

## RESEARCH ARTICLE

# Diet, Foraging, and Use of Space in Wild Golden-Headed Lion Tamarins

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Lion tamarins (Callitrichidae: *Leontopithecus*) are small frugi-faunivores that defend large home ranges. We describe results from the first long-term investigation of wild golden-headed lion tamarins (*L. chrysomelas*; GHLTs). We present data about activity budgets, daily activity cycles, diet, daily path length, home range size, home range overlap, and territorial encounters for three groups of GHLTs that were studied for 1.5–2.5 years in Una Biological Reserve, Bahia State, Brazil, an area characterized by aseasonal rainfall. We compare our results to those from other studies of lion tamarins to identify factors that may influence foraging and ranging patterns in this genus. Ripe fruit, nectar, insects, and small vertebrates were the primary components of the GHLT diet, and gums were rarely eaten. Fruit comprised the majority of plant feeding bouts, and the GHLTs ate at least 79 different species of plants from 32 families. The most common foraging sites for animal prey were epiphytic bromeliads. The GHLTs defended large home ranges averaging 123 ha, but showed strong affinities for core areas, spending 50% of their time in approximately 11% of their home range. Encounters with neighboring groups averaged two encounters every 9 days, and they were always aggressive. Data about time budgets and daily activity cycles reveal that the GHLTs spent most of their time foraging for resources or traveling between foraging sites distributed throughout their home ranges. The GHLTs spent much less time consuming exudates compared to lion tamarins in more seasonal environments. Additionally, the GHLTs had much larger home ranges than golden lion tamarins (*L. rosalia*), and did not engage in territorial encounters as frequently as *L. rosalia*. GHLT ranging patterns appear to be strongly influenced by resource acquisition and, to a lesser extent, by resource defense. *Am. J. Primatol.* 63:1–15, 2004. © 2004 Wiley-Liss, Inc.

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## INTRODUCTION

Diet is interrelated with many characteristics of territoriality, including the size of the home range, the ranging patterns, and the degree to which home ranges can be economically defended from intruders [Brown, 1964; Grant et al., 1992; McNab, 1963]. Primates exhibit particularly broad inter- and intraspecific variation in home range size and territorial behavior [Cheney, 1987; Clutton-Brock & Harvey, 1977; Grant et al., 1992; Mitani & Rodman, 1979]. Among primates, frugivores and insectivores generally have larger home ranges and travel longer daily paths compared to folivores, in order to obtain clumped, unpredictable, and/or easily depleted resources [Clutton-Brock & Harvey, 1977; Oates, 1987].

Lion tamarins (Callitrichidae: *Leontopithecus*) are small frugi-faunivores that defend relatively large home ranges (40–320 ha [Rylands, 1993]) in relation to their small body size (500–550 g). There are four species of lion tamarins: golden lion tamarins (*L. rosalia*), golden-headed lion tamarins (*L. chrysomelas*), black lion tamarins (*L. chrysopygus*), and black-faced lion tamarins (*L. caissarra*). These species are all endemic to different regions within the Atlantic Forest, Brazil. A review across lion tamarin studies indicates the average group size is four to seven individuals, and group sizes range from two to 11 individuals [Baker et al., 2002]. Their diet consists of ripe fruits, flowers, nectar, insects, small vertebrates, and gums [Kierulff et al., 2002; Rylands, 1993]. Lion tamarins generally use manipulative foraging to locate animal prey concealed in sites such as epiphytic bromeliads and tree bark [Rylands, 1996]. Home ranges may be large in order to provide a sufficient amount of easily depletable fruit and prey foraging sites over the long term [Dietz et al., 1997; Peres, 1989b]. In addition to being affected by the animals' need to meet current and future energy requirements, ranging behaviors may also be influenced by the need to defend boundaries [Peres, 2000]. At least two of the four species of lion tamarins are highly territorial and maintain boundaries through aggressive encounters with neighboring groups [Dietz et al., 1996; Peres, 1989b]. In contrast to more traditional definitions of territoriality [Schoener, 1968], space is not necessarily used exclusively, and lion tamarins groups may occupy areas that overlap to some extent at their borders [Peres, 2000].

