coefficient	T	P
	Constant	-0.595		
	% nitrogen	1.346	1.069	0.297
	% phosphorus	0.464	0.692	0.496
	% potassium	0.521	1.077	0.293
	% calcium	-1.948	-2.097	0.048
	Multiple r = 0.532 (r^2 = 0.283), df = 4,22, p = 0.106			
	Model y = 1.346(%N)+0.464(P_2O_5)+0.521(K_2O)-1.948(CaO)-0.595			
Dry season	Constant	0.155		
	% nitrogen	-2.438	-2.255	0.034
	% phosphorus	-1.048	-1.509	0.145
	% potassium	0.705	1.757	0.092
	% calcium	1.795	1.988	0.059
	Multiple r = 0.536 (r^2 = 0.287), df = 4,23, p = 0.087			
	Model y = -2.438(%N)-1.048(P_2O_5)+0.705(K_2O)+1.795(CaO)+0.155			

Hirola competed for shade (Chapter V) and subordinate animals were often excluded to the poorest shade. Some individuals could be observed lying in full sun, while others used inferior shade such as that besides a dry log. Hirola were generally observed in open areas in the early morning and late evening, but because of the need for shade, while, they moved to bushy sites during the hot times of the day. Because of this, hirola were most easy to find in early morning and late evening, times when they could be seen in the open. This may explain the difficulty of sighting hirola in the dry season when they used bushy areas more because of the increased need for shade.

Hirola preferred certain tree species for use as shade. *Delonix elata* was the most preferred shade tree in Tsavo (Table 7.17) and *Acacia tortilis* the most preferred in Garissa (Table 7.18). Generally, preferred shade trees were multi-stemmed, taller than 1.8 m with a canopy diameter ≥ 5 m, and with a cluster of other similar tree/shrub type plant nearby. Some of the shade trees were evergreen (non-deciduous) while others were deciduous. Non deciduous trees and shrubs were used all year round and formed an important component of the habitat. These include species such as *Boscia coriacea, Acacia tortilis, Eretia taitensis, Strichnos decusata, Anisotes pervifolius, Cassia abbreviata, Thylachium thomasii*, and *Dobera glabra*. Some shade plants were only used in the wet season when they had foliage. These included *Platycelithium voense, Cordia sinensis* and *Cordia monoica*. Some plants were used for shade all year round even though they were deciduous. These plants were provided moderate shade due to their multi-branched umbrella-like canopy that allowed little light penetration even when they had no leaves. Such plants included *Delonix elata, Premna racenosa*, and *Anisotes pervifolius*. The amount of these shade plants in a group range was used as a measure of shade quality.

An analysis of mean availability of preferred shade trees among different hirola group ranges in Tsavo indicated that some groups had better shade than others (F = 2.470, df = 8,79, $P < 0.05$). The MK group had the highest number of preferred shade trees while M2 had the least. Overall, the most abundant preferred shade tree was *Boscia coriacea* while the least abundant was *Strichnos decusata*.

Table 7.17: Tsavo trees and shrubs as sources of shade for hirola in order of their preference level (Electivity indices). Availability data were calculated from the total number of trees and shrubs taller than 1.8m with crown diameter (CD) greater than and less than 5m. Sampling was carried out in 540, 20x20m² randomly distributed sample plots within the entire hirola range. Data on use by hirola were calculated from total observed usage of different tree species by different hirola groups, each time hirola groups were sighted.

Shade tree species	Density (/km²)	Overall % availability	Overall % use	Overall Ei
Delonix elata	60.19	0.82	11.72	0.87
Acacia nubica	13.89	0.19	1.38	0.76
Dobera glabra	83.33	1.14	7.88	0.75
Platyceliphium voense	282.41	3.85	17.31	0.64
Anisotes pervifolius	92.59	1.26	4.46	0.56
Cordia monoica	166.67	2.27	6.93	0.51
Sesamothamnus rivae	74.07	1.01	2.67	0.45
Thylachium thomasii	83.33	1.14	2.17	0.31
Cassia abbreviata	180.56	2.46	4.21	0.26
Acacia tortilis	101.85	1.39	1.84	0.14
Boscia coriacea	620.37	8.46	10.89	0.13
Eretia taitensis	259.26	3.54	2.54	-0.16
Premna resinosa	740.74	10.1	6.68	-0.2
Cordia sinensis	1888.89	25.76	16.31	-0.22
Strychnos decussata	337.96	4.61	2.67	-0.27
Premna hildebrandtii	143.52	1.96	0.33	-0.71
Acacia bossei	23.15	0.32	0	-1
Acacia mellifera	4.63	0.06	0	-1
Acacia senegal	27.78	0.38	0	-1
Acacia zanzibarica	37.04	0.51	0	-1
Acalypha fruticosa	9.26	0.13	0	-1
Albizia anthelmentica	32.41	0.44	0	-1

Asparagus asiaticus	4.63	0.06	0	-1
Balanites orbicularis	13.89	0.19	0	-1
Cadaba heterotricha	9.26	0.13	0	-1
Caesalpinia trothae	87.96	1.2	0	-1
Calyprotheca taitensis	74.07	1.01	0	-1
Combretum aculeatum	138.89	1.89	0	-1
Commiphora africana	13.89	0.19	0	-1
Commiphora boiviniana	87.96	1.2	0	-1
Commiphora campestris	50.93	0.69	0	-1
Dirichletia glaucescens	240.74	3.28	0	-1
Gardenia jovis-tonantis	4.63	0.06	0	-1
Grewia bicolor	162.04	2.21	0	-1
Grewia forbesii	37.04	0.51	0	-1
Grewia lilacina	18.52	0.25	0	-1
Grewia nematopus	643.52	8.78	0	-1
Grewia tenax	74.07	1.01	0	-1
Grewia vilosa	60.19	0.82	0	-1
Hymenodictyon parvifolium	4.63	0.06	0	-1
Lannea alata	97.22	1.33	0	-1
Lannea triphylla	50.93	0.69	0	-1
Lycium europaeum	55.56	0.76	0	-1
Lawsonia inermis	13.89	0.19	0	-1
Maerua edulis	4.63	0.06	0	-1
Manilkara mochisia	4.63	0.06	0	-1
Melia volkensii	9.26	0.13	0	-1
Newtonia hildebrandtii	4.63	0.06	0	-1
Salvadora persica	13.89	0.19	0	-1
Xeromphis keniensis	4.63	0.06	0	-1
Strophanthus mirabilis	46.3	0.63	0	-1
Tarenna graveolens	18.52	0.25	0	-1
Vernonia hildebrandtii	9.26	0.13	0	-1

Table 7.18: Garissa trees and shrubs as sources of shade for hirola in order of their preference levels (Electivity indices). Availability data were calculated from the total number of trees and shrubs taller than 1.8m with crown diameter (CD) greater than and less than 5m. Sampling was carried out in 180, 20x20m^2 randomly distributed sample plots within the hirola range. Data on use by hirola were calculated from total observed usage of the different tree species by all hirola groups sighted during surveys in the hirola natural range.

Shade tree species	Density (/km^2)	Overall % availability	Overall % use	Overall Ei
Acacia tortilis	12.4	0.1	18.4	1.0
Albizia anthelmentica	24.8	0.1	2.5	0.9
Balanites orbicularis	136.1	0.6	6.9	0.9
Manilkara mochisia	74.3	0.3	3.3	0.8
Acacia zanzibarica	173.3	0.7	5.3	0.8
Salvadora persica	420.8	1.8	8.6	0.7
Maerua edulis	86.6	0.4	1.6	0.6
Dobera glabra	1386.1	5.8	25.7	0.6
Commiphora africana	99.0	0.4	1.2	0.5
Boscia coriacea	111.4	0.5	1.2	0.5
Acacia nubica	235.2	1.0	1.6	0.3
Commiphora campestris	259.9	1.1	1.6	0.2
Acacia reficiens	1002.5	4.2	5.7	0.2
Dobera loranthifolia	2425.7	10.2	13.9	0.2
Thylachium thomasii	185.6	0.8	0.8	0.0
Combretum aculeatum	1930.7	8.1	1.6	-0.7
Acacia bossei	928.2	3.9	0.0	-1.0
Acacia mellifera	198.0	0.8	0.0	-1.0
Acacia senegal	284.7	1.2	0.0	-1.0
Achyrances aspera	12.4	0.1	0.0	-1.0
Alovelus sp.	49.5	0.2	0.0	-1.0
Anisotes pervifolius	198.0	0.8	0.0	-1.0

Asparagus asiaticus	49.5	0.2	0.0	-1.0
Boscia agustifolia	12.4	0.1	0.0	-1.0
Cadaba heterotricha	24.8	0.1	0.0	-1.0
Maerua edulis	12.4	0.1	0.0	-1.0
Carissa edulis	346.5	1.5	0.0	-1.0
Sarcostemma viminale	24.8	0.1	0.0	-1.0
Rhoicissus revoilii	297.0	1.2	0.0	-1.0
Combretum hereroense	4814.4	20.2	0.0	-1.0
Commiphora holtziana	24.8	0.1	0.0	-1.0
Commiphora boiviniana	284.7	1.2	0.0	-1.0
Commiphora schimberi	37.1	0.2	0.0	-1.0
Cordia monoica	12.4	0.1	0.0	-1.0
Cordia sinensis	854.0	3.6	0.0	-1.0
Cordia somalensis	12.4	0.1	0.0	-1.0
Croton meyharthii	792.1	3.3	0.0	-1.0
Echbolium hamatum	272.3	1.1	0.0	-1.0
Eretia taitensis	12.4	0.1	0.0	-1.0
Erythrina melanacantha	12.4	0.1	0.0	-1.0
Euphorbia tirucalli	74.3	0.3	0.0	-1.0
Ficus ingens	160.9	0.7	0.0	-1.0
Grewia bicolor	74.3	0.3	0.0	-1.0
Grewia nematopus	49.5	0.2	0.0	-1.0
Grewia tenax	544.6	2.3	0.0	-1.0
Grewia tembensis	2561.9	10.7	0.0	-1.0
Grewia vilosa	730.2	3.1	0.0	-1.0
Lannea triphylla	24.8	0.1	0.0	-1.0
Libia caviodora	24.8	0.1	0.0	-1.0
Lawsonia inermis	86.6	0.4	0.0	-1.0
Maerua mungaii	457.9	1.9	0.0	-1.0
Maerua subcordata	210.4	0.9	0.0	-1.0
Maytenus heterophylla	37.1	0.2	0.0	-1.0
phyllanthus somalensis	12.4	0.1	0.0	-1.0
Sansevieria sp.	12.4	0.1	0.0	-1.0

Xeromphis keniensis	433.2	1.8	0.0	-1.0
Sesamothamnus rivae	12.4	0.1	0.0	-1.0
starculia africana	12.4	0.1	0.0	-1.0
Strychnos decussata	37.1	0.2	0.0	-1.0
Tarenna graveolens	37.1	0.2	0.0	-1.0
Terminalia orbicularis	37.1	0.2	0.0	-1.0
Vernonia hildebrandtii	99.0	0.4	0.0	-1.0

7.7 Conclusions

Hirola groups occupied specific home ranges that varied in size between the groups, perhaps indicating variation in essential resources. Each hirola group had 1 to 6 preferred core areas that contained high quality forage within their home range. These results suggest that ranges varied in their suitability to hirola. Home ranges showed a variable degree of overlap with neighbouring ranges. Most overlapping ranges had higher numbers of core areas, higher densities of seasonal waterholes and shorter grass. Such range overlapping could have been caused by competition for scarce resources between neighbouring groups. However, observations on neighbouring groups indicated that hirola did not actively defend their home ranges or even their core areas. Instead, neighbouring groups remained in separate parts of their ranges. In the rare cases when they came together the groups (although not their males) joined up to graze togather in a food patch (core area) before separating again. Thus, if competition occurred it did not involve direct conflict.

Results in Tsavo indicated that hirola preferred to use places with taller (>1.8m) trees in the dry season possibly as a source of shade. Not all bushy areas were used but rather those with a higher abundance of preferred shade tree species. Hirola require some trees and shrubs as a source of shade but excess bush may mean reduced herb cover for grazing and, possibly, a higher threat from predation. Observation indicated that amount of tree and shrub cover varied between Tsavo and Garissa, with Tsavo and TPNR having the least bush cover. The more open sites had a higher density of hirola suggesting that excess bush cover contributed negatively to hirola survival.

Observations on the herb layer in Tsavo and Garissa showed significant variation in grass and forb cover. Overall, Tsavo had the highest grass and forb cover, followed by Arawale Game Reserve. Realtively more hirola occurred in the Tana Primate N. R. and Galmagala than in Arawale. The low grass and forb cover in Arawale and Galmagala may have been as a result of heavy cattle grazing. High densities of topi, buffalo and hippo may sometimes have reduced herb layer cover, especially around the Tana Primate N.R. These results indicate that hirola preferred areas of short grass. The presence of coarse grazers may be essential in a hirola habitat to maintain the height and regeneration of the sward upon which hirola feeds.

Hirola mainly fed on grass although forbs were occasionally eaten. In Tsavo, the amount of forbs eaten increased during the dry season, indicating a possible shortage in general food availability and the need for succulent forage as source of moisture. Indeed most of the forbs eaten were succulent and of higher nutrient value than dry grass. Garissa hirola also fed mainly on grass although some forbs were eaten. Hirola preferred to graze on short grass and their bite heights were at about 7 cm from the ground. Hirola used slightly taller grass areas in the dry season and when it was very wet. Further, hirola preferred green grass but would avoid them as they grew tall in the wet season; instead they moved to areas where the grasses were shorter. The hirola's preference for short green grass may be partly a result of adaptations to a particular food source, but short grass areas also have better visibility and might be preferred as an anti-predator defense mechanism.

Different plant species contain different levels of nutrients at different stages of growth and hence season. Similarly some plants species occurring in different localities, at the same growth stage can have varying nutrient contents, partly due to variation in soil types. Herbivores thus have a number of options that could lead to a varying intake of nutrients. Not surprisingly, the results of the analysis of food plant nutrients revealed that there were higher nutrient concentrations in wet season forage than in the dry season. Tsavo forage was also found to contain higher values of nutrients in comparison with Garissa, although these differences are not reflected in the animal health as hirola at both sites appeared to be healthy.

Hirola food plants contained relatively low amounts of calcium in the wet season and low amounts of nitrogen in the dry season. These results may indicate possible deficiencies in these minerals during different seasons, and especially of nitrogen in the dry season. However, due to the hirola's feeding habits of searching for greener pasture underneath bushes and around drying water holes in the dry season, they could have avoided or reduced the effect of this bottleneck. The shortage of nitrogen may also explain why hirola fed on green succulent forbs in the dry season and why fairly high nutrient levels were still obtained from dry season faecal samples. Higher nutrient concentrations were found in dry season faeces than in wet season faeces in both Tsavo and Garissa. Studies on herbivore forage digestibility indicate that as grass swards mature, they increase in biomass and decrease in quality as they accumulate structural carbohydrates (Waite, 1963). Mature, poorly digestible grass often passes through the digestive system with little absorbtion (Illius & Gordon, 1992) whereas young high-quality grass is mostly digested and absorbed (Baile & Forbes, 1974). The high nutrient concentrations in faeces in the dry season could thus be for two reasons. First, it could be because nutrients are trapped within indigestible structural elements and are thus excreted undigested. Second the nutrient concentration could be high because of selective feeding on green elements in the herb layer. The methods used here cannot discriminate between these alternatives and further work is needed to resolve this issue. However, if hirola do manage to select a high quality diet, this ability must eventually become limited in protracted dry weather and the observed low levels of dry season nitrogen in hirola food plants could become more serious during periods of drought.

Shade appeared to be very important for hirola distribution in both Tsavo and Garissa. Hirola showed a high dependence on shade during the hot times of day when they rested. Particular trees and shrubs were preferred for shade. The abundance of these preferred shade trees affected hirola movements and varied greatly between hirola group ranges.

Chapter VIII:

Analyses of Limiting Factors

8.1 Introduction

Hirola are categorized as "critically endangered" under criterion A1a of IUCN Red List Categories, 1996, having demonstrated about 90% population reduction between 1973 (13,729 animals) (Wartson et al., 1973) and 1996 (1,504 individuals) within the natural range (Ottichilo et al., 1995). The factors responsible for this decline are thus of considerable practical importance. Factors that have been implicated in the decline include; predation, habitat degradation, competition with livestock, poaching, shortage of food and cover (physiological factors), and disease (Wargute & Aligula, 1993, Wargute, 1994, Agatsiva, 1995, Magin, 1996b)). In 1963, about 44 hirola (the exact number were not recorded) were translocated from Garissa to Tsavo (Grimwood, 1963; Donaldson, 1964). In 1996, a further 35 hirola were captured and added to the Tsavo population (Kock et al., 1998). Despite these efforts, the hirola population has increased only very slowly and remains at a low density (Chapter 4). Some of the factors that might limit the growth of the Tsavo population include inbreeding depression (Magin, 1996b; Andanje & Ottichilo, 1997), predation, the effects of translocation, competition with kongoni (Kingdon, 1997), the food supply, and a lack of suitable shade.

According to (Soule, 1983), "the extinction of a species has little to do with the death rattle of its final actor. The curtain in the last act is but a punctuation mark". Soule suggested that biologists should endeavor to understand what processes cause declines in both population range and size. Such an understanding could help wildlife managers make better decisions in conserving biodiversity by allowing more efficient allocation of resources for *in-situ* management, and for planning re-introductions. Most theory regarding extinction can be considered as belonging to the small-population paradigm (Simberloff, 1986; Caughley, 1994). It includes the genetic and demographic factors that influence a small population's risk of extinction (e.g., demographic stochasticity, environmental stochasticity, genetic drift, and inbreeding). The small-species paradigm has been contrasted with the declining-species paradigm that deals with those factors that contribute to the decline of species before their populations become rare (e.g., over-exploitation, habitat degradation, and the impact of introduced species: (Simberloff, 1986; Caughley, 1994; Green, 1994)). However, (Hedrick et al., 1996), suggested that this was a false dichotomy, and that processes from both paradigms contribute to extinction, and that both should be considered in conservation planning

Several studies have demonstrated that excessive emphasis on obvious deterministic factors can be misleading, resulting in conclusions that are too optimistic about the viability and persistence of a species (Hedrick et al., 1996). For example, it was accepted for many years that predation by Common Ravens (*Corvus corax*) on young desert tortoises (*Gopherus agassizii*) was the major factor jeopardizing their survival in some parts of the southwest America (Hedrick et al., 1996). A PVA showed, however, that the population was most sensitive by far to the mortality of mature females; an emphasis on reducing raven predation thus erred in mistaking a highly visible impact for a demographically significant one (Doak et al., 1994). Work on loggerhead sea turtles (*Caretta caretta*) has similarly shown the difficulty in assessing the relative significance of different vital rates when determining population growth (Crouse et al., 1987). The aim of this study is to identify possible limiting factors in preparation for a PVA that will be completed when these factors are more fully understood (see Appendix 3). PVA is useful in interpreting the significance of deterministic limiting factors (Hedrick et al., 1996).

Predation has often been suggested as a limiting factor for herbivore populations but, in practice, the consequences of antipredator behaviour for population dynamics are complex (FitzGibbon & Lazarus, 1995a). Predators have been observed to select just those individuals whose antipredator behaviour renders them most vulnerable when attacked (FitzGibbon, 1989). Studies in the Ishasha Sector of the Rwenzori National Park in Uganda indicated that a high density of predators (lions) was responsible for the decline of the topi population, in addition to poaching (Yoaciel & Van-Orsdol, 1981). Similarly, mountain lion predation was found to be the major factor preventing an increase in bighorn sheep (*Ovis canadensis*) numbers in the Peninsula Ranges of southern California (Hayes et al., 2000), and feral horse in Nevada (Greger & Romney, 1999). However, the role of predation as a population regulation mecahnism remaims controversial. Studies in the core of moose range in North American indicated that moose (*Alces alces*) numbers were regulated at low equilibrium density (0.4/km^2) by predation when wolves coexisted with bear species (Crete & Courtois, 1997). Also, the "predation-sensitive food" (PSF) hypothesis proposed that both food and predation necessarily limit populations, because as food becomes limiting animals take greater risks to obtain more food, and some of these are killed (Sinclair & Arcese, 1995). Alternative hypotheses are "predator regulation" where predators hold the prey population well below starvation levels; and "surplus" predation where predators kill only those prey that are excluded from optimal habitat and are already dying from starvation (Sinclair & Arcese, 1995).

It is widely agreed that many human activities are not compatible with wildlife conservation. Indeed the increase in human population worldwide has led to the apparent decline, and in some cases, extinction, of many wildlife species. Hence, conservation areas permitting human activities within their borders cannot be relied upon as a means of conserving large and middle sized mammals in Africa (Caro, 1999). Poaching or over hunting can have direct and negative effects on a species or wildlife community. This situation can be aggravated if, as in the case of hirola, the species in question is located in an arid environment with an increasing human density, if it suffers from droughts that strain the basic sources of livelihood, and if the species is locally distributed and in low numbers. Observations of large and medium-sized mammal densities in the Katavi Ecosystem in western Tanzania indicated that their densities were lower outside the National Parks (Caro, 1999). The factor responsible for these low densities was illegal hunting, especially in close proximity to big settlements (Caro, 1999). Similarly, subsistence poaching (sometimes called 'pot' poaching) has contributed to the decline of wildlife in the Masai Mara region of Kenya (Ottichilo et al., 2000), and of buffalo populations in the north-western and western corridor areas of the Masai Mara (Dublin et al., 1990).

Poaching, especially of large browsers such as elephants can lead to habitat degradation for other species. Elephants destroy woodlands thus creating grasslands and grassland patches (Laws, 1969; Caughley, 1976); they thus limit bush encroachment, acting as facilitators to grazers like hirola. Herbivory by large mammals also has a strong influence on the species composition, decomposition rates, nutrient recycling and microsite structure of the herb layer (McNaughton et al., 1988). Elephants seem to determine both structure and dynamics of tree community in Africa (Dublin et al., 1990) whereas the large mammal grazers determine the pattern and dynamics of the herb layer (McNaughton, 1983). Overall, these factors create microhabitats that may benefit certain species such as hirola.

An increase in the human population leads to an increase in demand for food and this may lead to overstocking of livestock (the most viable farming activity in arid environments). Overstocking leads to overgrazing, bare ground, the progressive growth of bush cover and thus a decline in range conditions (Oba et al., 2000; Andanje & Ottichilo, 1999; Prins & Olff, 1998; Rainy & Worden, 1997). The loss of habitat through overstocking is believed to be a major factor in the decline of wildlife populations (Morrison et al., 1992; Prins, 1992). Such declines may be through reduced reproduction rates, increased mortality rates and, ultimately, increased competition for food resources between wildlife grazers such as hirola and livestock. Studies of moose in North America in unproductive boreal forests indicated that sub-optimal nutrition in winter and summer was responsible for the relatively low rate of calf production (Crete & Courtois, 1997). In the Masai Mara Game Reserve in Kenya, land use and vegetation changes, drought effects and poaching were responsible for the decline in large and medium wildlife species (Ottichilo et al., 2000). Indeed, the main long-term threat to the future of wildlife populations in Kenya is due to the indirect effects on habitat resource destruction or alteration (Lado, 1996). In Africa overall, where herbivore species-richness remains high (Prins & Olff, 1998), the increasing conversion of natural lands to agriculture and human settlement is a consequence of increasing human population and is thought to be responsible for the increasing rate of decline in wildlife resources (Johan, 1995).

The association of wildlife, livestock and humans can also lead to exposure to novel diseases and parasites. Livestock can be restrained and treated or vaccinated, but, in general, these techniques are impractical for wildlife. Endangered species such as the hirola which share their range with people and livestock are thus at risk. Observation in Kruger National park indicated that zebra foals were being affected by African Horse Sickness (Lord et al., 1997). A similar observation in the Masai Mara Game Reserve indicated that the infection of canine distemper virus among wildlife species (hyenas, lions, wild dogs, cheetah) was derived from domestic dogs (Cleaveland et al., 2000); in this case the virus dramatically reduced the population size of hyenas (Alexander et al., 1995). Disease may also threaten long-term population viability, particularly when it acts with other limiting factors.

Many species in hot arid environments are dependent on behavioural mechanisms to reduce heat stress. Temperatures in the shade are significantly lower and thus a majority of animals seek shade during the hot times of day (Jackson, 1998). Artiodactyls and felids have a carotid rete that can cool the blood destined for the brain and consequently the brain itself, if the cavernus sinus receives cool blood returning from the nose (Jessen, 2001). This condition is fulfilled in resting, but during severe exercise hyperthemia, the venous return from the nose bypasses the cavernous sinus and suppresses brain cooling. The carotid rete system not only cools the brain to prevent thermal brain damage, but also prevents water loss through evaporative heat loss (Jessen, 2001). Studies on heat tolerance in donkeys and mules indicate that exposure to direct heat causes increase in body temperature, hence increased respiration leading to excessive water loss (Pal et al., 2000). A study on Brant's whistling rat (*Parotomys brantsii*) in the south-west arid biome of southern Africa indicated that the rats fed and foraged for shorter periods in summer and instead opted to spend more time in burrows; during winter, lower ambient temperatures allowed unrestricted diurnal activity (Jackson, 1998). Thus, the availability of shade is potentially a limiting factor for hirola both in its native range in Garissa and in Tsavo N.P where ambient temperatures are often very high.

Finally, it is probably rare for limiting factors to operate in isolation. Such factors may be more likely to bring a population close to extinction when other factors are already in operation. Thus disease may have a more important effect in a population that is already vulnerable due to habitat degradation.

This chapter attempts to explain relationships between the various candidate extrinsic limiting factors and patterns of abundance, reproduction and mortality in the hirola population in both Garissa and Tsavo. The chapter includes spatial and temporal relationships between limiting factors (e.g., vegetation characteristic, food availability, ungulate community structure, water, predation, poaching and competition) and the responses of the hirola population. A key technique in the study of the Tsavo population was to explore the action of these independent factors on variation between hirola groups, both in terms of variation in group size and in processes such as birth and mortality rates.

8.2 Garissa

8.2.1 Range decline

Surveys, and partial surveys of hirola in Garissa, carried out since 1963 indicated that the hirola range has been declining. Analyses of occupied ranges using mapinfo indicated that by 1963, hirola in Kenya occupied 16,820 Km². The range declined by 36% between 1963 and 1976 to about 10,810 Km². By 1996, the range declined further to the current 5,171 Km², indicating a further decline of 52% in 20 years period (Figure 8.1).

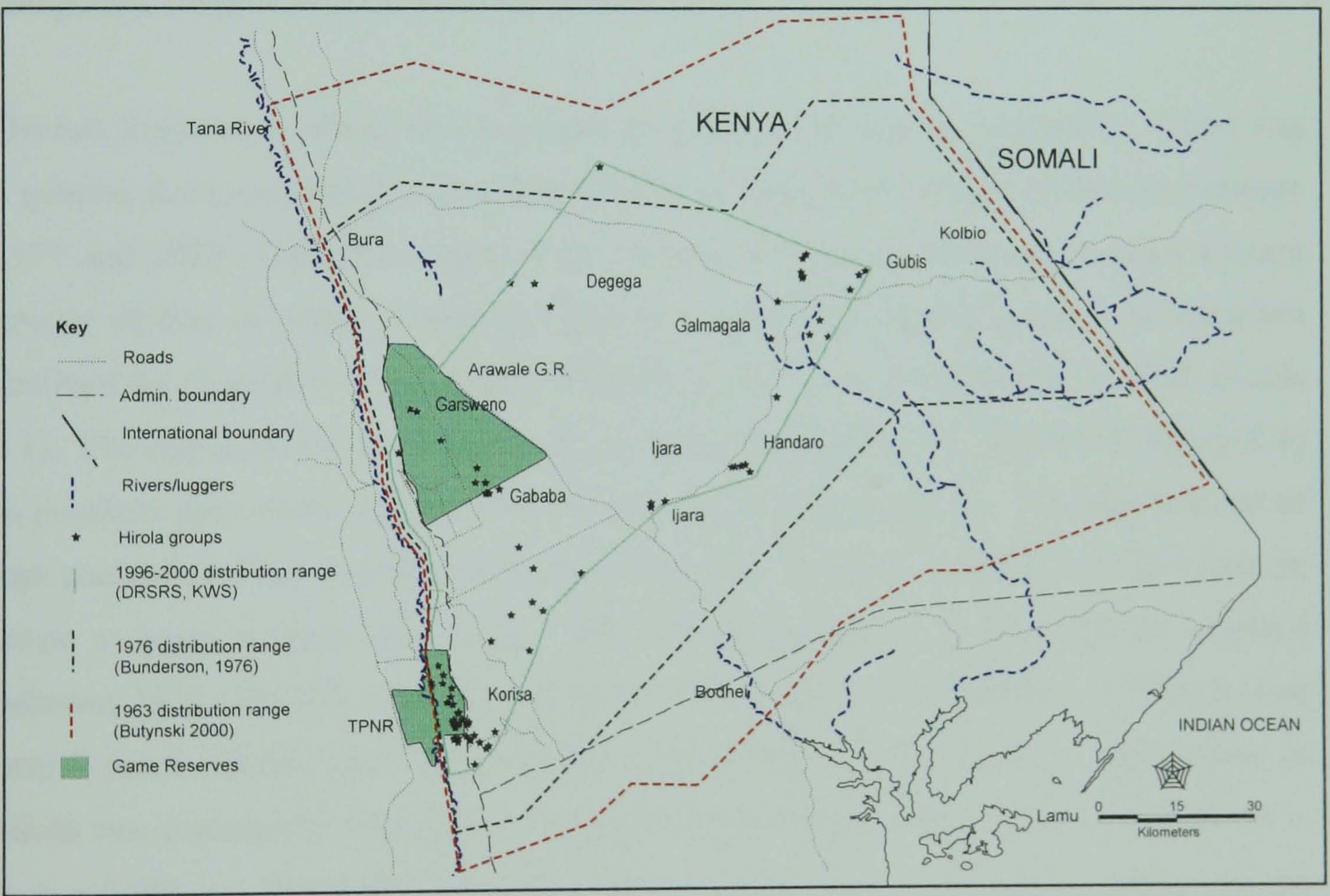


Figure 8.1: Analyses of hirola distribution and range decline in Garissa between 1963 and 1996.

8.2.2 Trends in the human population, livestock and wildlife species

There has been a general upward trend in the human population of Garissa, except between 1962 and 1969, when the population declined from 94,000 to 65,000 (Data from Central Bureau of Statistics, Ministry of Finance and planning, Kenya Population Census). This decline was attributed to inter-clan fighting in the region. However, there was a dramatic sharp human population increase between 1989 and 1999 from 127,000 to 390,000 due to the influx of fleeing Somalis from war torn Somalia (Figure 8.2a). The increase in the human population in a pastoral community caused a general increase in the number of livestock. However, as the human population rose, the number of cattle declined from 424,886 in 1977 to 254,681 in 1988 a decline of 40% in 11 years (Data from Central Bureau of Statistics, Ministry of Finance and planning, Kenya Population Census). This decline contrasted with a sharp increase in the number of shoats (sheep and goats), which more than doubled (Figure 8.2a).

Overall, livestock numbers far out-weigh those of wildlife species (Table 8.1). There was a general downward trend in the total number of large wild animals in Garissa between 1977 and 1988 (Table 8.1, Figure 8.2). Mixed feeders and browsers showed a much greater decline in numbers than did grazers. Combined, mixed feeders and browsers declined by about 64% from 42,443 animals in 1977 to 15,214 animals in 1988 (Table 8.1). The reason for these reductions may have been poaching (see Table 8.4, Figure 8.4) as poachers appeared to prefer them both for food and for trophies. The high number of topi counted in 1988 coincided with the wet season when topi move out of thick coastal forest to graze in more open areas. The sharpest decline in wildlife species occurred between 1978 (104,980 wild animals) and 1985 (31,611 wild animals), a 70% decline over 7 years. Hirola also declined at this time (Table 8.1, Figure 8.2). The decline in hirola was statistically correlated with the decline in lesser kudu (Pearson $r = 0.987$, $n = 4$, $p < 0.05$) and Burchell's zebra (Pearson $r = 0.992$, $n = 4$, $p < 0.01$). However, no significant correlations were detected with other animal species, including livestock. Because of the long intervals in human population censuses, the decline in hirola could not be statistically related although the general increase in the human population and in the livestock (Figure 8.2a&d) as hirola declined are strongly suggestive of a causal relationship.

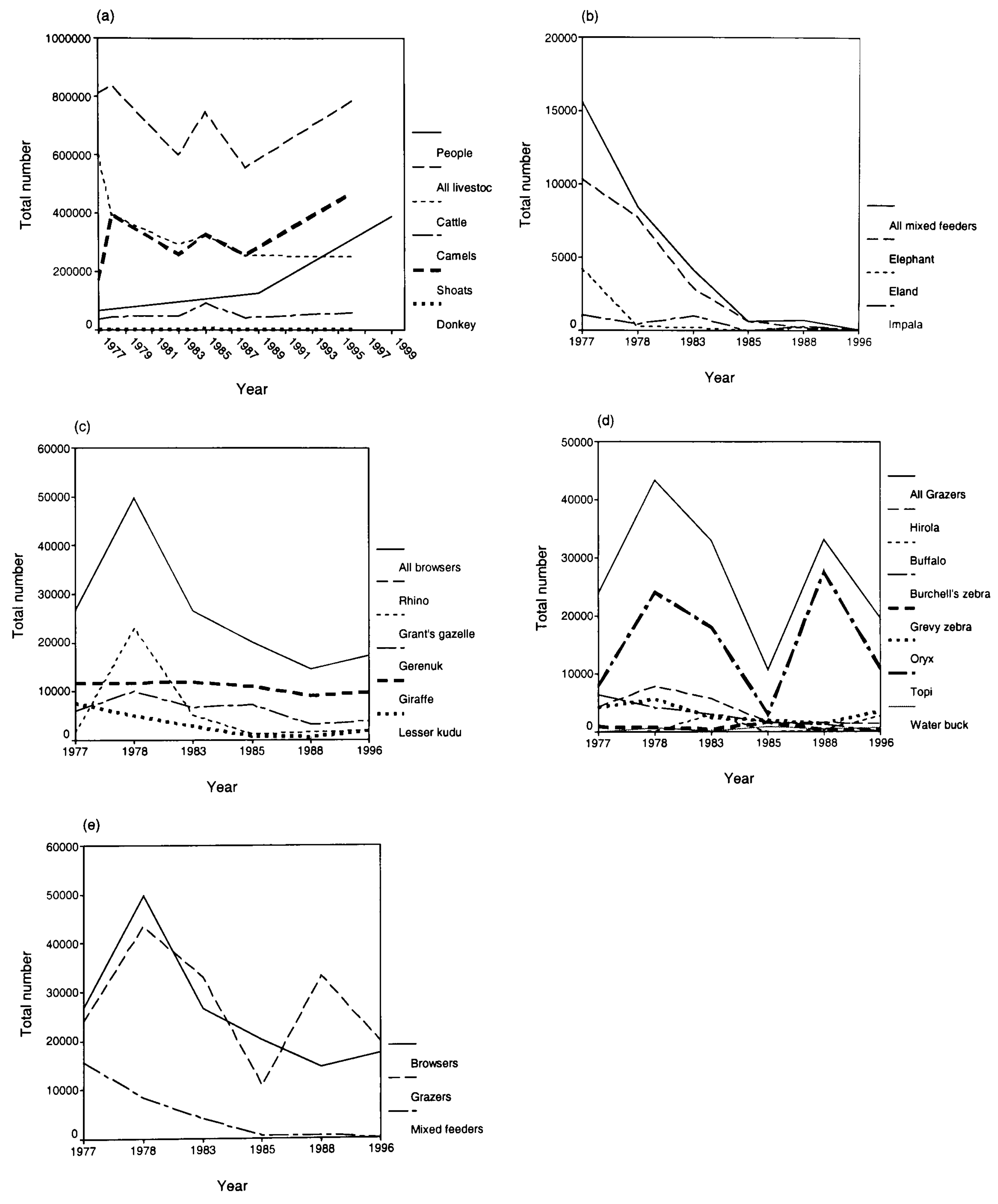


Figure 8.2: Changes in the number of people, domestic stock and wildlife (mixed feeders, browsers, and grazers) in the hirola's natural range (Garissa) between 1977 to 1996. Livestock and wildlife data from DRSRS census records 1977-1996 and population data from Ministry of Finance and Planning, Kenya Population Census.

Table 8.1: Changes in number of domestic stock and wildlife in the hirola natural range between 1977 to 1996. Livestock and wildlife data from DRSRS census summary records 1977-1996.

Species/Year	Mar-77	Sep-78	May-83	May-85	Apr-88	May-96
Livestock						
Cattle	603,110	394,339	291,366	324,751	254,681	251,865
Camel	36,438	45,987	47,372	91,018	41,901	60,143
Donkey	1,378	2,119	1,518	4,184	2,654	3,455
Shoats	169,784	393,949	258,823	326,992	257,070	468,588
Livestock sub-totals	**810,710**	**836,394**	**599,079**	**746,945**	**556,306**	**784,051**
Mixed feeders						
Elephant	10,340	7,725	2,904	642	176	30
Eland	4,234	278	220		230	0
Impala	1,083	446	1,012		318	18
Mixed feeders sub-totals	**15,657**	**8,449**	**4,136**	**642**	**724**	**48**
Browsers						
Grant's gazelle	1,477	23,063	5,104	1,203	1,645	1,926
Gerenuk	6,007	9,983	6,710	7,241	3,149	3,889
Rhino	98	0	0	0	0	0
Giraffe	11,621	11,740	11,947	10,980	9,077	9,819
Lesser Kudu	7,583	4,964	2,816	776	619	1,812
Browsers sub-totals	**26,786**	**49,750**	**26,577**	**20,200**	**14,490**	**17,446**
Grazers						
Buffalo		111	3,036		442	2,719
Hirola	15,950	11,282	10,843	1,595	1,592	1,359
Oryx	4,234	5,661	2,442	1,969	1,486	3,550
Topi	7,977	24,095	18,064	3,033	27,568	10,914
Waterbuck		697	176	875	477	717
Burchell's zebra	6,499	4,183	3,102	1,633	1,238	132
Grevy's Zebra		752	484	1,664	371	283
Grazers sub-totals	**34,660**	**46,781**	**38,147**	**10,769**	**33,174**	**19,674**
Grand total	887,813	941,374	667,939	778,556	604,694	876,196

8.2.3 Poaching

8.2.3.1 Hirola

Data on poaching in Garissa was mainly recorded by hirola community scouts (Chapter 3, Section 3.7). These data were thus limited to the areas where the scouts lived and did not cover the entire hirola range. However, the scouts were widely spread and I personally verified most of the information I was given by visiting the scenes to observe the remains of dead hirola. Table 8.2 indicates variation in hirola poaching between June

1998 and August 2000. The highest recorded numbers of poached hirola occurred at Gubis (10) and Galmagala (5), the two sites that are closest to the Kenya Somalia border (Figure 8.3).

The largest number of poached hirola (6) occurred in March 2000 and the majority of these were killed at Gubis. It was reported that this was the work of bandits harvesting wild animals in Kenya and using donkey carts to take the meat for sale in Somalia. Other animals (giraffe, zebra) were also killed. Overall, there were fewer hirola to the north of the TPNR along the Tana River and on the Kenya Somalia border (Figure 8.3). People from the Pokomo tribe were recorded to cross the Tana River and hunt for all types of game within the Somali pastoral land. Higher numbers of hirola within the east bank area of the TPNR is possibly due to KWS security patrols which exclude Pokomo poachers. Along the international border, bandits, commercial poachers and warring Somali factions were recorded as poaching, hence the lack of hirola in this area (Figure 8.3).

A total of 6 types of poachers were recorded in the hirola range (Table 8.3). These included the Pokomo hunters along the Tana River, government security personnel at manned stations within the entire range and bandits mainly along the Kenya/Somali border. Local Somalis were reported to have killed only one zebra, although they also consumed what others killed and were ready to buy poached game meat. The data obtained suggested that bandits took the highest number of hirola followed by Somali home guards (Kenya Police Reserve).

8.2.3.2 Poaching of other wildlife in relation to hirola

These data on poaching indicated that some animal species were poached more than others ($\chi^2 = 81.225$, df = 10, $p < 0.001$). Among the wildlife poached in Garissa, hirola was recorded most often, followed by lesser kudu and giraffe (Table 8.4, Figure 8.4a). When the poached species were lumped into specific feeding strategies, browsers and grazers proved to be poached more often ($\chi^2 = 109$, df = 2, $p < 0.001$) than mixed feeders (Table 8.4, Figure 8.4b). Further, a majority of poaching incidents were recorded close to the international border, followed by areas along the Tana River (Table 8.4).

Table 8.2: Number of hirola known to be poached with respect to location and period in the hirola natural range. The table also indicates higher poaching towards the Kenya Somalia border (Gubis). The numbers are probably an underestimate.

Date/Site	Jun-1998	Nov-1998	Jan-1999	Jun-1999	Sep-1999	Mar-2000	Aug-2000	Totals
Bura	0	0	0	0	0	0	1	1
Garsweno	1	0	0	0	0	0	0	1
Gababa	0	0	0	0	0	0	0	0
Kotile	3	0	0	0	0	0	0	3
Ijara	0	0	0	0	0	0	3	3
Handaro	0	0	0	0	0	1	0	1
Galmagala	0	2	0	1	2	0	0	5
Gubis	0	1	0	2	1	5	1	10
Totals	4	3	0	3	3	6	5	24

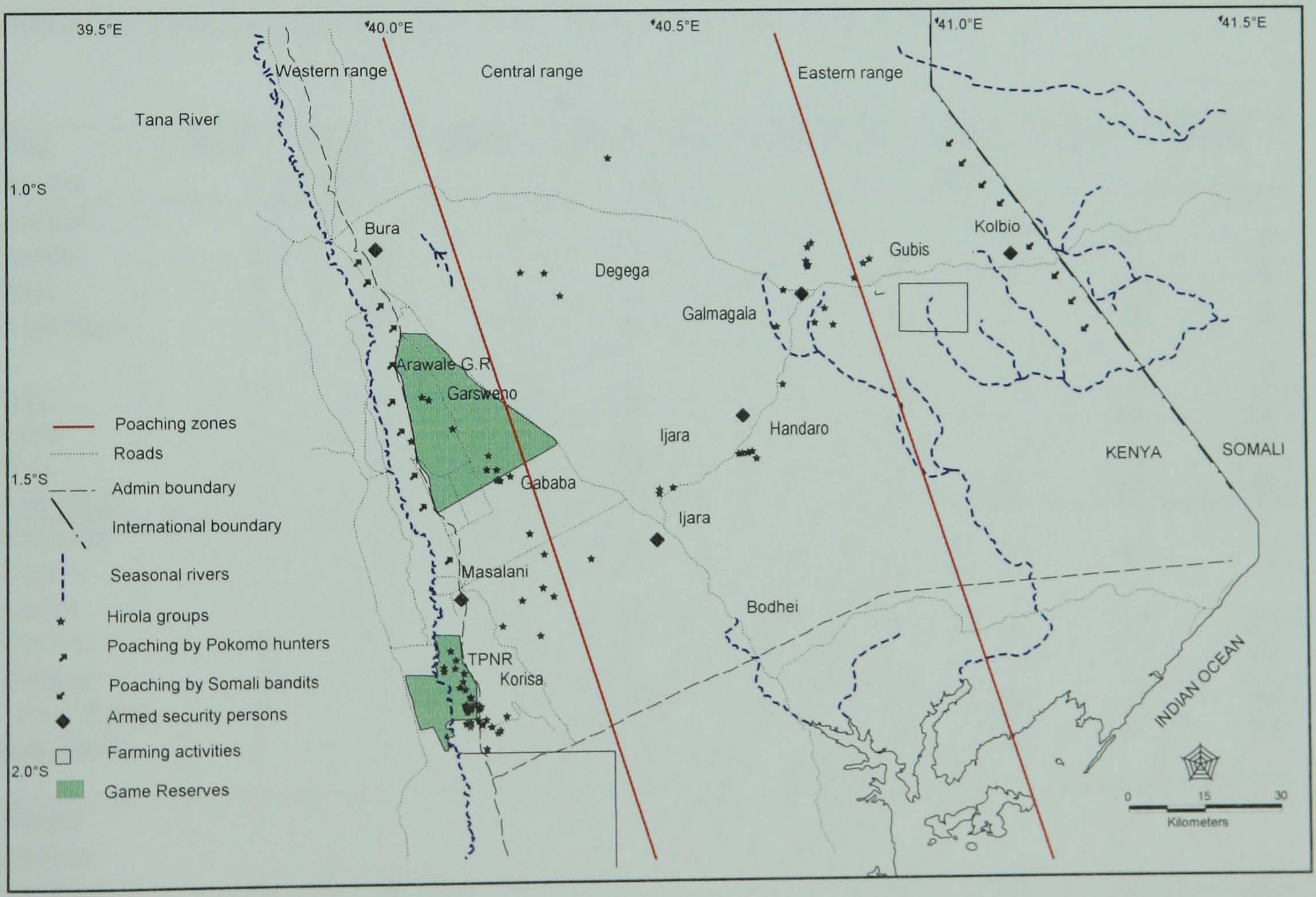


Figure 8.3: Centres of poaching activities in relation to hirola distribution in Garissa between September 1996 and December 2000.

Table 8.3: Summary of the different kinds of poachers recorded in the hirola's natural range, Garissa, and the numbers of hirola reported to be killed by each.

Site/ Poachers	Pokomo	Somalis	Admin. Police	Kenya Police	Kenya Army	Police Reserve	Bandits	Totals
Bura	0	0	0	1	0	0	0	1
Garsweno	1	0	0	0	0	0	0	1
Gababa	0	0	0	0	0	0	0	0
Kotile	2	0	0	0	0	0	1	3
Ijara	0	0	0	0	0	3	0	3
Handaro	0	0	0	0	0	1	0	1
Galmagala	0	0	2	0	1	2	0	5
Gubis	0	0	0	0	2	0	8	10
Totals	3	0	2	1	3	6	9	24

Table 8.4: Recorded poaching levels and areas where it occured on larger wildlife species within the hirola's natural range from January 1999 to August 2000.

Site/ Species	Bura	Gars-weno	Gababa	Kotile	Ijara	Handaro	Galma-gala	Gubis	Totals
Grazers									
Buffalo	0	2	2	3	0	0	0	0	7
Zebra	0	0	1	1	0	1	0	2	5
Waterbuck	0	0	0	0	0	3	0	0	3
Topi	0	0	0	0	1	0	0	4	5
hirola	1	1	0	3	3	1	5	10	24
Oryx	0	0	0	0	0	0	0	1	1
Sub-total	**1**	**3**	**3**	**7**	**4**	**5**	**5**	**17**	**45**
Browsers									
Grant's gazelle	0	1	0	0	0	1	1	0	3
Giraffee	0	0	3	1	0	0	6	7	17
Gerenuk	3	0	3	0	0	0	4	3	13
Lesser Kudu	0	1	0	0	0	0	19	0	20
Sub-total	**3**	**2**	**6**	**1**	**0**	**1**	**30**	**10**	**53**
Mixed feeders									
Elephant	0	0	0	0	2	0	0	0	2
Grand total	**4**	**5**	**9**	**8**	**6**	**6**	**35**	**27**	**100**

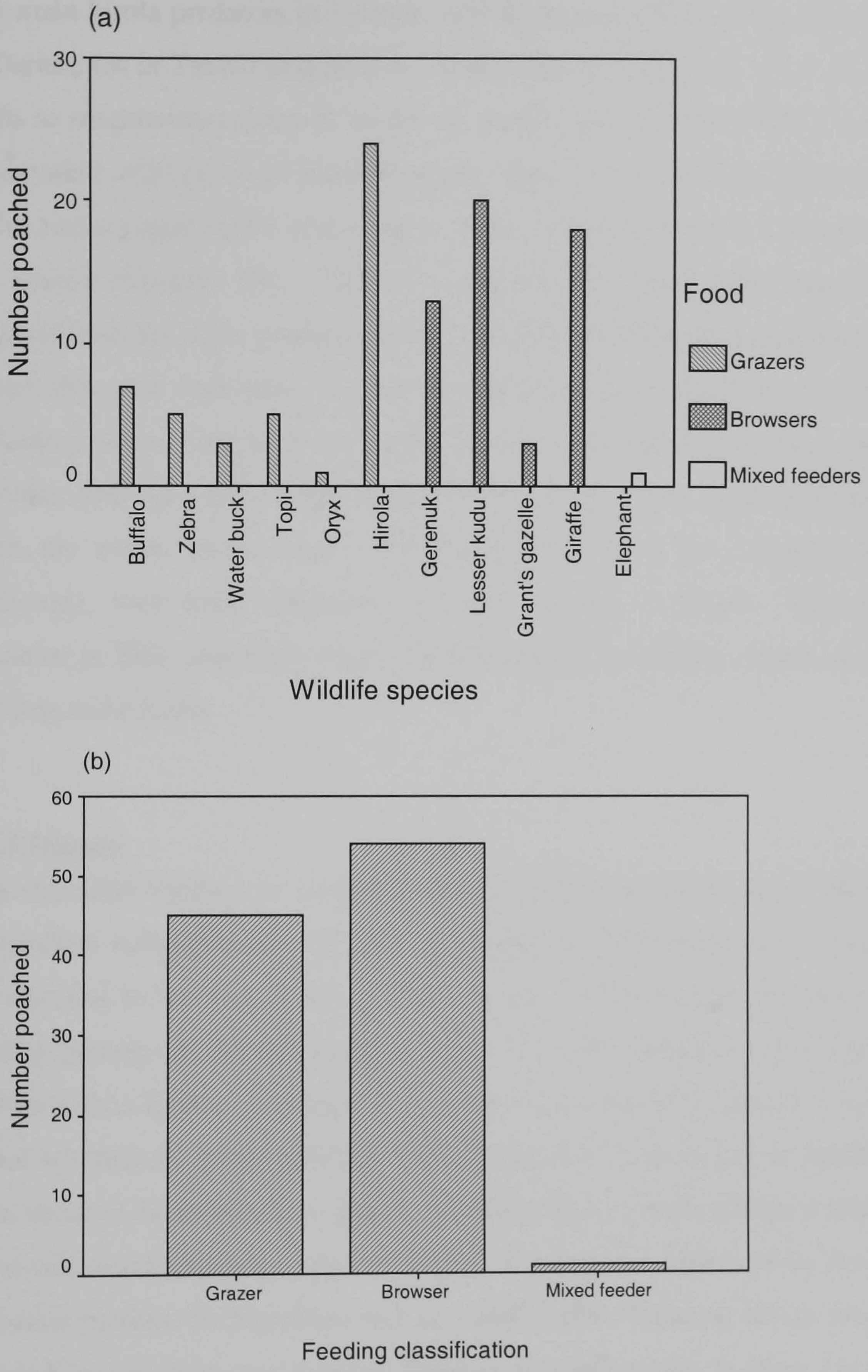


Figure 8.4: Comparison of poaching levels on various groups of wildlife within the hirola's natural range, Garissa.