In this study, we investigated patterns of resource acquisition, ranging, and territorial defense in golden-headed lion tamarins (GHLTs) in southern Bahia, Brazil. Little is known about GHLT behavior in the wild, with the exception of observations of one GHLT group that was studied for a 3-month period at Lemos Maia Experimental Station, Brazil [Rylands, 1989]. Specifically, we present data on activity budgets, daily activity cycles, diet, daily path length, home range size, home range overlap, and frequency of territorial encounters for three groups of GHLTs that were studied for 1.5–2.5 years in Una Biological Reserve, Brazil. We compare our findings to those available for other naturally occurring populations of lion tamarins. In particular, we emphasize similarities and differences in ranging behavior between GHLTs and golden lion tamarins (*L. rosalia*). Of the four *Leontopithecus* species, *L. rosalia* has been studied the longest and the most intensely. Such comparisons are valuable for increasing our understanding of the effect of demographic and environmental variations on lion tamarin foraging and ranging behavior [Kierulff et al., 2002].

## MATERIALS AND METHODS

### Study Site

We conducted our study at Una Biological Reserve in Southern Bahia, Brazil (15° 06'–12'S, 39° 02'–12'W). Una Reserve contains 7,059 ha of mature and regenerating forests, which are broadly characterized as lowland moist tropical forest [Mori, 1989]. The temperature in southern Bahia averages 24–25°C annually, and rainfall is aseasonal, averaging approximately 2,000 mm a year [Coimbra-Filho & Mittermeier, 1973; Mori, 1989].

### Data Collection

We documented the behavior and ranging patterns of 24 individuals from three groups of GHLTs: PIA (n = 8 individuals), ONÇ (n = 10), and ENT (n = 6). The age and sex composition of the groups varied according to the births, deaths, migrations, and maturation of young that occurred over the study period (Table I). The amount of degraded habitat differed between groups, with the ENT group ranging in mostly young secondary forest, and the PIA group ranging in mostly mature, tall forest [Raboy et al., 2004].

We followed the methods of Dietz et al. [1996] to capture and habituate individuals to the presence of human observers. We captured the tamarins in order to identify their age and sex class, dye-mark individuals, and fit two monkeys per group with radiotelemetry collars. Once the animals were habituated, B.E. Raboy and two field assistants observed each group one to three times a week throughout the study. Observers trained together for several months prior to the data collection period to ensure consistency of observations. The groups were followed on a schedule including two full and two partial observation days per week. On full days, the groups were followed from the time they left their sleeping site in the morning until they returned in the evening. The PIA, ONÇ, and ENT groups were observed for 92, 70, and 45 complete days, respectively, for a total of 991, 788, and 454 hr, respectively, for each group. On partial days, the groups were followed from 1100 hr until the tamarins entered their sleeping site, or from when they left their sleeping site until 1300 hr. The hours of overall observation (full and partial days) totaled 1,874, 1,596, and 1,048 for PIA, ONÇ, and ENT, respectively. The groups were observed throughout the year from the time they were habituated (June 1998, January

TABLE I. Age and Sex Distribution for Study Groups\*

Age and sex class	Group		
	PIA	ONÇ	ENT
Reproductive females	1–2	1	1
Non-reproductive adult females	0–1	0–1	0–1
Adult males	2–3	1–3	1–2
Sub-adult females	0–1	0–1	0
Sub-adult males	0–1	0	0
Juvenile females	0–1	0–2	0–2
Juvenile males	0	0	0
Total	3–7	2–7	2–6

\*Group compositions were not stable over the course of the study due to deaths, births, immigrations, emigrations, and maturation of young.

1999, and July 1999 for PIA, ONÇ, and ENT, respectively) to the end of the study (December 2000). The observers rotated their schedules to distribute observations across all groups.