8.2.4 Predation

The main hirola predators in Garissa were lions, and hunting dogs (Chapter **IV**). Hirola in Garissa (as in Tsavo) occupied the same range area all year round and made only local shifts to neighbouring areas in search of greener pasture and shelter (Chapter **VII**). Data on monthly availability of alternative prey species indicated that their availability on the entire hirola range varied with season, being abundant in the wet season and rarer in the dry season (Chapter **VI**). Field observations and information from the hirola scouts indicated that the main predator (lions) did not move and instead occupied areas close to waterholes, and manyattas (Somali homesteads) and preyed on livestock and wildlife including hirola. One male hirola was killed at the edge of a market centre's water dam at Roka, near Ijara by a single male lion in August 1998. Hunting dogs were known to roam the entire hirola range. During periods when they ranged closer to human settlement, they were sometimes reported to prey on hirola. One notable example occurred at Elbi, near Ijara where herders reported sighting a pack of six feeding on a yearling male hirola.

8.2.5 Disease

The inter-clan fighting in Somalia, which has been going on since 1991, has left many pastoralists vulnerable and unstable. Whether they are involved in fighting or not, they are exposed to the risk of being killed by the militia groups and their livestock taken. During periods of intense fighting, they are often forced to flee together with their livestock into Kenya. Because of a lack of governance in Somali, most economic and social systems are non-functional. Thus, there are no livestock vaccination programs or even markets for livestock products. All these factors make Kenya attractive. The influx of unvaccinated animals, some of which traverse the entire hirola range to end up in livestock markets in Mombasa and in ranches (for fattening before being sold) around Tsavo National Park, has brought diseases to wildlife and resident livestock. In 1992-1993, there was a rinderpest outbreak in the hirola range and it is thought to have greatly reduced the hirola population. The same outbreak greatly reduced the buffalo population in Tsavo. Further, more recent outbreaks of rinderpest have occurred in the hirola range and these have also been attributed to livestock coming in from Somalia (Dr. Richard Kock, pers comm.). During the 1997-1998 El-Nino floods a similar but reverse situation occurred: the entire hirola range was flooded and an aerial survey showed that both hirola and people had taken refuge on the same areas of raised ground (Daniel Woodley, pers. Comm.). I visited the range soon after the El-Nino rains and observed heaps of bones of goats and sheep that were reported to have died of pneumonia. Hirola may have died too from pneumonia but the hirola community scouts reported that some were poached. Immediately after the El-Nino rains, there was a disease outbreak within the hirola range that caused substantial deaths among wildlife including hirola and cattle. According to Dr. Richard Kock's report to the Hirola Management Committee, blood samples collected from sick cattle indicated foot and mouth disease, though the possibility of other diseases such as rinderpest, East Coast Fever (ECF), trypanosomiasis, and contagious bovine pleuro-pneumonia (CBP), that are prevelant within the hirola's natural range were not ruled out. The entire range was highly infested by brown ear ticks (known to transmit East Coast Fever) and tsetse flies (known to transmit trypanosomiasis). Perhaps, the increased bush cover that resulted from the heavy rains, tsetse flies dispersed further north from the coastal forests.

8.3 Tsavo

8.3.1 Trends in the herbivore community

The Tsavo ecosystem is a semi-arid environment and the parts of the range outside the Tsavo N.P. are owned by large scale ranching companies; in addition, subsistance pastoralists live within the ecosystem (Chapter II, Figure 2.2). Ranchers and subsistance pastoralist are notorious for tresspassing and grazing in the Park, especially during drought periods. At the same time, wildlife freely utilizes areas within the park and outside. Data on wild herbivores and livestock in the Tsavo Ecosystem indicate that there have been large fluctuations in numbers. One notable feature was a decline in early 1991 (Table 8.5, Figure 8.5). During this period, the livestock population declined by 74% from a total of 41,279 (1989) to 10,689 animals (1991). Comparable declines among wildlife species during the same period were: mixed feeders (25%), browsers (51%) and grazers (24%). Among the grazers, buffaloes were the most affected declining by 61% from a total of 6882 individuals in 1989 to 2681 in 1991, while among the browsers, lesser kudu declined by 69% during the same period (Table 8.5, Figure 8.5). There was no striking decline in rainfall (Figure 8.5e) in this period but it was associated with increased elephant poaching and a rinderpest outbreak that greatly reduced the buffalo and lesser kudu population in Tsavo NP. Hirola (which were too few to be detected in the DRSRS surveys) may also have been adversely affected during the same period but this was not monitored. Most wildlife seems to have increased after the 1991 decline but the 1997 counts were low and overall there appears to be a declining trend. Exceptions are cattle that are increasing and elephants that seem to be stable in recent years (Figure 8.5).

Table 8.5: Changes in number of domestic stock and wildlife in Tsavo Ecosystem between 1977 to 1997. Livestock and wildlife data from DRSRS census records 1977-1997.

Species	**Feb-77**	**Mar-78**	**Nov-89**	**Mar-91**	**Oct-91**	**Dec-92**	**Apr-94**	**Aug-94**	**Mar-97**
Livestock									
Cattle	4,429	15,523	29,208	9,133	29,282	4,143	2,301	6,589	12,945
Sheep & Goat	310	2,732	12,071	1,556	5,815	1,145	491	1,834	1,876
Livestock sub-totals	4,739	18,255	41,279	10,689	35,097	5,288	2,792	8,423	14,821
Mixed feeders									
Elephant	20,865	20,922	8,541	4,341	3,729	9,542	11,944	7,301	7,178
Eland	2,525	6,876	3,494	5,933	3,928	4,507	6,551	3,330	619
Impala	5,448	7,526	3,564	1,453	2,042	2,926	2,705	1,941	705
Mixed feeder sub-totals	28,838	35,324	15,599	11,727	9,699	16,975	21,200	12,572	8,502
Browsers									
Gerenuk	1,373	1,052	864	294	752	672	772	658	309
Giraffe	3,233	4,032	3,088	1,920	2,076	2,926	2,511	2,048	895
Grant's gazelle	2,126	7,011	5,594	2,646	6,360	6,252	5,708	7,088	3,993
Rhino	1,284	224					35		17
Lesser Kudu	797	1,142	1,164	363	899	636	1,686	872	430
Browser sub-totals	8,813	13,461	10,710	5,223	10,087	10,486	10,712	10,666	5,644
Grazers									
Buffalo	4,075	3,404	6,882	2,681	21,529	14,358	12,348	14,461	2,289
Hippo	44	380	105	69	224	199	579	106	241
Kongoni	9,347	10,528	6,847	5,916	7,381	7,797	7,271	5,236	3,391
Oryx	9,701	10,080	1,464	1,297	2,120	2,108	2,371	3,170	1,170
Waterbuck	487	963	211	640	406	127	316	267	723
Burchell's zebra	20,510	21,818	10,289	8,908	11,206	14,031	11,013	10,721	9,399
Grazers sub-totals	44,164	47,173	25,798	19,511	42,866	38,620	33,898	33,961	17,213
Overall totals	86,554	114,213	93,386	47,150	97,749	71,369	68,602	65,622	46,180

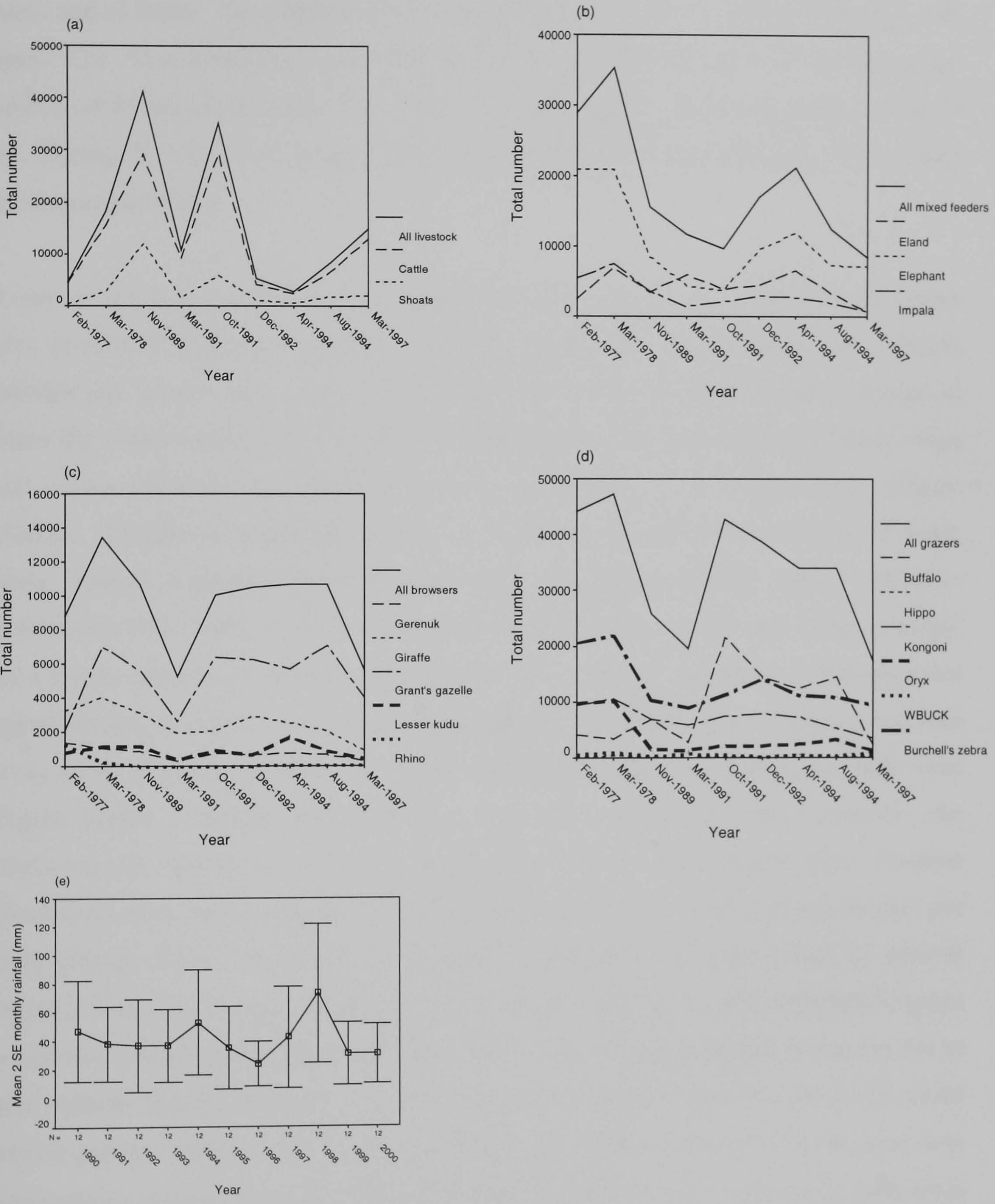


Figure 8.5: Changes in the number of domestic stock and wildlife (mixed feeders, browsers, and grazers) in the Tsavo ecosystem between 1977 to 1997, and rainfall pattern between 1990 and 2000. Livestock and wildlife data from DRSRS census records 1977-1997.

8.3.2 Habitat characteristics as a limiting factor

During the 1963 hirola translocation to Tsavo NP, hirola were released in the Ndara plains and at Irima. They later moved to settle in their current range (see Chapter VII, Figure 7.1). Thus hirola that were released at Irima (if they ever survived) moved a total distance of 45 km to the centre of the present range whereas the Ndara group moved 27 km. During the 1996 translocation, hirola were released at Satao Airstrip in Tsavo East and dispersed nearby.

In order to determine microhabitat preferences, hirola densities in different home ranges were correlated with various habitat structure parameters (see Chapter VII). Hirola densities per group range were calculated by adding all overlapping hirola groups to obtain the number using a particular home range and dividing by individual home range size. Data indicated that hirola densities were higher in more open areas (Figure 8.6a&d). Though no significant results were detected in other measurements of bush, hirola showed a general preference for more open areas (Figure 8.6bc). Positive correlations were found in relation to the abundance of bush lower than 1.8m in height and a crown diameter of more than 5m (Figure 8.6e). Further observations indicated that higher densities of hirola occurred in ranges with the greatest abundance of grass and forb cover, cover of grass and forb food plants and higher densities of preferred shade trees (Figure 8.6fgi). Though hirola sightings were often associated with waterholes, the results are not significant and display a generally negative trend (Figure 8.6j). Positive correlations with hirola densities were also found in relation to mean grass heights per range (Figure 8.6f). However this general correlation with grass height (a general property of the hirola range) is not sensitive to the fact that hirola often preferred to graze on patches of short green grasses (Chapter VII). This may indicate that hirola are not in their optimal habitat in Tsavo and that they may thus be forced to search for small suitable patches within an unfavourable environment. Hirola may have shifted from their initial release areas in Irima and Ndara because these sites are flat, completely open areas on black cotton soils and have tall, mostly pure stands of non-preferred grass species, and almost no short grass patches. The above results may indicate why some home ranges have higher group overlaps and why some hirola groups occupy distant places far away from other groups (See Chapter VII). Further, the patchy distribution and high overlaps in some places in Tsavo may indicate local microhabitat preferences.

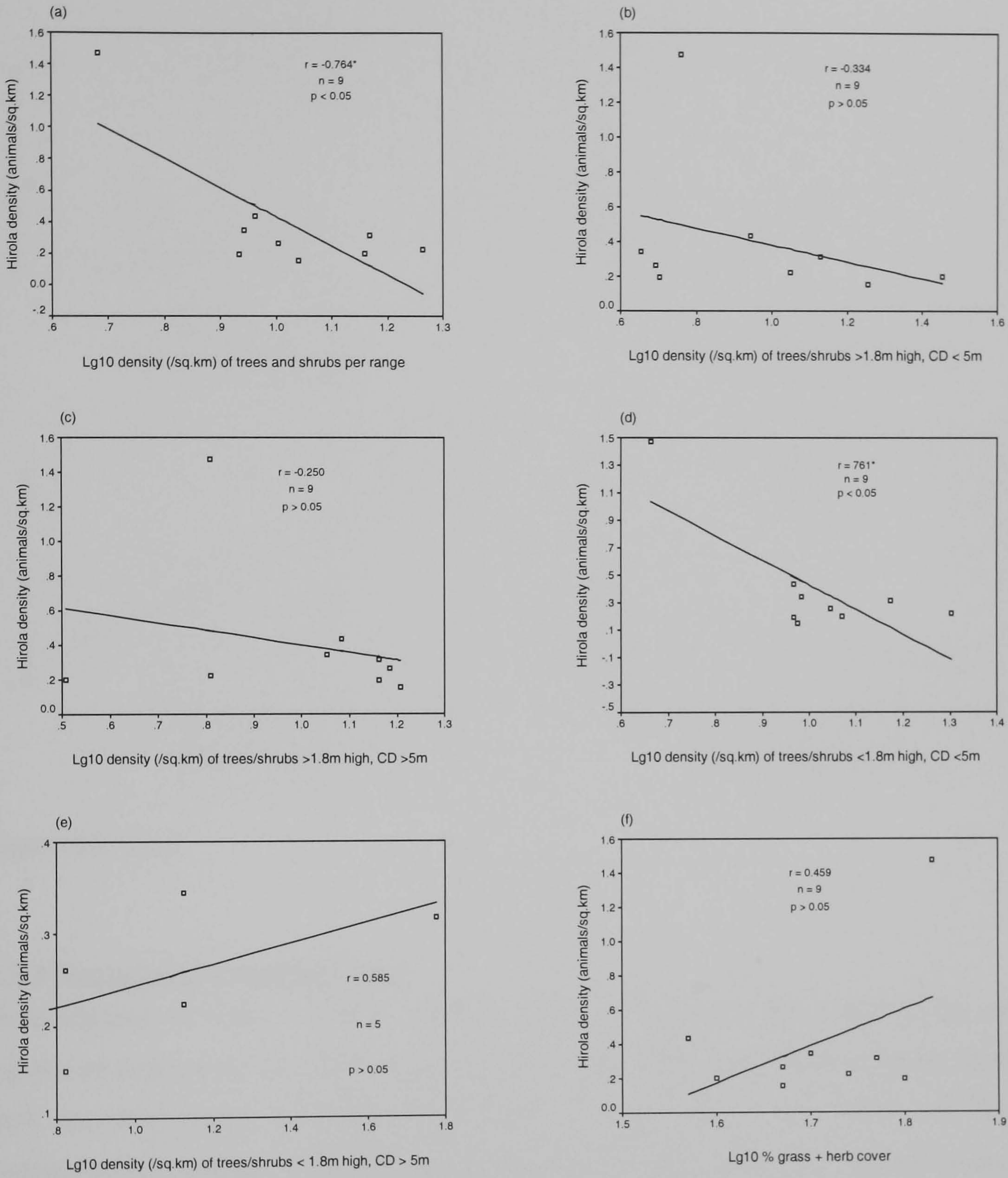


Figure 8.6: Relationships between hirola density and various habitat structure parameters

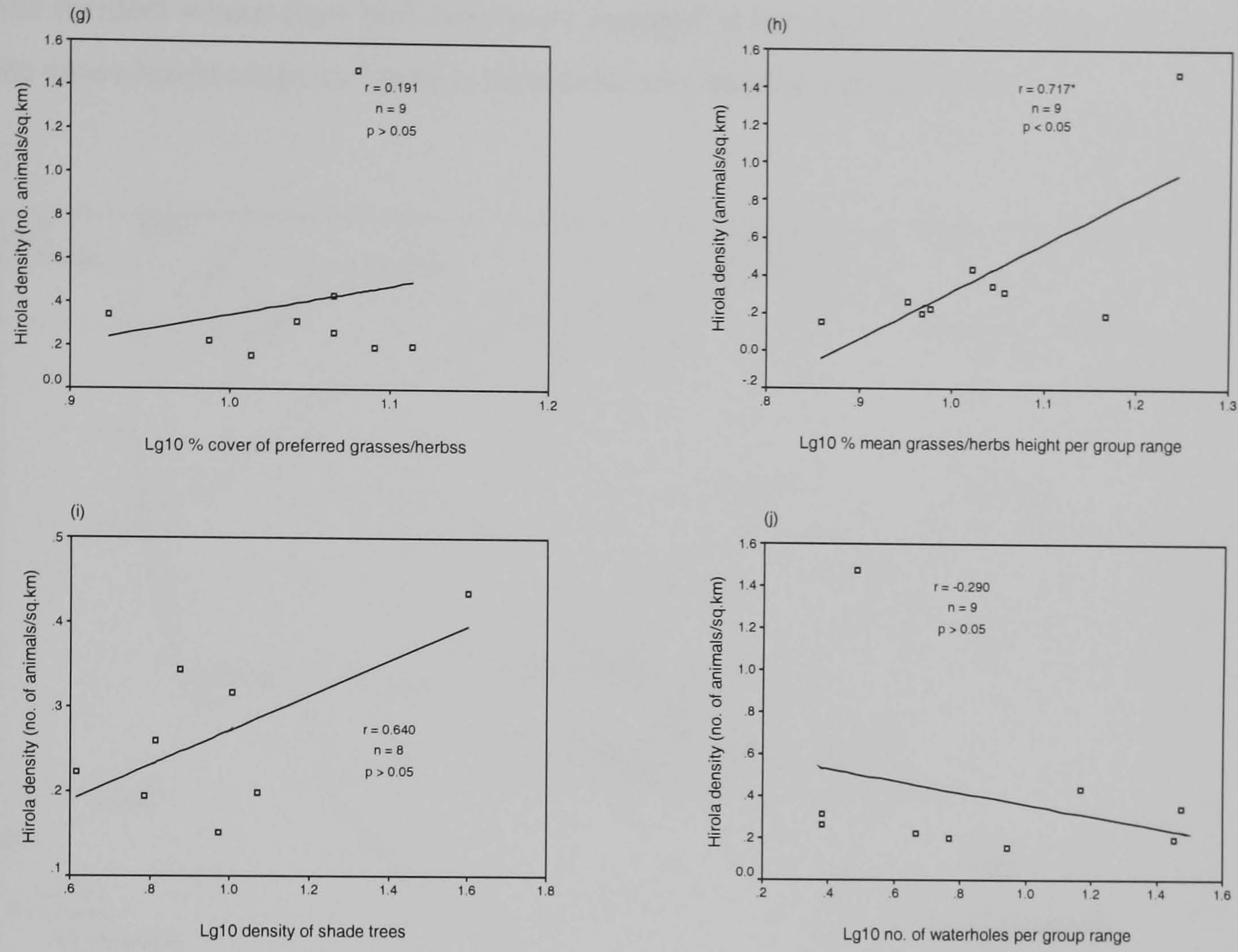


Figure 8.6: Cont.

8.3.3 Poaching as a limiting factor

Field sighting of hirola in Tsavo over the study area indicated that fewer hirola were sighted in areas prone to poaching (Figure 8.7). The MK group which occurred on the park boundary within the Kulalu Ranch was the most shy group, fleeing soon after sighting a car or people. Kulalu Ranch, is prone to night poaching by Giriama tribesmen and to some extent by cattle herders within the ranch. Most poaching was done on the darkest nights when there was no moon. The poachers are reported to confuse their victims using bright spotlight and a siren while one member approaches the standing animal and cuts its hind leg ligaments. Alternatively, funnel shaped thorn hedges are set along animal routes to grazing patches or water holes and wire snares are placed at the end of the funnel to trap passing animals. Numerous arrests of the night poachers have been made but Kulalu Ranch has many of the funnel trap networks. The current effort by KWS staff in collaboration with the David Sheldrick Wildlife Trust to remove laid snares has resulted in the removal of thousands of snare wires all around the park. However, one incident where three buffaloes were poached at the centre of hirola range shows that the entire hirola range in Tsavo is vulnerable to poaching (Figure 8.7).

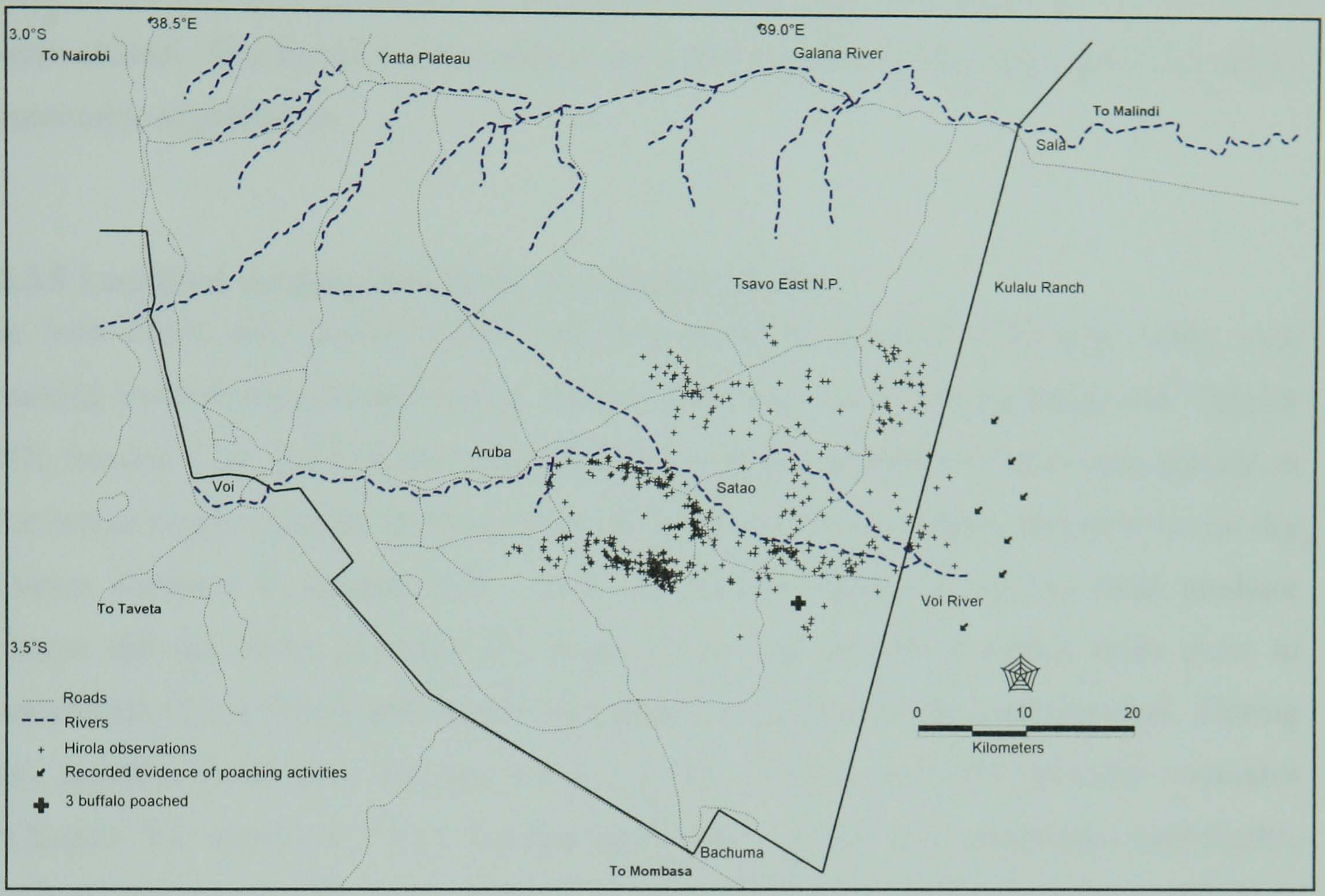


Figure 8.7: Hirola sighting points and evidence of poaching in the hirola range within Tsavo N.P. between September 1996 and December 2000

8.3.4 Reproductive behaviour patterns as a limiting factor

Observations on hirola groups in Tsavo showed that female hirola often separated from their group to graze alone with their calf and sometimes with their yearling offspring. Further, hirola yearlings often separated from the natal groups to graze alone or in temporary sub-adult groups (Chapter V, section 5.2). Overall, recruitment to the adult population was about 18.0% (see 4.2.4). Observations that female hirola were killed, together with their calves while in isolation and that only a few of the dispersing yearling survived to join or rejoin groups support the possibility that these may be periods of high risk. Hirola also appear to be timid in their response to predators when compared to Coke's hartebeest and Grant's gazelle. When predators approached, they generally ran slowly away in a line into the nearby bush. When they had lost visual contact with the predator, they were restless, walking around in circles and whistling, before eventually starting to graze again or walking further away. This behaviour differed from that of other fast-responding species such as Coke's hartebeest and Grant's gazelle that often kept watch over their predators, while alarm snorting, only running away fast when they were chased. The hirola's slow reaction gave the impression that they were particularly vulnerable to predators.