We conducted group scans [Altmann, 1974] at 20-min intervals. The identity and behavior of all visible tamarins were scored at the first instance an individual was observed during a period of 4 min. We scored the following behaviors: traveling, remaining stationary, foraging for and eating fruit, foraging for and eating flowers, foraging for animals, eating animals, socializing, resting, and "other." We recorded resting behavior whenever the individual being observed was lying down or resting its chest on a substrate, and stationary behavior whenever the individual was not moving and not involved in other behavior categories. "Socializing" included affiliative social interactions (such as grooming, resting while in contact with one another, and playing) and aggressive social interactions (such as threats and fights both within and between groups). When individuals were scored foraging for animal prey, the foraging substrate was noted. Whenever possible, we identified the species of fruit, flower, nectar, or gum consumed by the GHLTs. Every 20 min we also estimated the geographic location of the group's center, using maps and marked trails as a reference. All occurrences of intergroup encounters were documented, including the time of occurrence and termination. Information on the plant species consumed and the frequency of intergroup territorial encounters were the only data obtained from both full and partial days of observation. All other data were obtained only from full days of observation.

## Analysis

We determined individual time budgets by dividing the number of scans for which an individual was scored in a particular behavior by the total number of scans collected for that individual during full days of observation. We calculated group time budgets by averaging time budgets of individuals within groups. Averages for the study population are presented as weighted means.

We determined daily activity cycles based on four categories of behavior: traveling, resting and social behavior; foraging for animal prey, and foraging for and feeding on plant material. For each individual, the proportion of total scans for each behavior class was determined for each hour they were observed outside of their sleeping sites, based on full days of observation. Records from 0500 and 1600 hr were infrequent because the individuals were most often in their sleeping sites at those times, and thus we grouped those hours with the adjacent hour classes. Hourly measures were averaged across individuals within groups to determine the groups' overall daily activity cycles.

We used group positions collected every 2 hr to estimate home range areas using the fixed-kernel method [Worton, 1989] in the Animal Movement Analysis Extension for ArcView GIS 3.2 software (Environmental Systems Research Institute, Inc., Redlands, CA [Hooge & Eichenlaub, 1997]). We used least-squares cross validation [Seaman & Powell, 1996] to determine the appropriate smoothing factor for the kernel analysis, and determined the 25%, 50%, 75%, and 95% home range contours. Each contour represents the probability that the group was found within the specified area. We defined home ranges as the area within the 95% contour, and core areas as the area within the 50% contour. To determine daily path lengths, we calculated the sum of straight-line distances traveled between 20-min observation periods on full days of observation.

**RESULTS**

**Activity Patterns**

The time budgets (Fig. 1) did not differ greatly among the study groups. Foraging and feeding behaviors accounted for 34%, 35%, and 24% of the time budgets of PIA, ONÇ, and ENT, respectively. For PIA and ONÇ, this proportion was greater than that of scans allocated to traveling. Foraging for animal prey represented the greatest proportion of foraging and feeding behaviors.

Although patterns of daily activity cycles differed among groups (Fig. 2), there were common trends. Individuals in two of three groups foraged for and ate plant material more commonly in the earliest hour than during other times of day. In contrast, searching for animal prey occurred less frequently in the first hour than at other times of the day for all three groups. After the first few hours of the day, the rate of foraging for plants or animals showed less fluctuation than traveling or resting and social behavior for all groups. In addition, for all three groups, traveling was most common at the beginning and end of the day, and resting and social behaviors were most frequent during the middle of the day, between 1100 and 1300 hr.

**Diet**

The GHLTs in our study ate at least 79 different species of plants from 32 families (Table II). Our observers were trained to recognize 54 of these at the species level. Of these readily identifiable plant species, 44, 42, and 22 were eaten by the PIA, ONÇ, and ENT groups, respectively. Although fruit comprised the

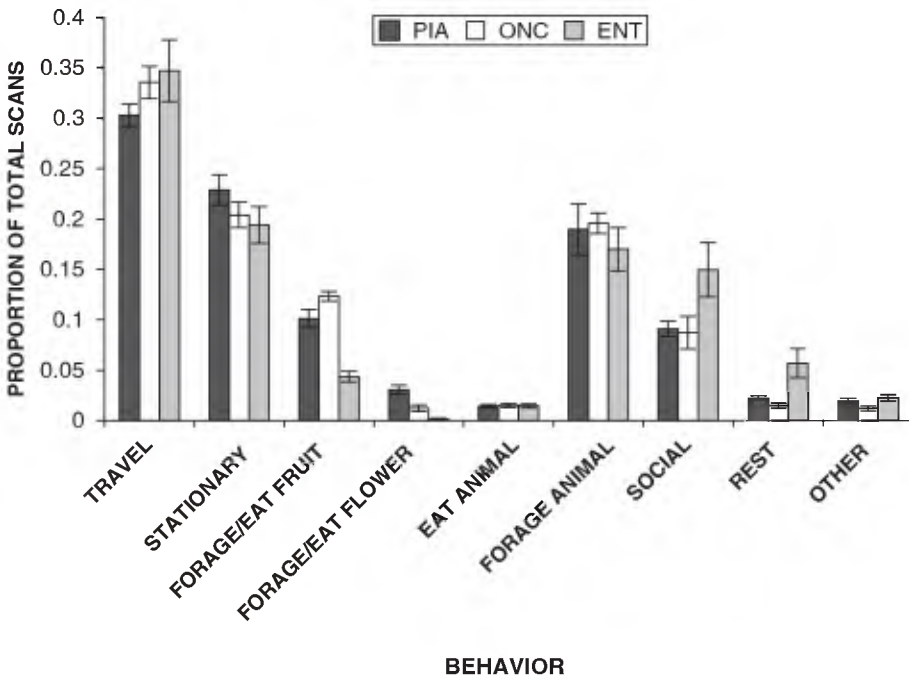


Fig. 1. Time budget of GHLT groups. Bars represent the mean ± standard error.

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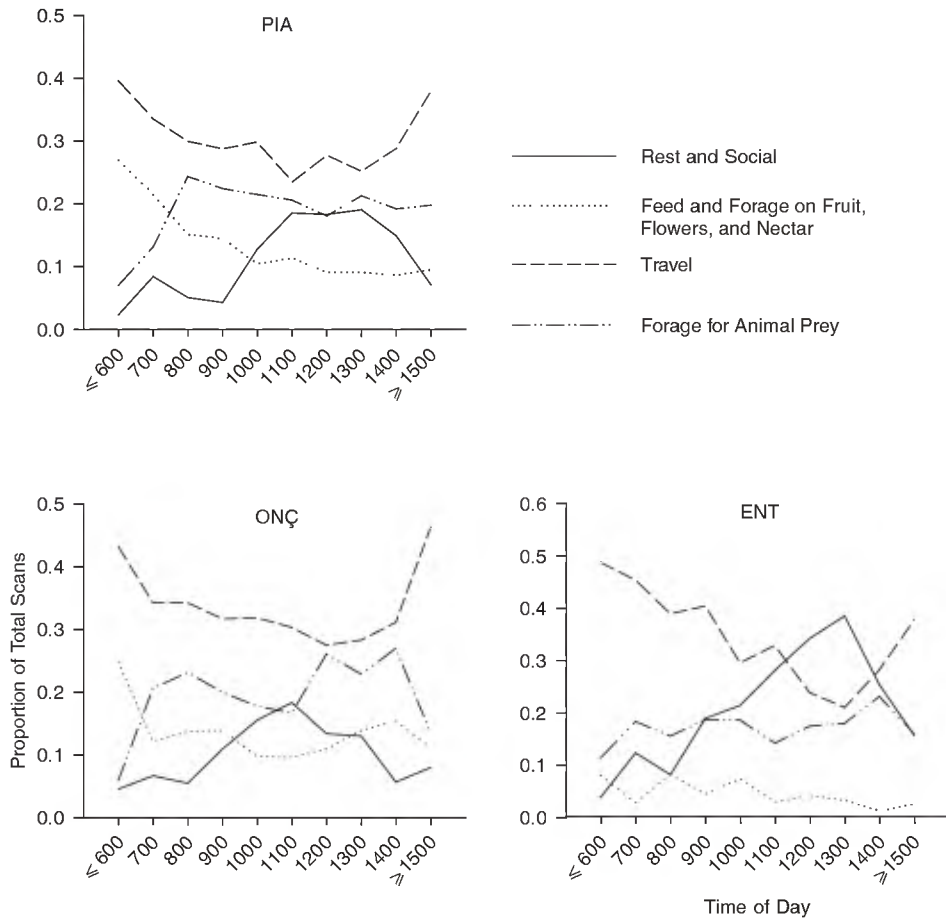