8.3.5 Localized ranging behaviour as a limiting factor

In both Tsavo and Garissa, hirola occupied the same range area all year round, only making local shifts to neighbouring patches (their other core feeding areas) (see Chapter VII, Section 7.2). Data on the seasonal and monthly availability of other prey species in the hirola range indicated that they were abundant in the wet season and rarer in the dry season (Chapter V, section 6.2). Field observations indicated that the main predator (lions) did not move (Chapter IV, Figure 4.11) and instead occupied areas close to waterholes (Satao Camp and Aruba Dam areas), and hunted in the neighborhood. During dry seasons, hirola were amongst the few resident species and with minimal associates (Chapter VI, section 6.2.2.1), though occasionally, a few bull elephants, waterbucks, impala, and lone buffalo bulls could move in to drink from drying waterholes. The lack of associates, coupled with fewer alternative prey to the resident predator population could have subjected hirola to higher predation risks. Further, during these periods hirola sought more shade and succulent forbs which could only be obtained in bushy areas (Chapter VII, section 7.5), places that give oportunities for predators. All direct predation observations (cases where a predator was seen feeding on a freshly killed hirola) were in the dry season.

8.3.6 Effect of limiting factors and hirola group dynamics

Regression analyses were carried out to test the possible effect of independent factors on variation between known hirola groups in Tsavo.

1. The dependent variables included in the analyses were:

a). Mean group size

b). Mean number of adult females per group

c). Mean number of female recruits per group
d). Mean number of calves per group
e). Ratio of calves per adult female per group
f). Calf mortality per group
g). Number of adult females emigrating from a group
h). Number of adult females immigrating into a group
i). Carcasses observed per hirola group range

2. The independent variable included in the analyses included:

a). Predator effects (Chapter III, sections 3.2.1.3 & 3.6)
i). Number of hirola killed by predators per group
ii). Number of observations of predators near a hirola group
iii). Number of hirola observed with predator scratch marks per group

b). Range effects (Chapter III, secction 3.2.1.1)
i). Group home range size
ii). Number of core areas per group home range
iii). Proportion of home range overlaps with neighbouring groups

c). Habitat structure effects (Chapter III, section 3.4.1)
i). Density (/km^2) of all trees and shrubs per hirola group range
ii). Density (/km^2) of all trees and shrubs 1.8m high with crown diameter less than 5m
iii). Density (/km^2) of all trees and shrubs 1.8m high with crown diameter more than 5m
iv). Density (/km^2) of all trees and shrubs shorter than 1.8m with crown diameter less than 5m
v). Density (/km^2) of all trees and shrubs shorter than 1.8m high with crown diameter more than 5m
vi). Density (/km^2) of all trees and shrubs 1.8m high with crown diameter less/more than 5m that were used by hirola for shade
vii). Height (cm) of grasses and herbs per hirola group range

d). Food availability (Chapter III, section 3.4.1)

i). Percentage cover of preferred grass species per group range
ii). Percentage cover of preferred herb species per group range
iii). Number of transient water holes per group range
iv). Mean monthly rainfall (mm) per group range

e). Associate species effects (Chapter III, section 3.2.1.4)

i). Overall percentage association with Coke's hartebeest per group
ii). Overall percentage association with Grant's gazelle per group
iii). Overall percentage association with zebra per group
iv). Overall percentage association with oryx per group
v). Overall percentage association with ostrich per group

The result presented below represent significant outcomes from the above parameters. Because variables were only obtained for nine hirola groups some otherwise important relationships could not be tested effectively.

8.3.6.1 Group size

Results on diurnal behaviour patterns (Chapter V, Section 5.41) showed that hirola rested during the hot hours of the day. Resting occurred mostly under the shade of certain preferred shade trees (Chapter VII, section 7.6). During the hot hours of the day, hirola groups in scanty shade areas always competed for the best shade, weaker individuals occupying poor quality shade or none at all. These observations underscore the importance of shade as an important ecological requirement for hirola. There was also a significant bivariate relationship that suggests that the availability of preferred shade trees in a hirola range favored larger hirola group sizes (Figure 8.8a). However hirola also appeared to be vulnerable to predators and bivariate analysis suggested that predators could be responsible for the small hirola group sizes observed (Figure 8.8b). Further, hirola group sizes were negatively related to the overall numbers of carcasses observed per group range (Figure 8.8c). Similarly, data showed a positive trend between the number of carcasses observed and the number of hirola killed by predators per group range, although the results were not significant (Figure 8.8d). A stepwise multiple regression analysis including these independent variables indicated that predators and lack of shade were the principle factors affecting hirola group sizes (Table 8.6).

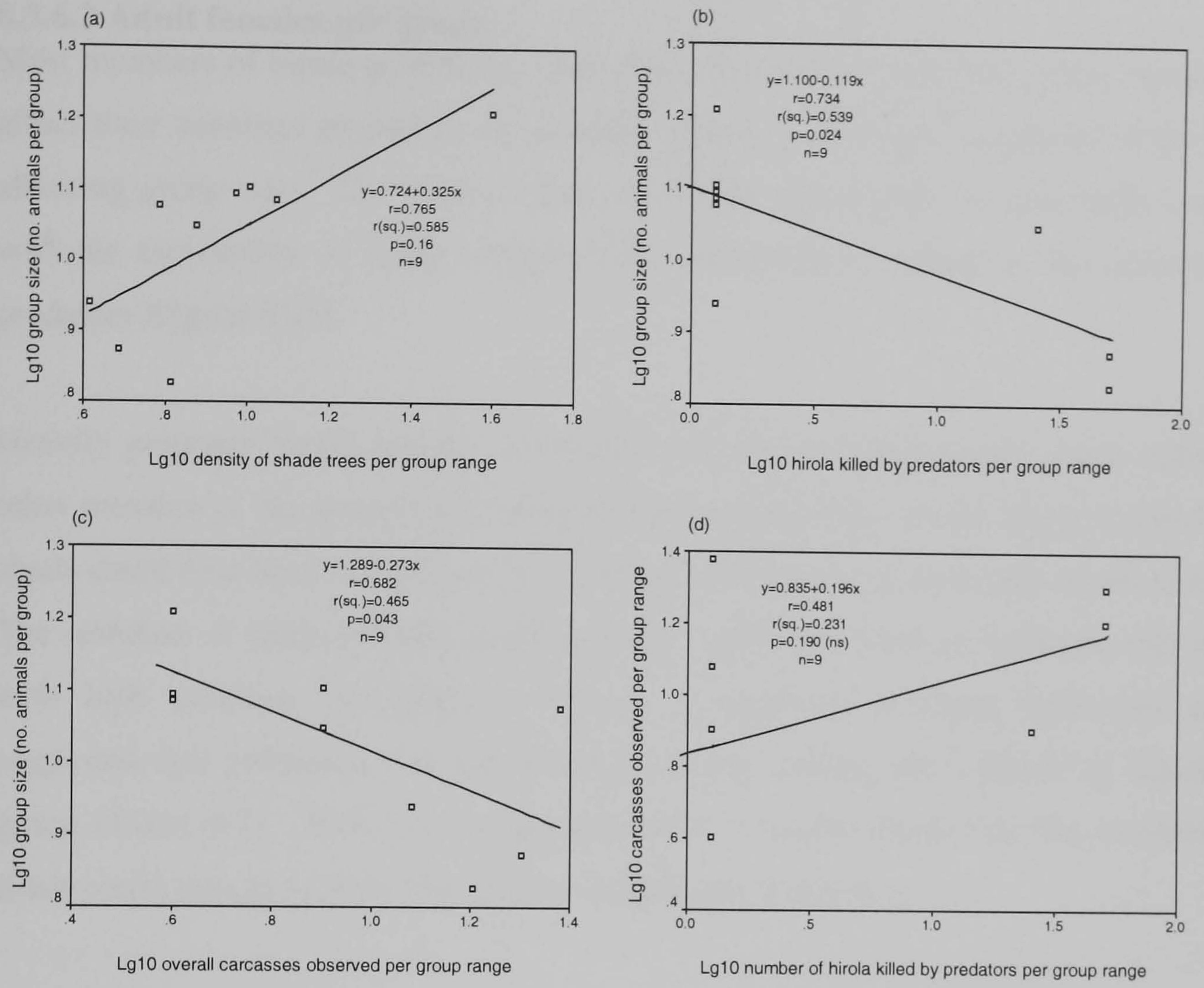


Figure 8.8: The relationship between hirola group sizes and availability of preferred shade trees (a) and effects of predators (bc&d) in Tsavo East National Park.

Table 8.6: Stepwise multiple regression analyses of hirola group size as dependent variable and number of observations of hirola killed by predators per group and the density of preferred shade trees per group range as independent variables.

Variable	B	t	P
Constant	0.854		
Number of hirola killed by predators per group	-0.084	-2.682	0.036
Density of preferred shade trees per hirola group range	0.241	2.944	0.026

Multiple r = 0.901 (r^2 = 0.811), df = 2,6, p = 0.007

Model: y =-0.084(number of hirola killed)+0.241(density of shade trees)+0.854

8.3.6.2 Adult females per group

Most members of hirola groups are adult females and so the analysis of the variables that affect their numbers proved to be broadly similar to the above analysis of the factors affecting group size. The number of adult females per group was positively correlated with the availability of shade (Figure 8.9a) and inversely related to the occurrence of predators (Figure 8.9b).

Heavily pregnant hirola females or females with young often sought shade earlier than other member in the group and tended to remain behind the group or get isolated. Poor shade could thus have contributed to limiting the numbers of such individuals in a group. The isolation of these animals could also have subjected them to predation risk in areas with high predator occurrence. Overall, a stepwise multiple regression analysis suggested that predation was the principle factor limiting the number of females per group (Table 8.7). However, as argued above, it seems likely that the availability of shade could also have been biologically significant (Table 8.7).

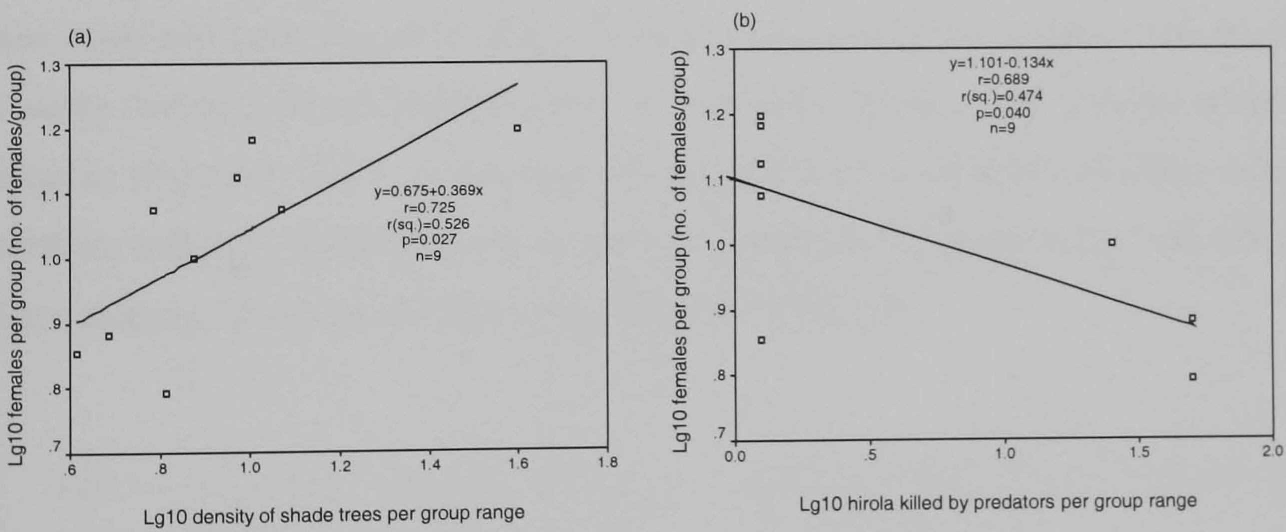


Figure 8.9: The relationship between various independent factors and variation in total number of adult females in the hirola groups in Tsavo East National Park.

Table 8.7: Stepwise multiple regression analyses of number of adult females per group as dependent variable and number of observations of hirola killed by predators per group and the density of preferred shade trees per group range as independent variables.

Variable	B	t	P
Constant	0.675		
Number of hirola killed by predators per group	-0.481	-2.061	0.085
Density of preferred shade trees per hirola group range	0.369	2.786	0.027
Multiple r = 0.725 ($r^2 = 0.526$), df = 1,7, p = 0.027			
Model: y =-0.481(number of hirola killed)+0.369(density of shade trees)+0.675			

8.3.6.3 Adult female emigration

Generally, field observations indicated that hirola groups moved out of grazing patches where predators were present. Data on emigration from groups indicated that adult females tended to emigrate more from groups that lived in areas where predators were most often detected (Figure 8.10a). However, apparently due to higher risk of predation in bushy habitats, hirola befitted more from group vigilance, and females tended not to emigrate (Figure 8.10b). A stepwise multiple regression analysis of these independent variables indicated that higher observation of predators per group range was the principle factor causing adult female hirola emigration (Tablele 8.8).

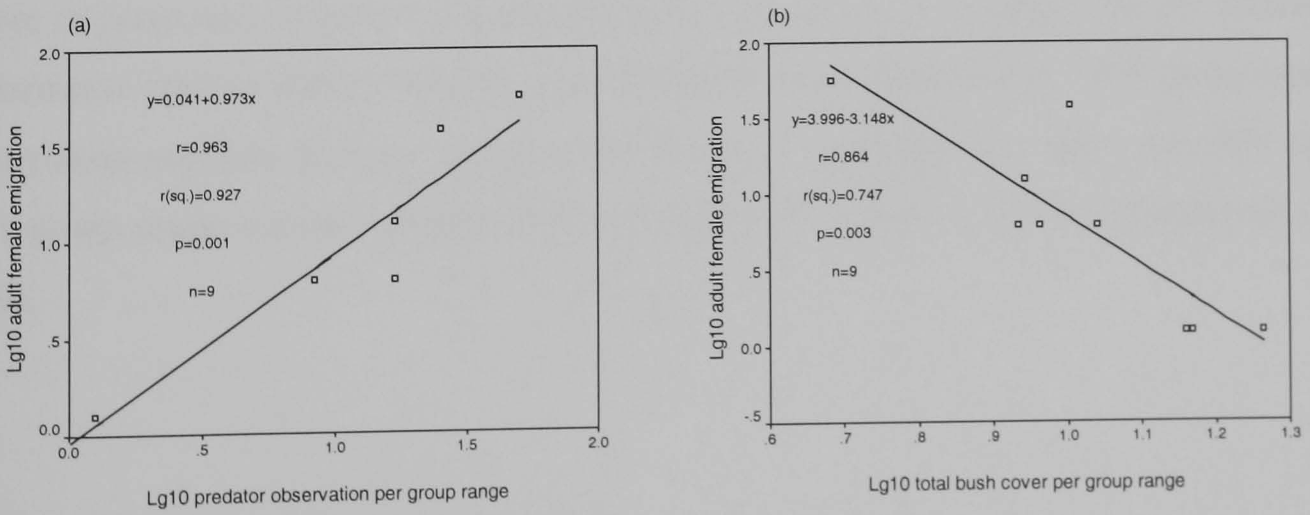


Figure 8.10: The relationship between various independent factors and variation in number of adult female hirola emigrating per group in Tsavo East National Park.

Table 8.8: Stepwise multiple regression analyses of number of adult females emigrating per group as dependent variable and number of predator observations per group range and the amount of bush coverper group range as independent variables.

Variable	B	t	P
Constant	-0.041		
Number of predator observation per group range	0.973	9.453	0.001
Density of bush cover per hirola group range	0.059	0.225	0.830

Multiple r = 0.963 ($r^2 = 0.927$), df = 1,7, p = 0.001

Model: y =-0.973(number of predators)+0.059(density of bush cover)-0.041

8.3.6.4 Adult female immigration

General observations on hirola groups in Tsavo indicate that they are located in areas ranges that receive lower rainfall compared to the surrounding areas (Chapter VII). Further, observation on hirola groups in the wet season indicated that they moved away from lush fast growing grasses (areas where it had rained) and grazed on shorter newly growing grasses. Data on adult female immigration indicate that immigration was higher in areas with lower mean monthly rainfall (Figure 8.11a). Analysis also suggested that adult female hirola immigrated to ranges where oryx were common (Figure 8.11b). The observed relationship may thus have been because of attraction to grazing sites with the short green grasses that hirola and oryx prefer, as well as anti-predator advantage in the form of increased vigilance and predation dilution effects resulting from the presence of alternative prey in similar habitats like zebra ond Coke's hartebeest. A stepwise multiple regression analysis of these independent variables indicated that mean monthly rainfall per group range was the principle factor causing adult female hirola immigration (Table 8.9).

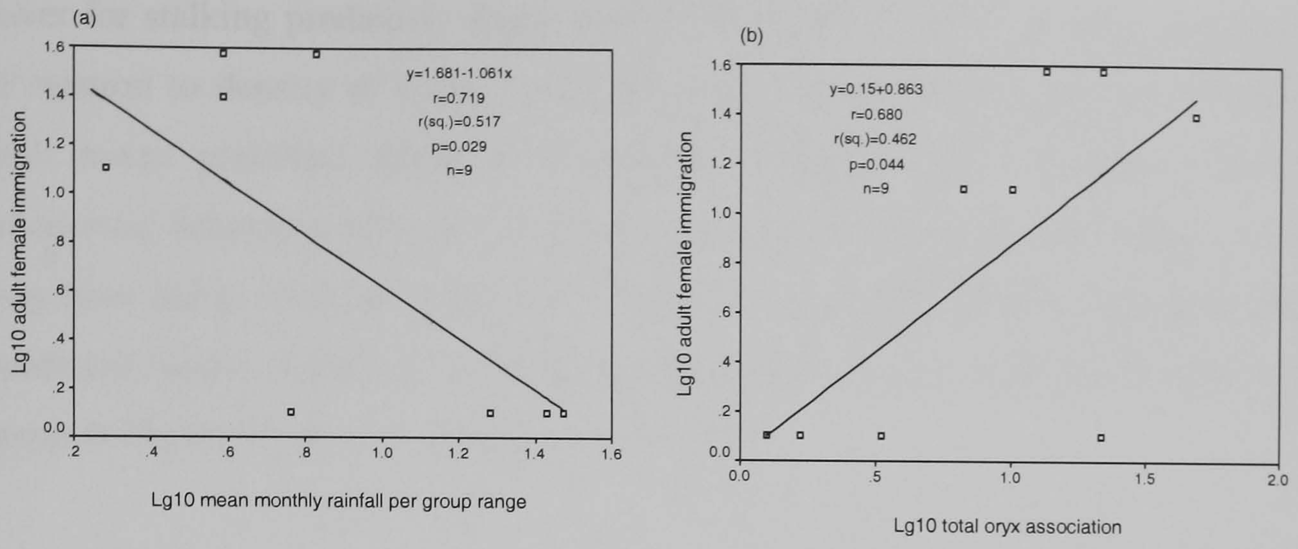


Figure 8.11: The relationship between various independent factors and variation in number of adult female hirola immigrating per group in Tsavo East National Park.

Table 8.9: Stepwise multiple regression analyses of number of adult females immigrating per group as dependent variable and mean monthly rainfall per group range and amount of oryx association per group as independent variables.

Variable	B	T	P
Constant	1.681		
Mean monthly rainfall per group range	-1.061	-2.737	0.029
Amount of association with oryx hirola per group	0.466	1.902	0.106

Multiple r = 0.719 (r^2 = 0.517), df = 1,7, p = 0.029

Model: y =-1.061(monthly rainfall)+0.466(Oryx association)+1.681

8.3.6.5 Mortality

69.8% of hirola calves died within the first 6 months of life in Tsavo. Similarly, only 18.0% of the calves born each year survived to the age of 2 years. Observations on diseases among hirola over the study period indicated that only one female and her calf had diarrhea, but soon recovered. The remaining animals always appeared to be healthy and calved normally. However, notable observations were made on the loss of calves and adults to predators (Chapter IV). Carcasses were found more often in areas with high grass cover (Figure 8.12a). This may because areas with high grass cover afforded better cover for stalking predators. Regression analysis of observed carcasses per group range in relation to density of shade trees indicated that more carcasses were found in areas with lower preferred shade trees density (Figure 8.12b). Perhaps, the extensive wandering behaviour seen when hirola searched for shade in areas where it was scant may have led to predation exposure. Overall, a stepwise multiple regression analyses of predicted factors related to mortality indicated that areas of high grass cover were more prone to higher levels of predation (Table 8.10).

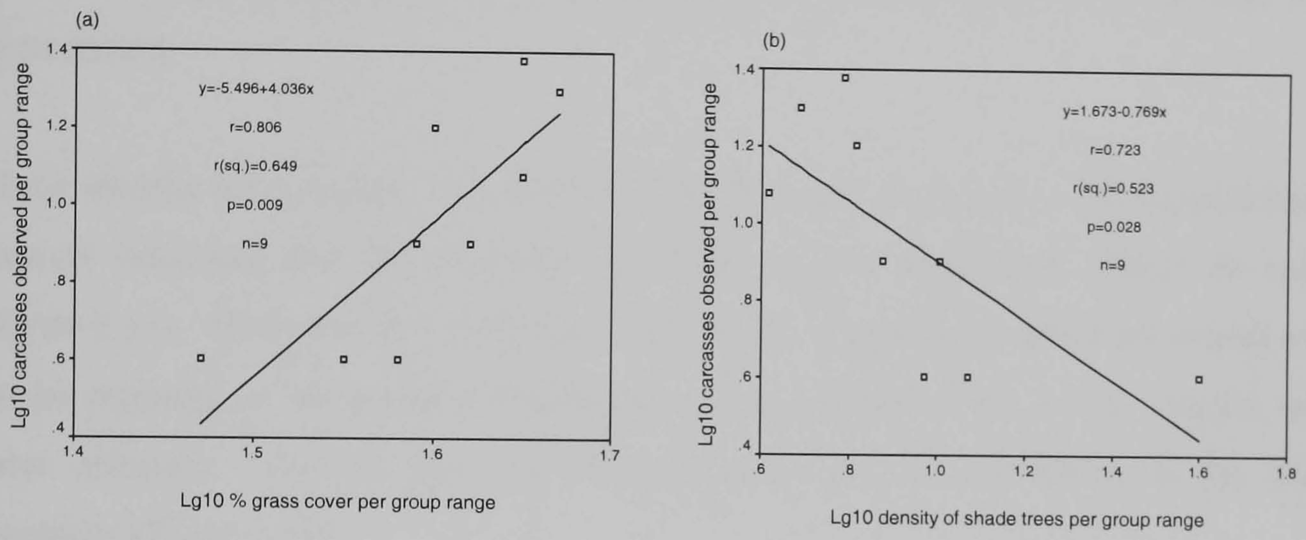


Figure 8.12: The relationship between various independent factors and variation in number of carcasses per group in Tsavo East National Park.

Table 8.10: Stepwise multiple regression analyses of number of number of carcasses observed per group range as dependent variable and % grass cover and density of preferred shade trees per group range as independent variables.