Fig. 2. Daily activity cycles for selected behaviors performed by GHLTs.

majority of plant feeding bouts, the GHLTs also ate nectar from five species of plants (*Symphonia globulifera*, *Manilkara af. salzmannii*, *M. longifolia*, *M. maxima*, and *M. rufula*) and the flowers of two species (*Hortia arborea* and one unidentified plant).

GHLTs were occasionally observed eating gum from the pods of *Parkia pendula* or obtained from holes that had been gouged in the branches and trunks of *P. pendula* by sympatric Wied's marmosets (*Callithrix kuhli*). Gum-eating was a rare behavior, occurring infrequently in PIA (the average proportion of time spent eating gum was 0.25% of the time budget or 0.74% of feeding and foraging scans), and it was not observed at all in the two other groups during scan-sampling. Gum-eating was grouped with "other" for the PIA time budget.

Epiphytic bromeliads were the foraging sites most commonly used by GHLTs in search of animal prey. The GHLTs also foraged in crevices and holes in trees, between palm fronds, and in leaf litter (Table III). We observed GHLTs eating insects (Orthoptera, Lepidoptera, and Coleoptera), insect larvae, spiders, snails, frogs, lizards, bird eggs, and small snakes.

## Foraging and Ranging Patterns of GHLTs / 7

**TABLE II. Plant Species Consumed by GHLTs**

Species	Family	Common name in Portuguese	Part consumed
<i>Aechmea</i> sp.	Bromeliaceae	Gravatá	Fr
af. <i>Myrciaria</i>	Myrtaceae	Murta	Fr
<i>Annona salzmanii</i> A.DC.	Annonaceae	Araticum/Pinha	Fr
<i>Artocarpus heterophyllus</i> Lamark	Moraceae	Jaca	Fr
<i>Brosimum rubescens</i> Taub.	Moraceae	Condurú	Fr
<i>Byrsonima laevigata</i> (Poir) DC.	Malpighiaceae	Murici	Fr
<i>Byrsonima</i> sp.	Malpighiaceae	Murici	Fr
<i>Coccoloba</i> sp.	Polygonaceae		Fr
<i>Compamanesia guaviroba</i> (DC.) Kiarer	Myrtaceae	Murta-guabiraba	Fr
<i>Cordia magnolifolia</i> Sham.	Boraginaceae	Baba-de-boi	Fr
<i>Croton macrobotrys</i> Baill.	Euphorbiaceae	Velame/Lava-prato	Fr
<i>Dialium guianense</i> (Aubl.) Sandw.	Caesalpinaceae	Gitai-preto	Fr
<i>Diplóon cuspidatum</i> (Hoehne) Cronquist	Sapotaceae	Bacumuxá	Fr
<i>Duguetia magnolioidea</i> Maas	Annonaceae	Pinha-brava	Fr
<i>Dyopyros</i> cf. <i>miltonii</i> P. Cavalcante	Ebenaceae		Fr
<i>Elaeis guianensis</i> Jacq.	Arecaceae	Dende	Fr
<i>Eugenia cerasiflora</i> Miquel	Myrtaceae	Murta	Fr