Variable	B	T	P
Constant	-5.496		
% grass cover per group range	4.036	3.597	0.009
Density of preferred shade trees per hirola group range	-0.354	-1.273	0.250

Multiple r = 0.806 (r^2 = 0.649), df = 1,7, p = 0.009

Model: y =4.036(% grass cover)-0.354(Density of shade)-5.496

8.3.7 The effects of translocation on hirola

8.3.7.1 Mortality of released animals

A total of 29 hirola were captured in Garissa and released in Tsavo in August 1996. These comprised 10 radio-collared and ear-tagged individuals (2 adult males, 7 adult females and 1 female yearling) and 19 ear-tagged (3 adult males, 6 male yearlings, 7 female adults and 3 female yearling). In total, the released population included 5 adult males, 6 sub-adult males, 14 adult females and 4 sub-adult females. Among these, were 21 animals that had been netted (2 adult male, 5 sub-adult males, 10 adult females and 4 sub-adult females), and 8 (3 adult males, 1 sub-adult male and 4 adult females) that had been darted.

Three months after release, a total of 13 (44.8%) individuals out of 29 released had died. Results indicated that the presence of collars had no significant effects on mortality (Table 8.11). However, the method of capture had a significant effect on overall survival as the majority of the animals that died had been darted (Table 8.12). Adults were the most affected. The sex and age of individuals did not contribute to the observed mortality (Table 8.13).

Table 8.11: Mortality in relation to collaring and ear-tagging up to 3 months after release (December 1996).

Class	Died	Survived	X^2	P
Collared & ear-tagged	5	5	0.165	>0.05
Ear-tagged	8	11		
Total	13	16		

Table 8.12: Mortality in relation to capture technique up to 3 months after release (December 1996). (Note: data analysis excludes mortality on foetuses and new-born calves that resulted from translocating pregnant females).

Age Class	Capture Technique	Number of animals Died	Survived	X^2	P
Total Capture	Netted	6	15	8.134	<0.05*
	Darted	7	1		
Adults only	Netted	4	8	4.866	<0.05*
	Darted	6	1		
Yearlings only	Netted	2	7	2.593	>0.05
	Darted	1	0		

Table 8.13: Mortality in relation to sex and age group up to 3 months after release (December 1996). (Note: data analysis) excludes mortality on foetuses and new-born calves resulting from the translocation of pregnant females).

Category	Classes	Number of animals Died	Survived	X^2	P
Age	Adults	10	9	1.357	>0.05
	Yearlings	3	7		
Sex	Males	6	4	1.42	>0.05
	Females	12	7		

8.3.7.1 Dispersal of the released animals

The released hirola dispersed individually in different directions. This was contrary to our expectation that they would retain their existing social groups. Figure 8.13 shows the furthest distances that identified individuals moved before settling. Three females moved furthest. These were individual number 386, an adult female that went outside the park to Taita Ranch, 396, an adult female with a young male that moved to Galana River, and 382, a young female that moved to Kulalu Ranch (Figure 8.13). These movements all occurred within the first 2 weeks after release and the animals involved had all been caught using nets.

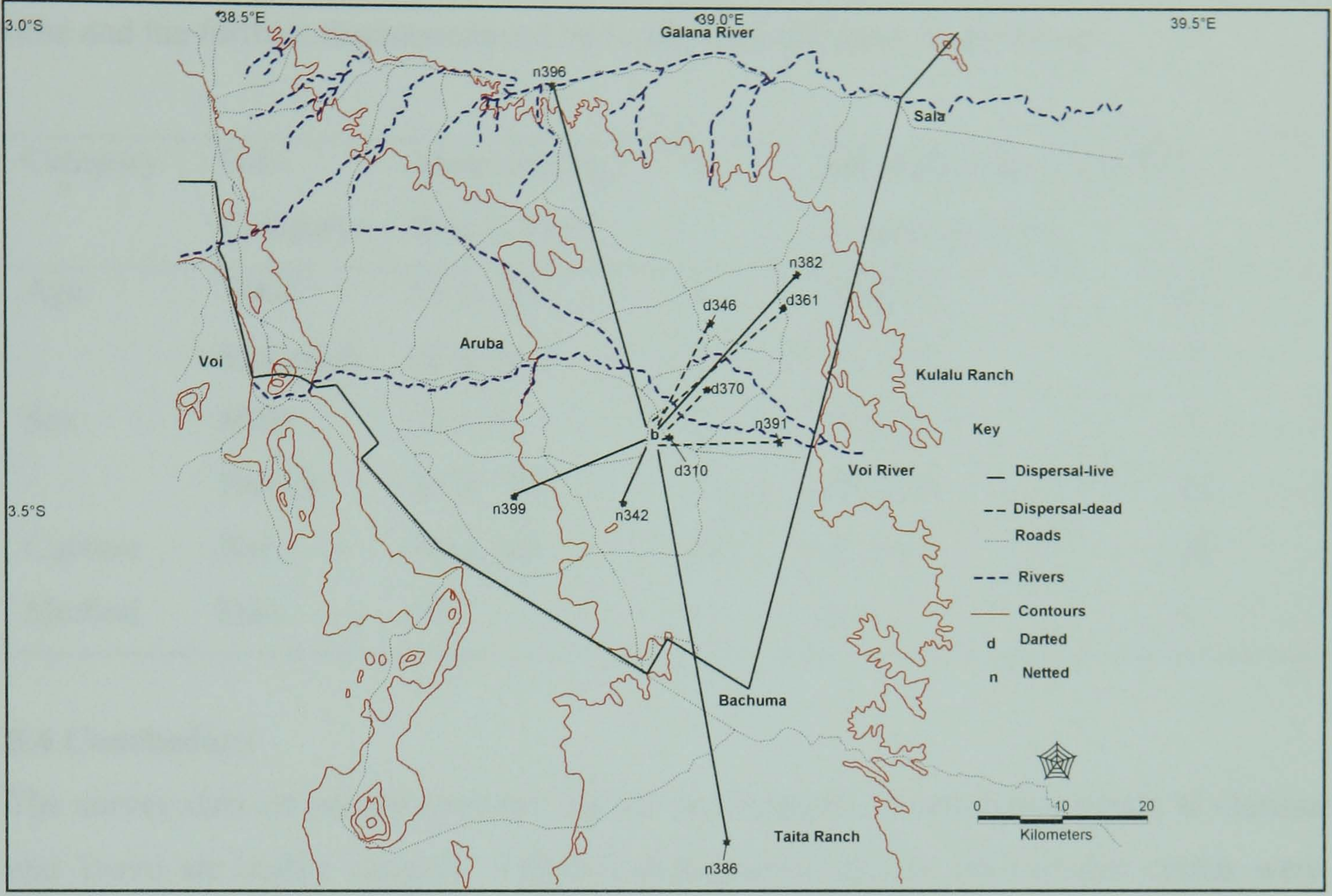


Figure 8.13: Map of Tsavo south of the Galana River showing the 1996 hirola release boma (b) and the extent of dispersal of known hirola individuals (Numbers). Solid lines indicate that the animals were alive and still moving when detected while broken lines indicate that the animal was dead when detected. Letters 'n' and 'd' denote whether the animal was netted or darted respectively when captured in Garissa.

There were no significant statistical differences in settling duration and distance in relation to sex, age and capture technique (Table 8.14). Results show that the time taken by an individual to settle was positively correlated to the distance moved (Pearson $r = 0.57$, $p < 0.05$)

Table 8.14. Mean differences among age, sex and capture technique in relation to settling time and the furthest distance moved by hirola from the pre-release boma.

Category	Sub-Category	Mean settling time (Days)	N	Mean distance moved to settling (Km)	n
Age	Adult	95 ± 134	9	30 ± 18	9
	Sub-adult	68 ± 59	7	31 ± 17	7
Sex	Male	51 ± 16	2	46 ± 31	2
	Female	88 ± 112	14	29 ± 15	14
Capture	Net	86 ± 108	15	31 ± 17	15
Method	Dart	39	1	28	1

8.4 Conclusions

The survey data on animal numbers used in the analyses of population trends in Garissa and Tsavo are highly variable. Possible explanations include the fact that counts were undertaken in different seasons (see Tables 8.1 & 8.5), that counts were undertaken at varying intensities (5 & 10 km transect spacings) and earlier data (1970s and 1980s) may have been affected by observer inexperience. Despite these problems, major trends in the data are apparent and, collectively, the data provide good evidence for a general decline in abundance.

8.4.1 Garissa

The hirola natural range has declined dramatically since 1963. The decline coincided with the increase in human population and their livestock, especially sheep and goats; cattle have also declined more recently, possibly as a result of range degradation and disease. All wildlife species have declined in number since 1963, including hirola, although browsers were the most affected.

The information provided by a network of hirola community scouts, indicated that hirola were the most poached animals in Garissa, followed by gerenuk and giraffe. Overall, bandits did most poaching. Much of the poaching may have been caused by political instability in the neighbouring republic of Somalia, where escaping militia men sought refuge just over the border in Kenya, an area which formed part of the hirola range.

Overall browsers were most preferred by poachers, followed by grazers and lastly mixed feeders. According to bushmeat eaters, browsers and species that are not water dependent animals, such as the hirola have sweeter meat. Most poaching occurred along the Tana River (Pokomo tribesmen) and the Kenya Somalia border (bandits).

Transmission of disease from wildlife to livestock and vice verse appears to have been common in the hirola range. This may have been exaccerbated by periodical influxes of unvaccinated livestock from Somalia, and the frequent movement of pastoralists from as far afield as Moyale in Kenya in search of pasture for their livestock during dry seasons. Disease appeared to be responsible for the largest numbers of hirola deaths. The diseases recorded during the study period included pneumonia, rinderpest, trypanosomiasis, foot and mouth and East Coast Fever.

Overall, the new information collected during this study supports the possibility that human induced factors rather than natural factors were responsible for the dramatic decline of hirola. Of the various possible factors linked to human intervention, disease and poaching seem to have been most important. Competition with livestock and habitat degradation may be important medium or long-term factors but were probably less important in the rapid short-term reduction in numbers.

Information from herdsmen and the hirola community scouts who worked on foot in this remote environment, suggested that some hirola were killed by predators. Lions and hunting dogs were known to have killed hirola but hyaenas, while common and a potential threat to hirola, were not recorded as killing hirola. The available data suggested that lions killed most hirola. However, it seems unlikely that predation was a major contributing factor to the observed population decline.

8.4.2 Tsavo

As human populations increase, conservation areas may suffer as a result of edge effect and lack of, or degradation of, dispersal zones. The Tsavo ecosystem is no exception. Census records show a general declining trend in the overall number of wildlife and livestock in Tsavo. The data indicated that the sharpest decline in the Tsavo wildlife and livestock occurred in 1991. Though the population recovered somewhat in 1997, subsequent counts indicate a log-term decline of most wildlife species; the exceptions are elephants which appear to be stable and cattle which are rising.

Apart from the potential threat of commercial poaching on elephants and rhinos, the main threat to other wildlife species is due to poaching for meat (known as 'pot' poaching). This mortality is often undetected because poachers use traditional (and silent) snares. The increasing levels of poverty in communities within the ecosystem and the increasing population size is likely to put more pressure on wildlife. The hirola groups occurring in areas prone to poaching were shy and small in size. In addition, the recent poaching of three 3 buffaloes at the core of the hirola range indicated that all of the Tsavo hirola population is potentially vulnerable to poaching. However, during the study period it seemed unlikely that poaching made a significant impact on the population.

Hirola preferred microhabitats with short diverse grass species, ample shade, raised, red soil areas with a high availability of transient waterholes. The presence and extent of these habitats affected the distribution of hirola group ranges: where they were present hirola groups overlapped and where they were scarce, hirola groups were more dispersed. This observation suggests that hirola in Tsavo may be ecologically limited by the availability of these relatively rare microhabitats.

Field observations of hirola reproductive behaviour indicated that females often wandered away from their family groups with their young calves and even with their yearling offspring. Further, both yearling females and males dispersed from their natal groups staying alone, or in the company of Grant's gazelle, before eventually (in the case of females) rejoining a family group or forming new groups; males joined bachelor groups before eventually becoming solitary. The solitary stages in the life of hirola may be a critical stage as such animals risk predation due to lack of protection afforded by the anti-predator advantages of group membership. Most observed predation was on lone adult females with their calves and only 18% of all young survived to recruitment. Studies on Coke's hartebeest in Nairobi National park showed that 70% of young survived to year of age (Gosling 1974). This may suggest a lower survival rate among hirola in Tsavo East National Park.

Hirola groups occupied home range areas which contained a number of preferred core feeding sites which were used regularly. This behaviour while important for forage utilization may also have made the group vulnerable to ambush predators, particularly lions, which probably take advantage of predictable movements by potential prey. This behaviour, in combination with the departure of alternative prey during the dry season may have placed hirola under severe predation pressure. One hirola group occupying the smallest home range area was completely decimated by lion predation.

Data on variation in the size of hirola groups suggested that predation and lack of shade may have been responsible for a reduction in the overall number of hirola per group. Similar results were obtained for the number of adult females per group and, by extrapolation, these results suggest that predation and shade availability could limit the hirola population. Further, higher numbers of observed carcasses were associated with sites with higher grass and herb cover that could have provided cover for stalking predators.

Finally, data on the survival of translocated hirola in Tsavo suggested that the capture method had an important effect on post-release adult survival: animals caught in nets were more likely to survive than those caught with tranquilizing darts. In contrast, age or sex, were not contributing factors. On average, adult females wandered less from the release site, although there were three notable exceptions. While females settled later than males, they were readily accepted and joined stable groups. Sub-adult females on the other hand stayed alone or joined groups of Grant's gazelle. While these factors did not have a long-term effect in Tsavo, they limited the number of animals that were added to the population and they need to be considered in future movements of hirola.

Chapter IX:

Discussion and Conclusions

9.1 Hirola behaviour and ecology

9.1.1 Population size and trends

This study has established that the average population size of hirola in Tsavo East National Park was 71±9.3 SD, and that these animals ranged over an 844 km² area (Chapter IV, section **4.2.1**). Further, there were about 672 hirola in Garissa in a 5,171 km² range (Chapter IV, section **4.3.2**). Since these are probably the only two populations of hirola, the total for the species is thus about 743. However, the Garissa figure is probably an underestimate and so the true figure may be between 750 and 1,000 animals.

Considering that about 11 hirola were first released in Tsavo in 1963 (Kock, 1996), and that an additional 16 animals were added to the population in 1996 (Kock et al., 1998), the Tsavo hirola population appears to be increasing only very slowly. Given the fact that female hirola can give birth as early 16 months of age (Smielowski, 1987), this slow growth suggests the operation of severe limiting factors. Tsavo East National Park is a protected area and over the years of the present study, the hirola population occurring there seems stable. However, its very slow growth rate casts doubt on the long-term viability of the population. Studies on relocated populations indicate that they are more likely to succeed if the founder population is >100 individuals (Fischer & Lindenmayer, 2000). In Garissa, the hirola population was 13,729 in 1973 (Watson et al., 1973). The fact that the current population represents about 5% of the previous population after a period of 27 years indicates that the population is diminishing at an alarming rate. Furthermore, the Garissa hirola range has considerably declined from its previous range of about 16,820 km² in 1976 (Bunderson, 1976) to the current 5,171 km², representing about 30.7% of the original. The Garissa hirola range is a pastoral land with intense and increasing human pressures, which are likely to continue to impact negatively on the population. Overall, there are factors at play that are affecting the growth and abundance of the two populations and, if unchecked, they are likely to cause the extinction of the hirola.

9.1.2 Group size and composition

The hirola social groups in Tsavo ranged between 2 to 15 in number with a mean group size of 7.3 ± 2.6 SD (Chapter IV, section **4.2.2**). In Garissa, hirola groups ranged between 1 and 25 individuals with a mean group size of 7.9 ± 4.15 SD (Chapter IV, section **4.3.3**). All groups were accompanied by an adult male hirola. Neighbouring groups sometimes joined together temporarily to graze on green patches that had received earlier showers at the end of the dry season (Chapter V, section **5.2**). These results compare well with previous studies. In Garissa, previous observations showed that family groups ranged from 5 - 40 with a mean group size of 7 - 9 (Bunderson, 1985; Kingdon, 1982); these groups were usually in the company of a mature male. Dahiye (Dahiye, 1999) while working in Garissa observed that family groups ranged from 5-17 with a mean group size of 8.7. The consistency of group size over the entire period indicates that these values represent the natural group size of hirola. However, the mixed aggregations of breeding and bachelor herds numbering up to 300 and occurring at the end of dry season, that were observed by Bunderson in 1976 (Bunderson, 1985) were not observed in the present study. This might indicate that the population density has declined due to some limiting factor(s) or that the available groups are now too scattered to join together in such numbers. Studies in the Mara-Serengeti ecosystem indicated that the eruption of large groups of ungulates were the result of the removal of a major mortality factor, rinderpest, through vaccination of surrounding domestic livestock (Sinclair, 1979). In Tsavo, slight increases in group sizes occurred during the calving period as a result of new calves being born and small numbers of recruits entering a group; however, such increases were usually temporary and the groups generally declined again as individuals were killed by predators.

Hirola groups were dominated by adults although, as mentioned, minor variations occurred in the number of younger individuals. In both Tsavo (Chapter IV, section **4.2.2**) and Garissa (Chapter IV, section **4.3.3**), the age structure before the onset of calving showed a bias towards adults and yearlings. After calving, the age structure was biased towards adults and calves. The occurrence of a low proportion of recruits in the population was probably a consequence of a combination of high juvenile mortality with additional mortality when yearlings were expelled from their family groups (Chapter V, section **5.3.5**). The sex ratio of the hirola population in Tsavo and Garissa was biased towards females. Only single mature males existed in a group and the number of males without females, either alone or in groups, were few. Populations with a preponderance of females can increase faster than those with few females (Hedrick et al., 1996) but this potential was not realized in the Tsavo population.

9.1.3 Reproductive behaviour and seasonality

This study has confirmed earlier findings that hirola males are polygamous (Kingdon, 1982; Bunderson, 1985). Hirola family groups are maintained and herded by a family male (Chapter V, section **5.3.1**). These adult males remain for long periods with their groups and are only replaced by solitary adult males when they are killed by predators or (in one case) when they become too ill to herd the family. Little physical contacts occurs between neighbouring males. During the study period, only one observation of a male-male encounter was observed and in this case one of the males avoided damaging encounter by running away. This male had been newly introduced in Tsavo and its behaviour could have been due to the fact that it was not yet established in its range. Isolated male hirola in Tsavo did not show any evidence of territoriality (Chapter V, section **5.3.2**). Instead, they appeared to forage in parts of the group home ranges that were not being used by the family group. However, group males appeared always alert and herded females together, possibly so that they could not join another male. Hirola males (and females) seemed remarkably free of injuries (such as scars and torn ears) that would indicate fighting. The change of adult males in family groups may thus have been through means other than fighting. One possible way could be pre-emptive defence. During diurnal observations on hirola groups, the male hirola sometimes left the family group suddenly and ran into the bushes as if chasing another animal. In cases where the cause of such chases was confirmed, it sometimes involved Coke's hartebeest and Grant's gazelle, but in areas with more bush cover, often the cause was not determined and it could have involved single male hirola. However, the observation that an injured and weak male hirola could keep a family group for about a year in the area where other solitary males existed suggests either a low level of intrasexual competition or a strong owner advantage in takeover attempts. Studies have shown that male mating strategy largely depends on the availability and distribution of resources, the density of females and/or males, and the degree of breeding synchrony (Emlen & Oring, 1977; Gosling, 1986; Clutton-Brock, 1989; Langbein & Thirgood, 1989). The low level of competition between male hirola may have been due to a low density of females and an even lower number of competing males; the reasons for the latter is probably due to a high risk of predation for isolated animals.

Tsavo hirola were seasonal breeders (Chapter IV, section 4.2.3). This conclusion is similar to previous findings (Kingdon, 1982). The peak mating season occurred between February and April at the start of long rains. A similar period was observed in zoo hirola (Smielowski, 1987). Calving occurred from August to March, with a peak at the end of November and beginning of October. Observations indicated that peak calving occurred shortly before or after the onset of the short rains. This may explain the importance of showers in the reproduction of hirola and the extent of the impact of drought on reproduction. The similarity in age structure between the Tsavo and Garissa populations indicated that the two populations displayed similar seasonal patterns of reproduction. Observations on related Alcelaphines (Skinner & Smithers, 1990) have shown that they give birth within the same period, even in the South African region. The synchronisation of births with the onset of rainfall may be selected for because it offers optimal grazing for lactating females (the most costly element of mammalian reproduction) and growing calves (Murray, 1995). Theoretically, it is possible that all adult females gave birth since all appeared to be in good physical condition; however, some studies indicate that individual females may not reproduce in some years, particularly after having weaned an offspring (Clutton-Brock et al., 1985; Kirkpatrick et al., 1996; Russell et al., 1998). Observations on hirola in captivity indicated that healthy females calved annually (Smielownski, 1987). My observations showed that 51% (Chapter IV, section **4.2.3**) of adult females in Tsavo were seen with calves while about 46% (Chapter IV, section **4.3.3**) had calves in Garissa. These values must be an underestimate because some calves would have died and not been recorded in the intervals between locating a group. If it is assumed that all adult females in Tsavo gave birth, then 68.9% of the calves born must have died within the first 6 months of life, while only 18% of them survived to 2 years of age. In captivity, all the adult females calved and 32% of calves died before they were 3 months of age (Smielowski, 1987). Calving occurred around the middle hours of the day and was accompanied by movements from the calving site, when the calf was able to move. Such movements may have been an anti-predator strategy. Early mortality among herbivores is usually caused by predators in habitats where predator occur (Linnell et al., 1995), and preweaning survival is generally <50% (Epstein et al., 1983), and can be as low as 1% (Byers, 1997). Maternal experience can also reduce the vulnerability of young ungulates to predators (Byers, 1997; Ozoga & Verme, 1986). The timing of birth may also account for temporal variation in preweaning survival. Late birth dates often lower survival in temperate ungulates (Clutton-Brock et al., 1987; Clutton-Brock et al., 1991; Fiesta-Bianchet, 1988) by shortening the period of access to growing forage. In the presence of predators, caribou calves born during the birth peak may enjoy higher survival than those born earlier or later (Adams et al., 1995). Other factors such as parasites (Logan, 1973), disease (Miller et al., 1988), and high levels of inbreeding (Lent & Davis, 1991; Sausman, 1984) may sometimes reduce preweaning survival but there was no evidence of the operation of these factors in the present study.

9.1.4 Dispersal from natal groups and the formation of new groups

Observations on hirola groups in Tsavo indicated that most offspring dispersed away from their natal groups during the first year of life. All male yearlings left their natal groups, some as early as 6 months of age while females started dispersing after about 9 months of age (Chapter V, section **5.3.5**). Dispersing young males, either i) joined groups of Grant's gazelle, ii) formed temporary mixed groups with other dispersing females, or iii) joined bachelor groups with older males. At over 32 months of age they were mature and solitary and could form a family group or replace a group male (Chapter V, section **5.3.5**). Females appeared to stay longer in family groups. During separations, they either i) stayed alone or joined groups of Grant's gazelle, ii) joined young males and formed temporary yearling groups (of up to 6 in number), iii) joined lone adult males where they matured and, in one case at least, formed a new group (Chapter V, section **5.3.6**), and, iv) those that did not disperse separated occasionally from their natal groups, but stayed within reach of the group. The group male and sometimes adult females were directly responsible of driving the yearling individuals out of the groups. Observations of developing young indicated that male hirola matured at about 30 months while females were able to mate at about 20 months of age (Chapter V, section 5.3.5). These field observations compared closely with zoo observations where males were observed to mature at between 20-24 months and females at 15-20 months (Smielowski, 1987).

Among the related wild *Alcelaphines*, male Coke's hartebeest mature at about 3 years of age and may be able to takeover territories at 4 years of age, whereas females mature at between 18 and 24 months and give birth to their first young at between 2 to 3 years (Skinner & Smithers, 1990). Female blesbok *Damaliscus dorcas phillipsi* and *bontebok Damaliscus dorcas dorcas* are sexually mature at 24 to 30 months of age (Skinner & Smithers, 1990). Female topi and tsessebe mature at about 28 months while their males become sexually mature at 30 to 42 months of age (Child et al., 1972; Kingdon, 1982). However, studies on the mountain goats have indicated that populations in poor habitats show late sexual maturity (Festa-Bianchet et al., 1994). Dispersal among hirola is thus a pre-requisite for the formation of new groups, but on the other hand may contribute to the slow growth of the population if dispersing young are at risk from predation. This interesting pattern of behaviour may explain why few hirola (about 18%) survive to recruitment (Chapter IV, section **4.2.5**). Studies on other herbivores indicate that the survival of young may be reduced through shorter nursing time (Sarno, 1999) experience when they are driven from the natal group at an early age, particularly in the case of males.

9.1.5 Ranging and daily activity patterns

Hirola groups occupied specific home ranges that varied in size. In some localities, home ranges appeared to overlap substantially (Chapter VII, section **7.3**), while in others they were far dispersed and separate. These differences may have been due to variations in food quantity and quality, interference from predators, and, possibly, competition from other grazers. Observations indicate that home ranges with more core areas were a result of scattered preferred microhabitats caused by localised rainfall that created patches of suitable grazing. Both predators and large herbivores such as elephants and buffaloes caused hirola to move away from an area. These results are similar to the observation in Saskatchewan that non-migratory woodland caribou (*Rangifer tarandus caribou*) movement rates were a response to local predator pressure (Rettie & Messier, 2001). Observations further indicated that the dispersed location of some hirola groups was a consequnce of the distribution of suitable microhabitats since all areas occupied by hirola groups, however far apart, appeared to have relatively similar vegetation. The core areas of hirola ranges were characterised by the presence of raised red soil areas with grazing patches interspersed by bush and surrounded by open, low-lying grazing areas. These areas had higher densities of seasonal waterholes, preferred shade trees and shrubs, and patches of short green swards consisting of preferred grass and forb species. Under suitable conditions hirola used such areas for up to three months, indicating that hirola could potentially use far smaller home ranges where environmental conditions were suitable. Most herbivores will move less if their essential requirements are met in a particular feeding area. The bongo (*Tragelaphus eurycerus*) in Dzanga National Park, Central African Republic, spent most of their time near natural salt licks where they grazed on preferred grasses and herbs, and consumed soils from the salt lick (Klaus-Hugi et al., 2000). In forests without salt licks, they ranged over much larger areas.

Hirola were most active during the early morning and late evening hours of the day, when the weather was cool, and they rested during the middle part of the day (Chapter V, section **5.4**). However, sporadic grazing occurred whenever there was prolonged cloud cover or during showers of rain. Active grazing took place in fairly open areas whereas resting took place on the edges of bushland. Many prey species avoid predators by using refuges in which they are less vulnerable to capture but foraging and other activities necessitate leaving this protection (Kramer & Bonenfant, 1997). During active grazing, hirola used open areas that were often in use by other herbivore species. These open areas were often on gently sloping plains with higher densities of transient waterholes that provided greener preferred pasture for hirola. Hirola appeared to spend the night in such places, moving very little and staying close to associated species such as Coke's hartebeest, zebra, and Grant's gazelle. However, studies on lion predation indicate that most kills are around watering points and on the edges of bushes (Ruggiero, 1991; Hanby et al., 1995). These nightime concentrations of hirola and other herbivores were common and may have provided some protection against predation. Larger groups accord better vigilance than smaller ones (Jarman, 1974; Roberts, 1996). Potentially, hirola could thus have been in danger at their resting sites where they were generally in small groups and could easily be attacked by predators like lions and cheetahs. However, predators are generally inactive at such times and during resting hours in or at the edge of scrubland, hirola showed their lowest levels of overall vigilance and some animals seemed to be fast asleep. Resting areas such as a group of shrubs surrounded by open areas may also have conferred some benefits in terms of the ability of hirola to detect potential predators.

Most social activities took place during the active feeding period (Chapter V, section **5.5**). However, some activities such as intra-specific aggression, and social grooming occurred during resting hours. There were continuous displacements from shade in some hirola groups particularly when the group was in an area with poor shade trees and bushes. At times the entire group moved off, apparently in search of better shade areas. The male generally occupied the best available shade followed by females arranged with respect to their social dominance. In good shade sites, the main activity was resting and grooming. Inter-specific aggression also occurred during grazing periods and were mostly over grazing patches. Zebra, Coke's hartebeest, and topi interactions with hirola were mainly over food patches, whereas Grant's gazelle was often chased when they attempted to nose hirola calves.

9.1.6 Ungulate community structure and association

A total of 14 animal species were seen commonly on the hirola range in Tsavo, while 7 occurred in Garissa (Chapter VI, sections **6.2.1&2**. In both places, the ungulate species showed seasonal trends in numbers with most occurring in the wet season. The main factor determining both the annual movements and variations in their numbers was found to be rainfall, presumably through its effects on the food supply. The benefits of seasonal migrations and aggregation may be to take advantage of seasonal spatial variation in food availability, maximise the growth potential of the vegetation through rotational grazing, and escape predation pressure (Fryxell, 1995). As a result, resident and migratory species could have different forms of regulation, with residents commonly regulated by predators and migrants regulated by food availability (Fryxell et al., 1988). Overall, migratory species tend to achieve highest levels of abundance while resident species tend to be fewer (Fryxell, 1995). Observation of lion predation on zebra and wildebeest in the Kruger National Park indicated that non-migratory wildebeest were the most affected as compared to zebra that were semi-migratory (Mills & Shenk, 1992). Hirola used the same ranges all year round while other herbivores moved depending on season. Differences in the amount of available food or dispersion of food items can cause seasonal variations in location, typical group sizes and concentrations of most ungulate species (Jarman, 1974). Observations on hirola groups indicated that they maintained their general range throughout the year (Chapter VII, section **7.3**). One reason why hirola could survive the dry season was that during this period, groups moved into bushy habitats where they obtained some green food material from the bases of bushes and trees as well as obtaining shade. At the same time, most grazing was done on the edges of or inside drying or dry waterholes where vegetation was relatively green. In addition, the most intensive grazing occurred in early morning on dew laden forage and hirola thus rarely needed to drink free water. However, the ability of hirola to survive through the dry season meant that they were resident throughout the year and thus subject to year-round predation pressure from resident predators. This may have been particularly intense when the migratory prey species moved out of the hirola range. A high density of prey species on a particular range should tend to reduce the risk of predation to all species involved through simple dilution effect (Hamilton, 1971; Bertram, 1978). Doubling the local density of herbivores while predator density remains unchanged would lead to a halving of the mortality risk.

In Tsavo, hirola associated with other species at a frequency that was related to their availability on the range (Chapter VI, section **6.3.1&2**). Grant's gazelle was the most common ungulate in Tsavo and the dominant associate of hirola and hirola appeared to benefit from the presence of Grant's gazelle through a reduced need for vigilance in mixed groups. However, in Garissa, warthogs were the most common on the range but topi formed the main associates. Though predation risk may have been reduced by association with other species, and by the availability of alternative prey, the use of the same range would have resulted in competitive interference over resources especially from zebra and Coke's hartebeest in Tsavo, and topi in Garissa. On the other hand, competition during the dry seasons may have been reduced due to the emigration of potential competitors.

9.1.7 Habitat selection and food choice

The pattern and structure of vegetation are determined largely by environmental and edaphic factors (Belsky, 1995). Further, rainfall, geology, soil moisture, soil characteristics on the slope (soil catena), and soil alkalinity, salinity, and sodicity are the dominant influences on pattern and structure in African savannah systems (Belsky, 1995). Large mammals, however, also have a strong influence on species composition, decomposition rates, nutrient recycling and microsite structure, through herbivory (McNaughton et al., 1988). Overall, these factors create microsites that suit certain species. Hirola were found to be highly selective of microhabits, choosing sites with a sparse short green grass/forb layer that provided food and relatively dispersed bush for cover and shade (Chapter **VII**). These findings are supported by earlier observations of patch selection trials showing that grazers tend to prefer short, sparse swards to tall, dense swards (Wilmshurst et al., 2000). Indeed, migratory herbivores often shift from areas of high to low sward biomass during the growing season (Vesey-Fitzgerald, 1960; Gwynne & Bell, 1968; Jarman, 1974; Langvatn & Hanley, 1993; Wilmshurst et al., 1990). As nutritional quality is an inverse function of grass abundance, herbivores appear to sacrifice short-term intake for nutritional gains obtainable by eating sparse forage of higher quality (Wilmshurst et al., 2000). The distribution of preferred shade trees and shrubs also influenced their location. Hirola preferred fairly open sites, though they required some bush for cover and shade. The amount of tree and shrub cover varied between Tsavo and Garissa, with more open sites (on flood plains along the Tana River dominated by the preferred grass *Sporobolus helvolus* and patches of the forb *Commelina forscalae*) holding higher densities of hirola. These sites were heavily grazed by cattle and wildlife especially hippos, buffaloes, zebra and topi. The occurrence of large numbers of hirola at such sites may indicate that hirola benefits from the presence of other species that help in reducing the overall heights of grass herb layer. Similarly, hirola ranges in Tsavo coincided with sites that were frequently used by other species such as zebra, Coke's hartebeest, oryx and buffalo. Hirola preferred sites with shorter grass and only used areas with taller grass in the dry season, and in places where they could get shade. The presence of high densities of hirola on sites with a short, sparse herb layer may indicate the occupation of a preferred habitat. However, it also suggests a lack of sufficient habitat with preferred food plants which could thus lead to local concentrations and over-utilisation.

The diet which savannah ruminants select vary in two principal ways: botanically, in the proportions of grasses, forbs and browse, and in quality, which approximates to the inverse of fibre content and its degree of lignification (Illius, 1997). All ruminants select against wood, stem and leaf sheath and in favour of leaf lamina, but this tendency is strongest in small species and almost absent in large species. Large species make less use of short grass than do small species, and are the first to move off swards high on the catena when they become depleted during the dry season (Illius, 1997). The most selective feeders, such as duikers, have botanically-diverse diets, avoiding fibrous components of the vegetation where possible. Intermediate selectivity is associated with lower-quality diets and is exhibited by animals in the range of 50 to 200 kg body weight (which includes the hirola), which may tend to specialise on either grass or browse, or switch from grass to browse as grass digestibility declines at the end of the wet season (Jarman, 1974). Hirola appear to feed mainly on grasses, selecting short stands and consuming whole plants (stem, leaf and inflorescence) at about 7 cm from the ground. However, forbs were eaten too. In Tsavo, the proportion of forbs increased in the diet during the dry season. Similarly, hirola in Garissa mainly grazed but ate forbs too. Two strange observations in Garissa were of a female hirola feeding on the leaves of *Combretum hereroense* and once I encountered a group in the riverine forest feeding on the dry (but highly nutritious) seeds of *Acacia tortilis*. Both of these observations were made in the dry season. In general, hirola used moderately tall grass areas in the dry season as they moved closer to bushy areas. Further, hirola preferred green grass but would avoid them as they grew taller in the wet season; they then moved in search of edge grasses that were less green but shorter. The avoidance of tall grass may have been a result of the threat from predation. Though hirola food plants appeared low in nutrients during the dry season, hirola seemed to tolerate this for a short period and they did not seem to change in body condition. According to White (White, 1980), loss of body condition in the dry season among tropical ungulates is usually explained by low quality of forage. Studies indicate that as grass swards mature, they increase in biomass and decrease in quality as they accumulate structural carbohydrates (Waite, 1963). Mature, poorly digestible grass requires longer retention in the rumen and/or reticulum to reduce particle sizes sufficiently to pass to the hind gut (Illius & Gordon, 1992). Faster passage of high-quality grass means that it can be consumed in greater quantity by ruminants than can low-quality grass (Baile & Forbes, 1974). Hirola may have overcome this condition as a result of their feeding around drying water holes that most times had greener grass and by the selection of nutritious, succulent forbs. This pattern of selection may also explain why their faecal material had higher nutrient contents and why hirola always appeared to be in good physical condition.

9.2 Factors limiting hirola populations

9.2.1 The Garissa hirola population

9.2.1.1 Habitat degradation

Observations on hirola feeding and on their habitat preference indicated that they preferred grassland patches with short grass/herb layer interspersed with bushes (Chapter VII, Section **7.5**, Chapter VIII, section **8.2.1&2**). Such areas in Garissa appear to be declining. Most sites are overgrown with bush (eg the Arawale Game Reserve that was formally created as a conservation site for hirola (Magin, 1996b)) while others are turning into scrubland with bare ground (eg the Bura area). Few hirola occur on sites where these processes are most advanced. This habitat degradation has been caused by recent increase in the human population, and especially by the influx of Somali refugees as a result of political instability in the Somali Republic. The increased human population has also led to an increase in livestock numbers and hence overstocking. An increase in livestock leads to overgrazing, an increase in bare ground and the progressive growth of bush cover leading to a general decline in range condition (Oba et al., 2000, Prins & Olff, 1998, Rainy & Worden, 1997). The loss of habitat is a major factor in the decline of most wildlife populations (Morrison et al., 1992). The decline in population can be through reduced reproduction rates, increased mortality rates or increased competition for food resources between livestock and wildlife grazers such as hirola (Prins, 1992). As a result of overgrazing, there may also be a reduction in fuel load that is necessary to promote the fire regimes that would help reduce bush encroachment (Dublin et al., 1990).

The increase in illegal immigrants, many of them ex-soldiers from Somalia led to increased poaching especially of elephants and rhinos (Chapter VIII, section **8.2.3**). During the 1990s large gangs of 100 – 200 men roamed the hirola range and lived off wildlife while poaching for ivory and rhino horn and robbing buses, villages, and market centers. Most locals believe that of all the wildlife in the range, hirola has the best meat and most poachers prefer it. There were about 10,500 elephant and about 100 rhinos in the hirola range by 1977 (DRSRS data base, 1977). Currently only about 35 elephants exist on the forest edges of the TPNR along the Tana River and no rhinos survive. Elephants destroy woodlands thus creating grasslands and grassland patches (Laws, 1969, Caughley, 1976), thus acting as facilitators to grazers like hirola. The decline in elephants and rhinos, may have led to bush encroachment and an overall decline in habitat quality for hirola.

9.2.1.2 Poaching

Bush encroachment in Garissa has in turn forced hirola to vacate overgrown sites and inhabit sites closer to Somali homesteads or vacated homesteads where through grazing and human activities, the bush cover is low and the sward layer is short (Chapter IV, section **4.3**). However, this location presents a further threat as poachers can find hirola within short distances of their settlements. The Garissa hirola had higher flight distances than those in Tsavo thus indicating a greater threat from poaching. Studies in the Katavi Ecosytem in western Tanzania have indicated that wildlife species tend to be fewer outside protected areas and that as a result of hunting, they are always shy (Caro, 1999).

Due to unstable government in Somalia, high incidences of organized poaching were recorded along the Kenya/Somalia border. As a result of high insecurity in the area, the Kenya government has deployed large numbers of mainly upcountry security personnel. Due to the remoteness and hardships of the area, re-supplies of food are sometimes unreliable and this may lead to poaching. The presence of Home Guards to help contain banditry and cattle rustling has also led to more guns for poaching in the region. Several people have played down the effect of poaching, but I believe it is one of the major factors affecting hirola in Garissa. The only animals that exist in large numbers in the Ijara/Galmagalla area are waterbuck, whose meat is regarded as unpleasant and warthogs, which are avoided by Muslims. Studies in the Ishasha Sector of Ruwenzori National Park, Uganda indicated that poaching was one of the key factors causing the decline of the topi population (Yoaciel & Van-Orsdol, 1981). Yoaciel's study showed that poaching increased even further after the establishment of a military garrison at the Ishasha border since these people were largely immune to prosecution. The current localized distribution of hirola away from areas where water is available indicates their response to this kind of threat. A study on buffaloes on the border between Botswana and Zimbabwe indicated that this water-dependent species settled far away from water reserves, in areas where they were least likely to encounter poachers (Hunter, 1996).

9.2.1.3 Diseases

Disease could be an important threat to hirola in the natural range and could potentially drive the species to extinction in a single disease episode. The most probable cause of such an outbreak would be transmission from livestock. This study indicated high movements of people and livestock within the hirola range (Chapter VIII, section **8.2.5**). These involved two main groups of people, the first from Somalia. The periodic movement of Somalis with their livestock into the hirola range was due to the ongoing inter-clan conflicts in Somali and were partly to ensure their personal security, partly to sell their livestock at markets along the Kenyan Coast and partly to graze their livestock within the coastal forest grasslands patches during periods of drought. The second form of livestock movements within the hirola range involved the Kenyan Somalis from as far as Wajir and Moyale who came southwards to graze their livestock in periods of extreme drought. Most of these people were heavily armed and they lived mainly on wildlife. These frequent and large-scale movements of livestock were a constant opportunity for disease transmission.

In captivity, hirola suffer from acidosis, bloat, tuberculosis and mycobacterioses (Smielowski, 1987). It also seems very likely that hirola, like most African bovids, are susceptible to rinderpest. Serological testing of four adult hirola in 1995 and of 35 hirola from the 1996 capture indicated that none of these animals had been exposed to rinderpest. However, in 1999, these samples were reassessed using a more sensitive test and at least one hirola tested positive (Kock et al., 1999). There is concern that rinderpest may now be endemic in the Garissa District and that each year a portion of the hirola population succumbs to it (Kock et al., 1999). The closely related *Damaliscus spp.*are moderately susceptible to rinderpest (Woodford, 1984). Reported cases of rinderpest outbreaks occurred in the hirola range in 1962-1963, and in 1982-1984 and it has been suggested that each outbreak may kill a part of the hirola population (Ottichilo et al., 1995). The rinderpest epidemic west of Tana River near Garsen and Tsavo East National park killed 55% of the buffalo population (Kock et al., 1999).

It also appears likely that hirola are susceptible to other diseases that affect livestock and the mortality of hirola in late 1998 was due to East Coast Fever and trypanosomiasis (Richard Kock pers comm.). Foot and mouth disease might cause some mortality among hirola but is likely that, like most other ungulates, hirola are wholly or partially resistant to this disease (Pratt & Gwynne, 1977; Kock et al., 1999). According to Kingdon (Kingdon, 1982), there are no reports of hirola suffering declines as a result of disease, however the dramatic decline in hirola during 1983 and 1985 may have been at least partly due to disease. In general, it seems probable that hirola have suffered massive mortality due to disease from time to time. Now that hirola have been reduced to such low numbers, any further major episode of disease may represent a serious threat to the survival of the species.

9.2.1.4 Climatic changes

Climatic changes may have also had some impacts on hirola. There was drought in the hirola range in 1965, 1970, 1973 - 1976, 1979, 1980, 1984 – 1985, 1990, 1992 (Dirschl et al., 1978; Decker, 1989; Wargute & Aligula, 1993; Wargute, 1994)). Droughts are certain to have reduced the hirola food resources and probably caused some level of death and low reproduction. In addition, starving people will have been more likely to poach hirola for food. Studies have shown that populations of herbivores are determined by the quantity and quality of food over a period sufficient enough to enable the animal to deposit reserves of energy and protein stored in the body (Prins & Olff, 1998). Skogland (Skogland, 1986) suggested that the fecundity of migratory populations should be less sensitive to environmental variation than that of sedentary populations such as hirola (Chapter VII, section **7.3**). Migratory populations such aswildebeest, caribou, and elk do show stable fecundity of prime-aged females, but constant adult fecundity has also been reported in sedentary populations of roe deer (*Capreolus capreolus*) (Gaillard et al., 1992) and fallow deer (Putman et al., 1996), indicating that the adult fecundity of many large herbivores is resilient to a wide variety of environmental conditions and may be a species-specific life history trait. Studies on moose (Boer, 1992), pronghorn (Byers, 1997), and gazelles (Baharav, 1983) confirm high resilience of adult fecundity in ungulates. Limited, density-independent year to year variation in adult fecundity usually originates from annual variation in weather such as rainfall (Berry, 1981). Since the quality and quantity of forage in semi-arid areas is largely influenced by rainfall, it is likely that droughts negatively influenced the hirola population through reduced reproductive and survival rates. These effects may have been enhanced by poaching and the spread of diseases as livestock are moved around, often concentrating in areas where some resources remain. During the 1997-1998 El-Nino floods a similar but reverse situation occurred. The entire hirola range was flooded and an aerial survey showed that some hirola had taken refuge on raised ground, indeed the very same areas that people were forced to occupy. Almost the entire stock of goat and sheep in the range died. Hirola may have died too and while none were reported, the hirola scouts recorded some poaching. An outbreak of East Coast Fever immediately after the El-Nino also caused substantial deaths among hirola and livestock.

9.2.1.5 Loss of dry season refuges

Observations of hirola occupying the area around the TPNR, indicated that the open patches used were typical flood plains, and constituted the highest concentration of hirola in Garissa (Chapter IV, section **4.3.1**). The Tana River typically discharges water onto the flood plains each year. In the past these floods have even been known to kill an entire forest along the river banks (Decker, 1989; Hughes, 1990). This process has been essential in maintaining flood plains that offer grazing habitat for hirola. Currently, parts of the flood plains have been converted to irrigation schemes as at Bura and Garsen, hence the loss of habitat for hirola. However, currently, flooding rarely occurs except during a major change in climate such as the El-Nino episodes and there are indications that slowly the riverine forest is expanding to cover the few existing flood plains. At the same time, bush encroachment is proceeding from the hinderland. In addition, dams for the generation of hydroelectric power have been constructed upstream at Masinga, Kiambere, Kindaruma and one is proposed for Mutonga. Such dams are reducing the discharge of the river and will lead to further loss of the flood plains. Comparable evidence for the impact of such changes in vegetation structure, is the encroachment of bush that led to the decline of roan antelope in Kruger National Park (Joubert, 1976).

9.2.1.6 Competition with livestock and other ungulates

Interspecific competition occurs when two or more species utilize a resource which is limited in supply. Field observations in Garissa indicated that most hirola were found in areas close to livestock bomas and along the flood plains on the banks of Tana River (Chapter IV, section **4.3.1**). Further, hirola were observed to graze close to cattle in the wet season, but during the dry season when grazing areas were scarce, hirola used the same areas as those utilized by livestock but occupied them very early in the morning before livestock arrived and late in the evenings after the livestock had been moved to homesteads for the night. However, when food was scarce and livestock could not feed for long enough during day light hours, the owners grazed them all night. This indicates the potential impact of the increased livestock population on hirola. Interestingly enough, there were 200, 000 cattle in the hirola range in 1973 (Duncan, 1974) and 126,730 cattle in 1995 (Ottichilo et al., 1995). This suggests an overall decline in carrying capacity on the hirola range, that is affecting both species. Further, studies on topi and wildebeest indicated that wildebeest, which have relatively wide mouths, can graze down vegetation swards to a height below that which can be tolerated by topi; and, the narrower-mouthed topi can reduce the leafy component of differentiated swards (i.e., swards in which seed-bearing stems have developed) through selective feeding to a level below that which can be tolerared by wildebeest (Murray & Illius, 2000). Although this kind of investigation was not undertaken in this study, it seems likely that the massive presence of livestock in areas occupied by hirola may be directly affecting the hirola's food resources.

9.2.1.7 Predation

Records of predation on hirola by lions and hunting dogs were common in Garissa. Though no data was available on predator density and actual impact on hirola, studies in the Ishasha Sector of Rwenzori National park indicated that the high density of predators (lions) was responsible for the decline of topi population, in addition to poaching (Yoaciel & Van-Orsdol, 1981). Lions, hyaenas, and hunting dogs were seen quite commonly in Garissa and a number of observations of predation were recorded by the hirola scouts (Chapter IV, section **4.3.4**). A number of cases of predation were recorded during the East Coast Fever outbreak, perhaps due to attacks on weak and sick hirolas. The numerous cases of predator attacks recorded on well protected domestic animals may also have been an indication of the high predation pressure on wildlife including hirola.

9.2.1.8 Overview of limiting factors in Garissa

Though data from the natural range is not conclusive, this study has established that disease, poaching, predation, habitat degradation and competition from livestock and/or other wildlife herbivores (Chapter VIII, section 8.2) are contributing to the decline on an already diminished natural hirola population. At the current mortality rates, the hirola population could remain static but poaching may exterminate some local groups that occur in high poaching zones (e.g., areas close to the Kenya-Somalia border) or drive the surviving members to sub-optimal habitats where they may eventually die out. On the other hand, a disease outbreak (section **9.2.1.3**) that affects both livestock and wildlife could potentially spread to the peripheral groups (those that are not under direct threat from poachers currently, particularly the groups within the Tana River Primate N.R.) and wipe out the entire population. Poaching and disease might thus be the biggest and immediate threats to the natural hirola population. Competitive interference and habitat destruction might be the most important long-term threats.

9.2.2 The Tsavo hirola population

9.2.2.1 Microhabitat selection

This study indicated that hirola were highly selective in their choice of microhabitat in Tsavo (Chapter VIII, section **8.3.2**). Range observations indicated that such microhabitats were limited in their availability. The relationships between the preferences of animals to an objective classification of the habitats in a particular area might give an indication of the balance between habitat requirements and resource availability. Studies have shown that there is often a trade-off between habitat selection and predation risk (Cowlishaw, 1997), resulting in greater use of less risky microhabitats. Further, an antelope selects the vegetation type that best satisfies its feeding requirements, then selects the stand of plants that most suit it and lastly the plant parts that it prefers to eat (Jarman, 1974). The fact that some hirola group ranges were clustered on particular microhabitat types while others were dispersed at low density is an indication of the preference of this species for particular habitat conditions and of the limitations of such habitats in Tsavo East N.P.

9.2.2.2 Local ranging behaviour and predisposition to predation

Hirola were observed to occupy the same range area all year round, only making local shifts to neighbouring habitat patches (core areas) (Chapter V). Observation on other ungulates indicated that they made seasonal movements away from the area in the dry season in search of resources, whereas the main predators (lions) did not move (Chapter IV, section **4.2.8**) (Hanby et al., 1995). Hirola may thus have been exposed to high predation pressure during these periods. Studies on lion prey selection in Kruger National Park indicated that lions selected the most abundant small to medium sized ungulates namely impala, wildebeest and zebra (Funston et al., 1998). Similarly in the Mara, pride lions killed topi, Coke's hartebeest, impala and warthogs during periods when the preferred migratory species (wildebeest and zebra) had migrated to the Serengeti (Bertram, 1979). Also, because a particular area was likely to contain wildebeest for a small proportion of the year, while zebra, with their less aggregated distribution, were likely to be present for a longer part of the year, more zebra were killed despite their being less abundant than wildebeest (Bertram, 1979). Studies in the Serengeti also indicate that lion prides did not migrate alongside prey but instead preyed on the few available non migratory prey species (Hanby et al., 1995). Further, lion prides in the Ngorongoro Crater (where prey species were abundant most of the year) had smaller home ranges than the Serengeti plains prides, which had to survive on seasonally available prey (Hanby et al., 1995). The fact that the antipredator benefits of interspecific association were also reduced makes predation a more serious threat to hirola in the dry season when other prey have moved. The Garissa population may experience similar threat as a result of seasonal topi migrations between the hinterland and the coastal forests.

9.2.2.3 Reproductive behaviour and predisposition to predation

Observations on hirola groups in Tsavo revealed that female hirola often separated from their family groups to graze alone with their calves or with their yearling offspring (Chapter V, section **5.3.4**). Further, hirola yearlings separated from their natal groups to live alone or in temporary sub-adult groups (See 5.2). Two females and their calves were killed by lions while in isolation from the group. Probably, only about 68.9% of calves born survived up to 6 months of age and only about 18.0% of calves born survived to the age of 2 years. Studies have shown that membership of larger groups confers anti-predator advantages (Jarman, 1974; Roberts, 1996). Hirola live mainly in groups and may not be able to effectively conceal themselves to avoid predators, unlike solitary antelopes that can conceal themselves in closed habitats and that sometimes freeze in the event of predation risk (Jarman, 1974; Sinclair, 1985; Hamilton, 1971; FitzGibbon & Lazarus, 1995b). Similarly, a lone hirola amongst a group of Grant's gazelle or zebra or ostrich may be easily recognisable to predators. Observation on lion predator selection in Kruger National Park indicated that lions selected buffalo calves and old bulls that they encountered away from herds (Funston et al., 1998). Studies on moose (*Alces alces gigas*) in the eastern Talkeetna Mountains, Alaska, indicated that annual mortality from grizzly bear (*Ursus arctos*) and wolf (*Canis lupus*) predation was higher for solitary yearlings than for dependent yearling (those with adults) and for solitary adults (White et al., 2001). Field observations that some female hirola were killed, together with their calves while in isolation and that only a few of the dispersing yearling survived to rejoin groups supports the common finding that solitary animals are vulnerable (Chapter VIII, section **8.3.4**). However, it is also possible that young hirola may be better able to hide from predators when alone than when in groups. The overall costs and benefits of dispersal behaviour have yet to be clarified and deserve further study.In general, hirola appear to be timid and vulnerable animals; they responded to approaching predators by running slowly away. Overall, observations of their anti-predator behaviour suggests that predation could be an important factor limiting hirola numbers.

9.2.2.4 Poaching

Field observations indicated that Tsavo hirola are not free from the threat of poaching. Tsavo National Park currently faces a serious threat of loss of game through poaching for meat by local people. So called 'pot poaching' is believed to be a major factor contributing to the decline of wildlife in the Masai Mara region in Kenya (Ottichilo et al., 2000). The decline of buffalo populations in the north-western and western corridor areas of Masai Mara was also attributed to illegal hunting (Dublin et al., 1990).

9.2.2.5 Disease

Between 1995 and 2000, two hirola, a mother and calf, were observed to have diarrhoea but they soon recovered. No other evidence of disease was observed in Tsavo during this study and disease did not appear to be an important factor in this population. However, there was a rinderpest outbreak in Tsavo between 1994 and 1995 (Kock et al., 1999), which greatly reduced the ruminant population and hirola may have been affected. The rinderpest outbreak in Tsavo was thought to have been caused by the movement of infected livestock from Somalia to the ranches around Tsavo National Park (Richard Kock pers. comm.).

9.2.2.6 Predation and shade

Analysis of the effect of a range of candidate limiting factors on variation across hirola groups suggested that predation and shade may have important effects on the overall numbers of hirola per group (Chapter VIII, section **8.3.5**). Predation was known to be the cause of some of the observed mortalities and the abundance of carcasses was related to variation in predator occurrence (Chapter IV, sections **4.2.6&7**). Other studies have demonstrated that predation can be a limiting factor especially on species with a small population, e.g., topi (Yoaciel & Van-Orsdol, 1981), bighorn sheep (Hayes et al., 2000) and feral horse (Greger & Romney, 1999). Studies on prey selection by lions in Manovo-Gounda-St-Floris National Park in the Central African Republic indicated that grazers were taken more frequently than browsers or mixed feeders, and the majority of the kills occurred on rivers floodplains or the surrounding woodlands (Ruggiero, 1991). Hirola groups grazed on the edges of drying waterholes, which occurred mostly in open areas and used the surrounding bushes for shading. This environment may have predisposed them to predation. The high intensity of aggressive displacements over shade (Chapter V, section **5.5.1**) suggested that this variable might be important and the abundance of prefrred shade trees and bushes was correlated with observed variation in group size (Chapter VIII, section **8.3.6.1&2**); temperature is known to be a major influence on ungulate diurnal activity cycles (Roberts & Dunbar, 1991).

9.2.2.7 Overview of limiting factors in Tsavo East N.P.

Observation of hirola groups in Tsavo indicated that predation, the availability of a spatially limited food resource (short green grass) and lack of shade could have limited group sizes and hence the population. However, the incidence of predators and the abundance of shade were inversely correlated and thus confounded in multivariate analysis. This intercorrelation may have been because lions were attracted to open areas where prey concentrations formed ansd where shade trees and bushes were minimal. In spite of this, competition for shade caused considerable competition and thus seemed to be biologically important; however, it seems unlikely that it would be a primary limiting factor. Predation emerged as the most important factor in multivaraite analysis and this result, together with a variety of observational data suggest that predation is by far the most important factor limiting the Tsavo population. The limited availability of a preferred food supply is potentially important but seems unlikely to be placing a ceiling on hirola numbers at the present low population size. If food were limiting there would be some indication of poor body condition and reduced reproductive performance. However hirola nearly always seemed to be in excellent condition, even in the dry season, and there was no indication that female reproduction was constrained. This suggests that the hirola population was below carrying capacity and that it has never been at carrying capacity since its introduction in 1963. The reason seems likely to be the high level of predation that the population experiences, particularly during the dry season when the population is exposed by the departure of the migratory alternative prey.

9.3 Conservation management strategies

9.3.1 In-situ conservation (Garissa)

9.3.1.1 Re-establishment of existing conservation areas

The findings of this study indicates that about 60 hirola exist in the Arawale Game Reserve and about 200 in and around the Tana Primate National Reserve. There is an urgent need to re-establish these partially protected or unprotected areas as real National Parks. National Parks enhance local security, promote tourism and wildlife protection, exclude people and livestock, and, ideally, provide income from tourism that can be directed to help projects within the local community. While there is no direct evidence that upgrading such areas will necessarily result into an increase in the number of wildlife, studies have shown that higher numbers of wildlife occur in protected areas than outside (Caro, 1999). The Kenya Wildlife Service should attempt to convert the area on the east bank of the TPNR into full Park status to protect the high concentration of hirola there, degazette parts of the Arawale Game Reserve (which now have no value as wildlife refuges) and extend its southern range (which has some groups of hirola) into a National Park. The two parks could then form breeding grounds for hirola in their natural range. These areas could act as a focus for future management plans and at the same time could reduce conflict with local people. Studies elsewhere show that the absence of active protection in non protected areas, either by central authorities or through local agencies, has resulted in declining numbers of wildlife (Leader-Williams et al., 1990).

9.3.1.2 Develop community based conservation schemes

In order to alleviate the conflict that exists at present between KWS and the local community, it is imperative that the local community is involved in hirola conservation measures. For example, the area around Galmagala which harbours substantial numbers of hirola could be converted into a community based conservation zone. This objective could be achieved through the formation of local conservation groups (Lewis et al., 1990); (Wilkie et al., 1998), and the upgrading of protection. However, community-based conservation programs will only succeed if the communities involved receive tangible benefits. The elders of the community around the Galmagala area have consistently expressed to me their desire to allocate part of their land to a community based hirola conservation zone. In return, they wish to be assisted in building dams and bore holes to provide water to the community as well as their livestock, and to be provided with armed protection against banditry from neighbouring Somalia. In Tanzania, such schemes are being undertaken by the Tanzania National Parks Authority in collaboration with the German Development Agency (GTZ) around the Selous Game Reserve, (Krishke et al., 1996) and the Cullman Wildlife Project, which is providing funding for schools and clinics to the villages adjacent to its hunting concessions (Robin-Hurt-Safaris, 1996).

9.3.1.3 Active habitat management

With the knowledge that is now available about hirola habitat requirements parts of Arawale Game Reserve that once supported high densities of hirola could be reinstated to their original form. This could be achieved partly through controlled burning to restore grassland patches (Dublin et al., 1990). In areas where there is no enough fuel to sustain fire (the areas near Bura), mechanical and possibly, chemical means could be used to reduce bush cover. In addition, the area could be easily supplied with permanent watering points at selected sites by piping from the nearby Tana River. Such developments could be achieved by relatively modest levels of funding and would represent an investment for future income from wildlife.

9.3.1.4 Monitoring microhabitat changes

Taking note of the microhabitat selectivity revealed in the present study of hirola, future management should attempt to monitor the availability and dynamics of the preferred short grass habitats so that any change can be quickly noted. Attempts should also be made to develop and refine techniques (such as controlled burning) that could be used to increase the availability of such limiting resources.

9.3.1.5 Monitoring of the impact of diseases

This study supports the suggestion made elsewhere that disease is a potential threat to hirola in Garissa. The major declines in hirola numbers that have been observed may be partly a result of diseases that have been transmitted through livestock movements. There is a need to monitor the spread of diseases between livestock and wildlife especially in the dry seasons and periods of extreme drought. This could be achieved through frequent monitoring of diseases among wildlife, by monitoring livestock movements throughout the range, and enforcing livestock vaccination programmes against possible diseases. Livestock vaccination programs in the Mara/Serengeti region led to tremendous increase in wildlife population (Sinclair, 1979). It may also be useful to determine the impact of the topi migration on hirola in terms of disease transmission. Topi migrate between the hirola's natural range, through the tsetse fly infested coastal forest to the open glades on the edges of the Indian Ocean, where they come into contact with the Swahili people's livestock.

9.3.1.6 Benefits of other associate species

This study established that hirola appeared less vigilant while in association with Grant's gazelle (Chapter VI, section **6.4**). However, this data was acquired during the mid hours of the day. There is need to establish further the advantages of other associate ungulates during all hours of the day and especially morning and evening when hirola appear to have many and varying associate species like Coke's hartebeest and zebra among others.

9.3.1.7 Hirola energy requirements

Energy (calories) is a major component of an animal's daily diet requirement (Illius, 1997), a procedure that lacked in this study. There is need to carry out captive experiment to understand the energy requirements, energy content of natural hirola foods during different seasons.

9.3.2 Ex-situ conservation

9.3.2.1 Establishment of wild and semi-wild populations

There are only two existing populations of hirola worldwide. These are the *in-situ* population occurring in Garissa District in a non-protected pastoral rangeland and the *ex-situ* population which exists mainly within Tsavo East National Park, a protected area. Results of this study indicate that the two populations breed effectively, but their overall numbers remain low if not declining. There is no indication that the factors responsible for their low numbers have been corrected and so they face an uncertain future. While the protection of the *in situ* population should be given high priority, the chance of extinction in both existing populations is so high that there is a compelling argument for the establishment of further ex-situ populations in better protected and, if possible, predator-proof sanctuaries. This would allow the risk of extinction can be spread geographically and would allow the total numbers of hirola to be increased to a level where stochastic factors would be less likely to cause chance extinction. According to the IUCN/SSC Antelope Specialist Group, the decline of hirola since the 1970s within its restricted natural range suggests that it is in danger of extinction in the short to medium term (East, 1998). This conclusion is supported and reinforced by the findings of the present study.

The establishment of *ex-situ* populations in addition to that in Tsavo National Park, in areas where a high level of protection and management can be assured, is an urgent priority to reduce the risk of extinction. Hirola survival will remain precarious until secure populations have been established in a larger number of sites both within and outside its natural range. The present study has also established that hirola groups can probably thrive in than previously supposed (about 3.5 km^2, Chapter VII, section **7.3**) if sufficient food and shelter is available and if disturbance is minimised. In order to save hirola, a carefully planned distribution of hirola to willing farms around the country, could be undertaken as a first step. The issue of ownership of the animals on private farms should not be an obstacle and could be tackled through legal agreements with the respective farms and ranches. The initial objective of KWS should be to help establish a reasonable number of groups of hirola in different parts of the country in protected, predator free environmen. The aim of establishing such groups should not be to establish semi-natural populations but rather to encourage numbers to increase so that the risk of species extinction is reduced and so that animals are available for future conservation measures (such as reintroduction to Garissa, if it becomes necessary).

However, the aim of creating further *ex-situ* groups is bound to face problems. The local Somali pastoralists in whose range hirola occurs have been encouraged to believe that hirola belong to them. During 1996 translocation, great efforts were made to stop the translocation. To help avoid this kind of scenario, KWS should be prepared to take decisive direct action in support of its role as the main statutory custodian of Kenyan wildlife. Such action should however take place in the context of programmes of conservation education and would be most effective as part of an integrated plan for hirola conservation in Garissa that included the restoration of protected areas (as discussed above), and the chanelling of benefits from hirola conservation to the local community.

At a practical level, the question of how animals should be moved in order to establish new groups requires serious consideration. Lessons from the 1996 translocation indicate that the best method devised so far is the capture using nets (Chapter VIII, section **8.3.7**) of entire family groups and movement by plane as quickly as possible into spacious pre-release pens in the recipient range. Helicopter darting is less successful and should be used only sparingly. Habituated individuals can be darted efficiently from the ground but this requires a rapid operation (one vehicle with an experienced darting team and enough loaded dart guns for each animal) so that the animal can be immobilised before the other members of the group can react to the disturbance.

Magin (Magin, 1996b), and Butynski (Butynski, 2000) have recommended several candidate areas for future hirola translocation. These are in two categories; the KWS managed National Parks and private ranches. KWS National Parks include the nothern area of Tsavo East National Park between the Yatta and Lali Hills, the Maktau-Jibe-Ziwani area of Tsavo West National Park, Nairobi National Park, and Meru National Park. The proposed private ranch areas include Baobab Farm - Mombasa, Hilton Wildlife Sanctuary - Taita Hills, Athi River Game Ranching, Lewa Downs Wildlife Sanctuary, and Oljogi (Pyramid) Wildlife Sanctuary. However, before any translocation is made, these sites should be surveyed for possible limiting factors that have been documented in this study (Chapter VIII, section **8.3.6**) and for any negative impact on the area. This study suggests that a thorough evaluation and comparison of these sites in relation to current sites occupied by hirola should be undertaken before any animals are moved. The ecological factors to be considered include grass/herb and shrub layer composition and structure, predation levels, availability and density of transient water holes and herbivore prey densities.

Any introductions should also take into account possible negative effects of competitive interference with indigenous species. The introduction of alien species is generally undesirable and should only be taken when there are compelling overriding reasons.

Hirola are believed to be ecological competitors of hartebeest and this may be the reason for their exclusive allopatric geographical distributions (Kingdon, 1997). While hartebeest are currently reasonably abundant, their populations are declining across Africa (except in southern Africa where they are farmed) and their conservation needs must not be forgotten during efforts to conserve hirola. Introductions to sites such as Nairobi National Park should thus be reconsidered. All of the ex situ introductions of hirola should also be regarded as interim measures. The preferred location for hirola in the long-term is the native range in Kenya and Somalia and they should be re-established there in large numbers when local conditions permit.

9.3.2.2 Captive animals (relevance of dispersal behaviour)

The hirola is Africa's only critically endangered species/genus of antelope which is not represented in captivity by a viable population. Establishing a viable population of hirola in captivity would provide new research opportunities on the species, enhance donor and zoo support and help ensure hirola survival. Much progress has been made by zoos with respect to their ability to maintain and breed antelopes in large naturalistic exclosures, but also in their commitment to conservation, particularly through research, public education, re-introductions such as the Arabian oryx (Price, 1989), and financial assistance for *in-situ* conservation activities.

A number of ungulates have been saved from extinction through captive breeding include the Arabian oryx (Price, 1989), scimiter-horned oryx (East, 1998) and the European bison (*Bison bonasus*) (Akimov et al., 2001). The addax (*Addax nasomaculatus*) and mountain bongo (*Tragelaphus eurycerus isaaci*) are nearly extinct in the wild but viable populations for re-introductions exist in captivity (East, 1998). It should be noted that the ultimate success of such breeding programs not only depends on proper demographic and genetic management of the captive population, but also on the successful collaboration of all scientific and captive breeding institutions, and more important, the on-the-ground conservation agencies, who provide facilities for re-introductions and/or introductions (Frantzen et al., 2001). A self-sustaining captive population of hirola should be established as soon as possible to provide an important security back-up measure and to secure the long term survival of the species. At the moment, there are only two hirola existing in captivity (Butynski, 2000). Hirola have been in captivity since 1950s and some individuals have survived and bred well (Smielowski, 1987). There have, however, been serious disease problems which affected individuals from time to time, causing their eventual decline and elimination. There have also been behavioural problems in captivity mainly through aggression between individuals kept in close contact (Andanje, 1997). However, these problems can potentially be avoided if the social system described in this study (Chapter V) is taken into account and if the dispersal patterns described are simulated in captive breeding conditions.

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Appendix

Appendix 1: Checklist of plant species observed in Tsavo and Garissa hirola range. G = Growth form, s = Shrub, h = Herb, sg = Sedge, t = Tree, X = Observed, 'Blank' = Not observed.

Plant Species	Family	G	Observed in	
			Garissa	Tsavo
Anisotes tanensis C.Buden	*Acanthaceae*	s	X	
Anisotes parvifolius Oliv.	*Acanthaceae*	s		X
Barleria argentea Rolf.f.	*Acanthaceae*	s	X	
Barleria ramulosa C.B.Cl.	*Acanthaceae*	s		X
Berleria acanthoides Vahl	*Acanthaceae*	s		X
Barleria prionitis	*Acanthaceae*	s		X
Berleria eranthemoides C.B.Cl.	*Acanthaceae*	s		X
Blepharis maderaspatensis Lindau	*Acanthaceae*	h		X
Blepharis linarifolia Pers.	*Acanthaceae*	h		X
Blepharis fruticosa C.B.Cl.	*Acanthaceae*	h		X
Echbolium hamatum C.B.Cl.	*Acanthaceae*	h		X
Monechma debile (Forsk.) Nees	*Acanthaceae*	h		X
Neuracanthus ukambensis C.B.Cl.	*Acanthaceae*	h		X
Thunbergia holstii Lindau	*Acanthaceae*	h		X
Justicia heterocarpa T. Anders.	*Acanthaceae*	h		X
Justicia flava Vahl	*Acanthaceae*	h		X
Asystasia somalensis (Franch.) Gillett	*Acanthaceae*	h		X
Echbolium sp. Verdcourt	*Acanthaceae*	h	X	
Echbolium revolutum (Lindau) C.B.Cl.	*Acanthaceae*	h		X
Ruttya fruticosa Lindau	*Acanthaceae*	s		X
Thunbergia holstii Lindau	*Acanthaceae*	h		X
Echbolium hamatum C.B.Cl.	*Acanthaceae*	h		X
Sansevieria sp.	*Agavaceae*	s	X	
Sansevieria sp. (spotted)	*Agavaceae*	h		X
Sanseveria intermedia N.E.Br.	*Agavaceae*	h	X	X
Gizekia pharnaceoides L.	*Aizoaceae*	h		X
Achyranthus aspera L.	*Amaranthaceae*	s	X	X
Amaranthus aschersonianus Thellg.	*Amaranthaceae*	s		
Amaranthus graecizans L.	*Amaranthaceae*	s	X	
Digera mucronata L. Mast.	*Amaranthaceae*	h	X	
Aerva lanata (L.) Schultes	*Amaranthaceae*	h		
Aerva pasca	*Amaranthaceae*	h		X
Pupalia lappacea (L.) A. Juss.	*Amaranthaceae*	h	X	X
Sericocomopsis hildebrandti Schinz	*Amaranthaceae*	s		X
Sericocomopsis pallida (S. Moore) Schinz	*Amaranthaceae*	s		X
Lannea alata (Engl.) Engl.	*Anacardiaceae*	s	X	X
Lannea schweinfurthii (Engl.) Engl.	*Anacardiaceae*	t		X
Lannea triphylla (A. Rich.) Engl.	*Anacardiaceae*	s		X

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Lannea stuhlmannii (Engl.).	*Anacardiaceae*	s		X
Adenium obesum (Forssk.) Roen & Schult.	*Apocynaceae*	s	X	X
Carissa edulis (Forssk.) Vahl	*Apocynaceae*	s	X	X
Strophanthus mirabilis Gilg.	*Apocynaceae*	s		X
Sarcostemma viminale (L.) P. Br.	*Asciepiedaceae*	s	X	
Asparagus falcatus L.	*Asparagaceae*	s	X	X
Asparagus racemosa Willd.	*Asparagaceae*	s		X
Balanites rotundifolia (Van Tiegh) Blatter	*Balanitaceae*	s	X	X
Balanites orbicularis Sprague	*Balanitaceae*	s		X
Bourreria teitenis (Gurke) Thulin	*Boraginaceae*	s		X
Heliotropium steudneri Vatke	*Boraginaceae*	h	X	X
Trichodesma zeylanica (L.) R. Br.	*Boraginaceae*	s		X
*Cordia somalensis**	*Boraginaceae*	s	X	
Cordia monoica R. Br.	*Boraginaceae*	s	X	X
Cordia siniensis Lam	*Boraginaceae*	s	X	X
Ehretia teitensis Guerke	*Boraginaceae*	s	X	X
Commiphora africana (A.Rich.) Engl.	*Burseraceae*	s	X	X
Commiphora campestris Engl.	*Burseraceae*	t	X	X
Commiphora edulis (Kl.) Engl.	*Burseraceae*	s	X	
Commiphora holtziana Engl.	*Burseraceae*	t	X	X
Commiphora riparia Engl.	*Burseraceae*	t	X	X
Commiphora schimberi	*Burseraceae*	t	X	X
Commiphora boiviniana Engl.	*Burseraceae*	t		X
Caesalpinia trothae Harms ssp. Erlangeri (Harms) Brenan	*Caesalpiniaceae*	s		X
Cassia abbreviata Oliv. Ssp. Kaessneri (Bak.f.) Brenan	*Caesalpiniaceae*	s	X	X
Cassia longiracemosa Vatke	*Caesalpiniaceae*	s		X
Delonix elata (L.) Gamble	*Caesalpiniaceae*	t		X
Cassia mimosoides L. Group E.	*Caesalpiniaceae*	h	X	
Tamarindus indica L.	*Caesalpiniaceae*	t	X	
Boscia angustifolia A.Rich.	*Capparidaceae*	t	X	X
Boscia coriacea Pax	*Capparidaceae*	s	X	X
Cleome hirta (Klotsch) Oliv.	*Capparidaceae*	h	X	X
Boscia mossambicensis Klotzsch	*Capparidaceae*	s	X	
Cadaba farinosa Forssk.	*Capparidaceae*	s	X	X
Cadaba glandulosa Forssk.	*Capparidaceae*	s		X
Cadaba heterotricha Hook.	*Capparidaceae*	s		X
Maerua decumbens (Brongn.) De Wolf	*Capparidaceae*	s	X	X
Maerua subcordata (Gilg) De Wolf	*Capparidaceae*	s		X
Maerua denhardtiorum Gilg.	*Capparidaceae*	s	X	X
Maerua edulis (Gilg & Ben.) De Wolf	*Capparidaceae*	t		X
Maerua grantii Oliv.	*Capparidaceae*	s	X	
Maerua mungaii Beentje	*Capparidaceae*	s	X	
Maerua triphylla A.Rich.	*Capparidaceae*	s	X	
Thylachium thomasii Gilg	*Capparidaceae*	s	X	X
Maerua subcordata (Gilg) De Wolf	*Capparidaceae*	s		X

Caparis sp	*Capparidaceae*	h	X	
Maytenus heterophylla (Eckl. & Zeyh.) Robson	*Celastraceae*	s	X	
Combretum aculeatum Vent.	*Combretaceae*	s	X	X
Combretum hereroense Schinz	*Combretaceae*	s	X	
Terminalia orbicularis Engl. & Diels	*Combretaceae*	s	X	X
Terminalia parvula Pampan	*Combretaceae*	t	X	
Terminalia sp.	*Combretaceae*	s	X	
Terminalia spinosa Engl.	*Combretaceae*	t	X	
Commelina africana L.	*Commelinaceae*	h	X	
Commelina latifolia A.Rich.	*Commelinaceae*	h	X	
Commelina albescens Hassk.	*Commelinaceae*	h	X	
Commelina forskalaei Vahl	*Commelinaceae*	h	X	X
Commelina benghalensis L.	*Commelinaceae*	h	X	X
Aspilia mossambicensis (Oliv.) Willd	*Compositae*	s	X	X
Emilia discifolia (Oliv.) C.Jeffrey	*Compositae*	h	X	
Vernonia colorata Drake	*Compositae*	s		X
Vernonia cinerea (L.) Less	*Compositae*	s		X
Vernonia hildebrandtii Vatke	*Compositae*	s	X	X
Aspilia mossambicensis (Oliv.) Wild	*Compositae*	s	X	X
Notonia sp.	*Compositae*	s		X
Evolvus alsinoides L.	*Convolvulaceae*	h	X	X
Ipomea mombassana Vatke	*Convolvulaceae*	h	X	X
Crassula schimperi Fisch. & Mey.	*Crassulaceae*	h	X	X
Kalanchoe sp.	*Crassulaceae*	h	X	X
Momordica boivinii Baill.	*Cucurbitaceae*	l		X
Cyperus bulbosus Vahl	*Cyperaceae*	sg	X	
Cyperus esculentus L.	*Cyperaceae*	sg	X	
Cyperus distans L.f.	*Cyperaceae*	sg	X	X
Cyperus rotundus L.	*Cyperaceae*	sg	X	X
Kyllinga alba Nees	*Cyperaceae*	sg	X	
Kyllinga erecta	*Cyperaceae*	sg	X	
Diospyros cornii Chiov.	*Ebenaceae*	t	X	
Euclea natalensis A.DC. Ssp. Obovata	*Ebenaceae*	s	X	
Acalypha fruticosa Forssk.	*Euphorbiaceae*	s		X
Croton dichogamus Pax	*Euphorbiaceae*	s		X
Croton meyharthii Pax	*Euphorbiaceae*	s	X	
Erythrococca bongensis Pax	*Euphorbiaceae*	s	X	
Euphorbia cuneata Vahl (E. spinescens)	*Euphorbiaceae*	s	X	
Euphorbia polyantha Pax	*Euphorbiaceae*	s	X	
Euphorbia hirta L.	*Euphorbiaceae*	h	X	
Tragia arabica Baill.	*Euphorbiaceae*	h		X
Tragia subsessilis Pax	*Euphorbiaceae*	h	X	
Euphorbia tirucalli L.	*Euphorbiaceae*	s	X	
Euphorbia spinescens Pax	*Euphorbiaceae*	h		X
Givotia gosai A.R. Smith	*Euphorbiaceae*	s		X
Phyllanthus maderaspatensis L.	*Euphorbiaceae*	h	X	

Phyllanthus somalensis Hutch.	*Euphorbiaceae*	s	X	
Securinega virescens (Willd.) Baill.	*Euphorbiaceae*	s		X
Aristida adoensis Hochst	*Gramineae*	g	X	X
Aristida adscensionis L.	*Gramineae*	g	X	X
Brachiaria leersoides (Hochst) Stapf	*Gramineae*	g	X	X
Brachiaria eruciformis (J.E.Sm.) Griseb.	*Gramineae*	g	X	X
Brachiaria deflexa (Schumach.) Robyns	*Gramineae*	g	X	X
Brachiaria serrifolia (Hochst.) Stapf	*Gramineae*	g	X	
Cenchrus ciliaris L.	*Gramineae*	g	X	X
Chloris barabata Sw.	*Gramineae*	g	X	X
Chloris roxburghiana Schult.	*Gramineae*	g	X	X
Chloris pygnothrix	*Gramineae*	g	X	X
Chrysopogon aucheri (Boiss.) Stapf	*Gramineae*	g	X	X
Chrysopogon plumulosus	*Gramineae*	g	X	
Cynodon plectostachyus (K.Schum.) Pilg.	*Gramineae*	g	X	
Cynodon dactylon (L.) Pers.	*Gramineae*	g	X	X
Dactyloctenium aegyptium (L.) Willd	*Gramineae*	g	X	X
Dactyloctenium australe Steud.	*Gramineae*	g	X	
Digitaria macroblephora (Hack) Stapf	*Gramineae*	g	X	X
Digitaria milanjiana (Rendle) Stapf	*Gramineae*	g	X	X
Digitaria rivae (Chiov.) Stapf	*Gramineae*	g	X	X
Echinocloa haploclada (Stapf) Stapf	*Gramineae*	g	X	X
Enteropogon macrostachyus (A.Rich.) Benth.	*Gramineae*	g	X	X
Enteropogon rupestris (J.A. Schmidt.) A.Chiov.	*Gramineae*	g	X	
Enteropogon somalensis	*Gramineae*	g	X	
Eragrostis caespitosa Chiov.	*Gramineae*	g		X
Eragrostis cilianensis (All.) Lut.	*Gramineae*	g		X
Eragrostis tenuifolia (A.Rich.) Steud.	*Gramineae*	g		X
Eragrostis horizontalis A. Peter	*Gramineae*	g	X	X
Eragrostis superba Peyr.	*Gramineae*	g	X	X
Tragus berteronianus Schult.	*Gramineae*	g		X
Tragus heptaneuron	*Gramineae*	g		X
Oropetium thomaeum (L.f.) Trin.	*Gramineae*	g	X	X
Latipes senegalensis Kunth	*Gramineae*	g	X	X
Panicum coloratum L.	*Gramineae*	g	X	X
Leptochloa obtusiflora Hochst.	*Gramineae*	g	X	X
Bothriochloa radicans (Lehm.) A. Camus	*Gramineae*	g	X	X
Panicum maximum Jacq.	*Gramineae*	g	X	X
Panicum infestum Anderss.	*Gramineae*	g	X	X
Schmidtia bulbosa Stapf	*Gramineae*	g	X	X
Paspalum vaginatum Sw.	*Gramineae*	g	X	
Paspalum commersonii	*Gramineae*	g	X	
Cymbopogon pospischilii (K. Schum.) C.E. Hubb.	*Gramineae*	g	X	X
Heteropogon contortus (L.) Roem. & Schult.	*Gramineae*	g	X	X
Setaria verticullata (L.)P.Beauv.	*Gramineae*	g	X	
Setaria holstii	*Gramineae*	g	X	X

Sporobolus fimbriatus (Trin.) Nees	*Gramineae*	g		X
Sporobolus helvolus (Trin.) Dur. & Schum	*Gramineae*	g	X	X
Sporobolus pyramidalis P.Beauv.	*Gramineae*	g	X	X
Sporobolus spicatus (Vahl) Kunth	*Gramineae*	g	X	X
Tetrapogon bidentatus Pilg.	*Gramineae*	g	X	X
Tetrapogon tenellus (Roxb.) Chiov.	*Gramineae*	g	X	X
Pyrenacantha malvifolia Engl.	*Icacinaceae*	s	X	X
Becium sp.	*Labiatae*	h		X
Leucas martinicensis (Jacq.) Ait.f.	*Labiatae*	h	X	X
Leucas nubica Benth.	*Labiatae*	h	X	X
Ocimum americanum L.	*Labiatae*	h	X	X
Plectranthus lanuginosus (Benth.) Agnew	*Labiatae*	h	X	
Aloe deserti Berger	*Liliaceae*	h		X
Scilla kirkii Bark	*Liliaceae*	h	X	
Asparagus asiaticus L.	*Liliaceae*	s		X
Asparagus falcatus L.	*Liliaceae*	s	X	
Strichnos decusata (Pappe) Gilg.	*Loganieceae*	s	X	X
Agelanthus cehleri (Engl.) Polh. & Wiens	*Loranthaceae*	s		X
Viscum sp.	*Loranthaceae*	h	X	
Lawsonia inermis L.	*Lythraceae*	s	X	X
Caucanthus albidus (Nied.) Nied.	*Malpighiaceae*	s		X
Abutilon hirtum (Lam.) Sweet	*Malvaceae*	h		X
Abutilon fruticosum Guill. & Perr.	*Malvaceae*	s	X	X
Abutilon mauritianum (Jacq.) Medic	*Malvaceae*	s	X	X
Abutilon racemosa	*Malvaceae*	h	X	X
Hibiscus micranthus L.f.	*Malvaceae*	h	X	X
Hibiscus palmatus Forsk	*Malvaceae*	h	X	X
Sida ovata Forssk.	*Malvaceae*	s	X	X
Sida tenuicarpa Vollesen	*Malvaceae*	h	X	X
Thespesia danis Oliv.	*Malvaceae*	s	X	
Melia volkensii Guerke	*Meliaceae*	t		X
Acacia brevispica Harms	*Mimosaceae*	s	X	X
Acacia bussei (Sjostedt)	*Mimosaceae*	s	X	X
Acacia elatior Brenan	*Mimosaceae*	t	X	X
Acacia mellifera (Vahl) Benth	*Mimosaceae*	s	X	X
Acacia nilotica (L.) Del.	*Mimosaceae*	t	X	X
Acacia nubica Benth.	*Mimosaceae*	s	X	X
Acacia reficiens Wawra	*Mimosaceae*	s	X	X
Acacia senegal (L.) Willd.	*Mimosaceae*	s	X	X
Acacia tortilis (Forssk.) Hayne	*Mimosaceae*	t	X	X
Acacia zanzibarica (S.Moofe) Taub.	*Mimosaceae*	s	X	X
Albizia anthelimintica Brongn.	*Mimosaceae*	s	X	X
Newtonia hildebranddtii (Vatke) Torre var. hildebrandtii	*Mimosaceae*	t		X
Ficus ingens (Miq.) Miq.	*Moraceae*		X	
Commicarpus stellatus (Wight) Berhaut	*Nyctaginaceae*	h		X
Coccinia grandis (L.) Voigt	*Nyctaginaceae*	h		X

Ochna inermis (Forsk.) Schweinf.	*Ochnaceae*	h	X	X
Ochna inermis (Forsk.) Schweinf.	*Ochnaceae*	h		X
Opilia campestris Engl.	*Opiliaceae*	s	X	
Erythrina melanacantha Taub.	*Papilionaceae*	s	X	X
Indogofera arrecta A. Rich.	*Papilionaceae*	h	X	X
Indigofera hochstetteri Bak.	*Papilionaceae*	h		X
Crotalaria agatiflora Schweinf.	*Papilionaceae*	h	X	
Indigofera volkensii Taub.	*Papilionaceae*	h	X	X
Indigofera spinosa Forsk	*Papilionaceae*	h	X	X
Sesbania sericea (Willd.) Link.	*Papilionaceae*	h	X	X
Stylosanthes fruticosa (Retz.) Alston	*Papilionaceae*	h		X
Tephrosia pumila (Lam.) Pers.	*Papilionaceae*	h	X	X
Tephrosia subtriflora Bak.	*Papilionaceae*	h	X	X
Tephrosia villosa (L.) Pers.	*Papilionaceae*	h	X	X
Tephrosia noctiflora Bak.	*Papilionaceae*	h	X	X
Platycelythium voense (Engl.) Willd	*Papilionaceae*	t		X
Adenia globosa Engl.	*Passifloraceae*	s		X
Sesamothamnus rivae Engl.	*Pedaliaceae*	s	X	X
Polygala sphenoptera Fres.	*Polygalaceae*	h		X
Calyprotheca taitensis Pax & Vatke) Brenan	*Portulacaceae*	s		X
Portulaca oleracea L.	*Portulacaceae*	h		X
Talinum caffrum (Thunb.) EcK. & Zey.	*Portulacaceae*	h		X
Tallinum portulacifolium (Forsk.) Schweinf	*Portulacaceae*	h		X
Calyptrotheca somalensis Gilg	*Portulacaceae*	s	X	
Helinus integrifolius (Lam.) Kuntze	*Rhamnaceae*	s		X
Dirichletia glaucescens Hiern	*Rubiaceae*	s		X
Gardenia jovis-tonantis (Welw.) Hiern	*Rubiaceae*	s		X
Hymenodictyon parvifolium Oliv.	*Rubiaceae*	s		X
Meyna tetraphylla (Hiern) Robyns	*Rubiaceae*	s		X
Xeromphis keniensis Tennant sp. Nov.	*Rubiaceae*	s	X	X
Tarenna graveolens (S.Moore) Brem.	*Rubiaceae*	s	X	X
Tennantia sennii (Chiov.) Verdc. & Bridson	*Rubiaceae*	s	X	
Vepris glomerata (F.Hoffm.) Engl.	*Rutaceae*	s		X
Zanthoxylum chalybeum Engl.	*Rutaceae*	s	X	
Dobera glabra (Forssk.) Poir.	*Salvadoraceae*	t	X	X
Dobera loranthifolia (Warb.) Harms	*Salvadoraceae*	t	X	
Salvadora persica L.	*Salvadoraceae*	t	X	X
Allophylus rubifolius (A.Rich.) Engl.	*Sapiudaceae*	s	X	
Manilkara mochisia (Bak.) Dubard	*Sapotaceae*	t	X	X
Lycium europaeum L.	*Solanaceae*	s		X
Solanum hastifolium Dunal	*Solanaceae*	h	X	
Solanum somalense Franch.	*Solanaceae*	h	X	
Solanum teitense Vatke	*Solanaceae*	h		X
Solanum incanum L.	*Solanaceae*	s	X	X
Melhania taylori Bak.f.	*Sterculiaceae*	s	X	X
Waltheria indica L.	*Sterculiaceae*	s		X

Sterculia africana (Lour.) Fiori	*Sterculiaceae*	h	X	X
Sterculia stenocarpa H. Winkl.	*Sterculiaceae*	h		X
Grewia bicolor Juss	*Tiliaceae*	s	X	X
Grewia forbesii Mast.	*Tiliaceae*	s		X
Grewia lilacina K.Schum	*Tiliaceae*	s		X
Grewia nematopus K. Schum.	*Tiliaceae*	s	X	X
Grewia stuhlmannii K. Schum.	*Tiliaceae*	S	X	
Grewia tenex (Forssk.) Fiori	*Tiliaceae*	s	X	X
Grewia tembensis Fres var. kakothamnos (K.Schum.)	*Tiliaceae*	s	X	X
Grewia villosa Willd.	*Tiliaceae*	s	X	X
Triumfetta flavescens A.Rich.	*Tiliaceae*	s		X
Premna resinosa (Hochst.) Shauer	*Verbenaceae*	s	X	X
Premna hildebrandtii Guerke	*Verbenaceae*	s		X
Cissus rotundifolia (Forssk.) Vahl	*Vitaceae*	l	X	
Rhoicissus revoilii Planch.	*Vitaceae*	l	X	
Tribulus terrestris L.	*Zygophyllaceae*	h		X
*Alovelus**		h	X	X
*Libia caviodora **		h	X	X
*Opuntia opposita**		s		X
Prosopis chilensis		s	X	
Circostema		h	X	X

Appendix 2: A checklist of mammals and bird species commonly observed in Tsavo and Garissa hirola ranges. X = Observed, 'Blank' = Not observed.

Species/Classification	Scientific Name	Observed in	
		Garissa	Tsavo
Primates			
Senegal Galago	*Galago senegalensis*	X	X
Vervet Monkey	*Cercopithecus aethiops*	X	X
Yellow Baboon	*Papio cynocephalus*	X	X
Carnivora			
Black-backed Jackal	*Canis mesomelas*		X
Bat-eared Fox	*Otocyon megalotis*		X
Zorilla	*Ictonyx congica*		X
Honey Badger	*Mellivora capensis*	X	X
African Civet	*Civettictis civetta*	X	X
Small-spotted Genet	*Genetta genetta*	X	X
Slender Mongoose	*Herpestes sanguinea*		X
Bushy-tailed Mongoose	*Bdeogale crassicauda*	X	X
Dwarf Mongoose	*Helogale parvula*		X
White-tailed Mongoose	*Ichneumia albicauda*	X	X
Banded Mongoose	*Mungos mungo*		X
Spotted Hyaena	*Crocuta crocuta*	X	X
Aardwolf	*Proteles cristatus*	X	X
Cheetah	*Acinonyx jubatus*		X
Caracal	*Felis caracal*		X
Serval	*Felis serval*		X
African Wild Cat	*Felis sylverstris*	X	X
Lion	*Panthera leo*	X	X
Leopard	*Panthera pardus*		X
African hunting dog	*Licaon pictus*	X	X
Proboscidae			
African Elephant	*Loxodonta africana*	X	X
Perissodactyla			
Common Zebra	*Equus burchellii*	X	X
Grevy's Zebra	*Equus grevyi*	X	X
Black rhino	*Diceros bicornis michaeli*		X
Hyracoidea			
East African Rock Hyrax	*Proavia jonstoni*		X
Bush Hyrax	*Heterohyrax spp.*		X
Tubulidentata			
Aardvark	*Orycteropus afer*		X

PHOLIDOTA			
Cape Pangolin	*Manis temminckii*		X
Artiodactyla			
Warthog	*Phacocherus africanus*	X	X
Bushpig	*Potamochoerus porcus*	X	
Masai giraffe	*Giraffa camelopardalis m.*		X
Coke's hartebeest	*Alcelaphus buselaphus*		X
Grant's gazelle	*Gazella grantii*	X	X
Fringe-eared Oryx	*Oryx beisa callotis*	X	X
Eland	*Taurotragus oryx*	X	X
Impala	*Aepycerus melampus*	X	X
Waterbuck	*Kobus ellipsiprimnus*	X	X
Buffalo	*Syncerus caffer*	X	X
Topi	*Damaliscus korrigum*	X	X
Hirola	*Beatragus hunteri*	X	X
Gerenuk	*Litocranius walleri*	X	X
Steinbuck	*Raphicerus campestris*		X
Lesser kudu	*Tragelaphus imberbis*	X	X
Dik dik	*Madoqua kirkii*	X	X
Hippopotamus	*Hippopotamus amphibius*	X	X
Reticulated giraffe	*Giraffa camelopardalis r.*	X	X
Common birds			
Somali ostrich	*Struthio camelus molybdophanes*	X	X
Sacred ibis	*Threskiornis aethiopicus*	X	X
Hadada ibis	*Hagedashia hagedash*	X	X
Egyptian goose	*Alopochen aegyptiaeus*	X	X
Secretary bird	*Sagittarius serpentarius*	X	X
White-backed vulture	*Pseudogyps africanus*		X
Egyptian vulture	*Neophron percnopterus*	X	X
Verreaux's eagle	*Aquila verreauxii*		X
Bateleur	*Terathopius ecaudatus*	X	X
African goshawk	*Accipitor badius*	X	X
Tawny eagle	*Aquila rapax*	X	X
Greater kestrel	*Falco rupicoloides*		X
Crested francolin	*Francolin sephaena*		X
Yellow-necked spurfowl	*Pternistis leucoscepus*		X
Quail	*Coturnix coturnix*	X	X
Helmeted guinea-fowl	*Numida mitrata*	X	X
Kenya crested Guinea-fowl	*Cuttera pucherani*	X	X
Vulturine Guinea-fowl	*Acryllium vulturinum*	X	X
South African Crowned Crane	*Balearica regulorum*	X	X
Kori Bustard	*Ardeotis kori*	X	X
Crested bustard	*Lophotis ruficrista*		X
Black-bellied Bustard	*Lissotis melanogaster*	X	X

Chestnut-bellied Sandgrouse	*Pterocles exustus*	X	X
Black-faced Sandgrouse	*Eremialector decoratus*	X	X
Ring-necked Dove	*Streptopelia capicola*	X	X
Namaqua Dove	*Oena capensis*	X	X
Green pigeon	*Treron australis*	X	
European Rollar	*Coracias garrulus*		X
Lilac-breasted Roller	*Coracias caudata*		X
Pied Kingfisher	*Ceryle rudis*	X	X
Carmine Bee eater	*Merops nubicus*	X	X
Red-billed Hornbill	*Tockus erythrorhynchus*	X	X
Ground Hornbill	*Bucorvus leadbeateri*	X	X
South African Hoopoe	*Upupa africana*	X	X
Pearl-spotted Owlet	*Glaucidium perlatum*	X	X
Verreaux's eagle-owl	*Bubo lecteus*	X	X
Speckled Mousebird	*Colius striatus*	X	X
Blue-eared glossy Starling	*Lamprocolius chalybaeus*	X	X
Superb Starling	*Spreo superbus*	X	X
Red-billed Oxpecker	*Buphagus erythrorhynchus*	X	X
White-headed Buffalo Weaver	*Dinemellia dinemelli*	X	X
Red-billied Buffalo-weaver	*Bubalornis niger*		X

Appendix 3: Summary of population ecology and reproductive biology of hirola.

Factors	Hirola data from Tsavo, Garissa and Dvur Kralove n.Zoo
Population size	Tsavo 71.1±9.3 SD, Garissa 672 (range 259-1085)
Family group size	Tsavo 7.3±2.6 SD, Garissa 7.9±1.15 SD
Female sexual maturity	One female from the DH family group, monitored and ear-notched since birth, was observed mating at an age of 23 months. Data from captivity (Smielowski, 1987) shows that hirola females mated first at between 15 and 24 months. Coke's hartebeest (Stanley-Price, 1974) mated at 3 years.
Male sexual maturity	One male from the M2 family group, monitored and ear-notched since birth was mature and solitary at 28 months and formed a family group at 32 months age. Data from captivity (Smielownski, 1987) showed that males attempted mating at between 20 months 3 days – 24 months 4 days. Data on Coke's hartebeest (Stanley-Price, 1974) indicated that males were mature at 3 years and able to mate after 4 year.
Gestation	Field observation on hirola in Tsavo indicated that most mating occurred between March and April. Peak calving occurred between October and November. This gives an estimated gestation period of between 7 and 8 months. Data from captivity (Smielownski, 1987) indicates that gestation lasted about 7.5 months. Coke's hartebeest has a gestation period of 8 months (Gosling, 1974, Kingdon, 1982).
Weaning	The frequency of suckling among hirola in Tsavo East N.P. declined after about 3 months.
Female maternal attachment	Observation on hirola groups in Tsavo indicated that female hirola separated from their natal groups at about 9-14 months of age. Data from Coke's hartebeest indicate that females stayed with the mother up to about 3 years age (Stanley-Price, 1974).
Male maternal attachment	Observation in Tsavo showed that male hirola separated from family groups at between 6 and 12 months of age.
Longevity	Assuming that the young hirola captured in August 1971 and taken to Dvur Kralove n.L (Smielowski, 1987) Zoo were yearlings, one of the males in this zoo lived for 11 years, 3 months.
Breeding system	Sex ratios for both Garissa and Tsavo indicated that there are generally more females than males. Hirola family groups with single males and a number of females occurred in both Tsavo and Garissa, indicating a polygynous breeding system.
Males access to females	An injured male from VR group in Tsavo East managed to remain with a family group for 1 year. Further, few changes of group males occurred. This indicates that healthy males in family groups may exclude lone males from access to females for long periods.
Litter size	Hirola females gave birth to only one young, as in all other alcelaphines.
Calving rate	In Tsavo, the ratio of observed calves to adult females was

	51%±1.7%, but this was known to be an underestimate and a more realistic assumption may be that all or nearly all females calved. In Garissa, the ratio of observed calves to adult females was 46%; again, this was probably an underestimate. In captivity, all adult females except one calved annually (Smielowski, 1987).
Juvenile mortality	Due to early dispersal from natal groups by young hirola, it was not possible to monitor juvenile mortality up to 1 year's age. However, the data collected indicated that 40.5±13.8% survived to 6 months of age. In captivity, 31.7% survived to one year (n=19, Smielowski, 1987). Gosling (1974) observed a 30% mortality between 0-1 year among Coke's hartebeest. In Tsavo, assuming that all females calved, 69.8% may have died before 6 months of age.
Adult mortality	Data from 52 individually identified hirola indicated an annual adult mortality rate of 11.9%±1.9.
Recruitment	Comparing the number of calves born per group and the number of individuals observed at the age of about 2 years in the Tsavo hirola population, about 34.9% may have survived to this age. Assuming that all females calved, 18.0% of calves born survived to the age of 2 years.
Population sex ratio	Data from the hirola population in Tsavo indicated a sex ratio of 1:2.7, while that in Garissa was 1:3.2 M:F. These ratios were not significantly different from unity.
Adult sex ratio	The adult sex ratio was 1:3.8 in Tsavo and 1:4.4 M:F in Garissa. In Coke's hartebeest, young males are expelled from territories at from 10 months to over 2 years of age; when expelled at young ages they suffer higher mortality rates and this partly accounts for the adult sex ratio of about 1:1.5 (M:F)(Gosling, 1974).
Calf sex ratio	The calf sex ratio in Tsavo was 1:1.85, while that in Garissa was 1:1.9 M:F. In captivity, the calf sex ratio was 1:1.7 (n=19, Smielowski, 1987).
Effect of inbreeding	One known female in Tsavo rejoined her natal group and was mated by her father. Hirola groups rarely changed males.
Home range size	Observation on 9 hirola groups for 4 years indicated an average home range of 81.5±38.4 km^2.
Core area size	Hirola group core areas in Tsavo were about 3.45±1.28 km^2.
Diseases	4 disease outbreaks occurred in the natural range (Garissa) between 1970 and 2000. During this period, the population declined from 14000 to 1000. The probability of occurrence was thus about 13.3% per annum. The highest population decline after a disease episode was between 1983 and 1985 when the population declined from 10,843 to 1,595 (85.3% decline).
Drought	6 droughts have occurred in the hirola natural range between 1970 and 2000. During this period, the hirola population declined from 14000 to 1000. The probability of occurrence of a drought is thus about 20% per annum (occurring every 7-8 years).