<i>Eugenia mandioccencis</i> Berg.	Myrtaceae		Fr
<i>Eugenia</i> sp.	Myrtaceae	Murta	Fr
<i>Ficus</i> sp. A	Moraceae	Gameleira	Fr
<i>Ficus</i> sp. B	Moraceae	Gameleira	Fr
<i>Ficus</i> sp. C	Moraceae	Gameleira	Fr
<i>Gomidesia</i> sp.	Myrtaceae	Murta	Fr
<i>Guapira</i> cf. <i>obtusata</i> (Jacq.) Little	Nyctaginaceae	Farinha-seca	Fr
<i>Guettarda platyphylla</i> Muell. Arg.	Rubiaceae	Arariba	Fr
<i>Gurania</i> sp.	Cucurbitaceae		Fr
<i>Henrietea succosa</i>	Melastomataceae	Mundururú-ferro	Fr
<i>Hortia arborea</i> Engl.	Rutaceae	Limao-bravo	Fl
<i>Hydrogaster trinerve</i> Kuhlman	Tiliaceae	Bomba-d'água	Fr
<i>Inga edulis</i> Mart.	Mimosaceae	Ingá-cipó	Fr
<i>Inga nutans</i> Mart.	Mimosaceae	Ingá	Fr
<i>Lacmellea aculeate</i> (Ducke) Monach	Apocynaceae	Chanana	Fr
<i>Licania</i> sp.	Chrysobalanaceae		Fr
<i>Mabea piriri</i> Aubl.	Euphorbiaceae	Leiteiro	Fl
<i>Macoubea guianensis</i> Aublet	Apocynaceae	Mucugê	Fr
<i>Macrolobium latifolium</i> Vog.	Caesalpinaceae	Óleo-cumumbá	Fr
<i>Manilkara</i> af. <i>salzmanii</i> (A.DC.) Lam.	Sapotaceae	Bapeba	Fr
<i>Manilkara logifolia</i> (DC.) Duband	Sapotaceae	Parajú	Ne
<i>Manilkara maxima</i> Penn.	Sapotaceae	Parajú/Massaranduba	Ne
<i>Manilkara rufula</i> (Miquel) Lam.	Sapotaceae	Massaranduba	Ne
<i>Manilkara</i> sp.	Sapotaceae	Parajú/Massaranduba	Ne

TABLE II. (continued)

Species	Family	Common name in Portuguese	Part consumed
<i>Marlierea cf. claussemiana</i> (Gardner) Kiaerskou	Myrtaceae		Fr
<i>Marlierea obversa</i> Legrand	Myrtaceae		Fr
<i>Mendoncia blanchetiana</i> Prof.	Mendonciaceae		Fr
<i>Miconia mirabilis</i> (Aubl.) L. Wms.	Melastomataceae	Mundururú	Fr
<i>Miconia rimalis</i> Naudin	Melastomataceae	Mundururú	Fr
<i>Micropholis guianensis</i> (DC.) Pierre	Sapotaceae	Bapeba-vermelha	Fr
<i>Micropholis venulosa</i> (Mart. & Eichl.) Pier	Sapotaceae	Bapeba	Fr
<i>Musa paradisiaca</i> L.	Musaceae	Banana-prata	Fr
<i>Myrcia acuminatissima</i> Berg.	Myrtaceae	Murta	Fr
<i>Myrcia cauliflora</i> (C.Mart.) O.Berg.	Myrtaceae	Jaboticaba	Fr
<i>Myrcia cf. bergiana</i> Berg.	Myrtaceae	Murta	Fr
<i>Myrcia rostrata</i> Berg.	Myrtaceae	Murta	Fr
<i>Myrcia</i> sp.	Myrtaceae	Araçá	Fr
<i>Myrcia thyrsoidea</i> Berg.	Myrtaceae	Araçá	Fr
<i>Myrciaria</i> sp.	Myrtaceae	Araçá	Fr
<i>Neea floribunda</i> Poepp. & Endl.	Nyctaginaceae		Fr
<i>Neomitranthes</i> sp.	Myrtaceae	Murta	Fr
<i>Ocotea nitida</i> (Meissn.) Rohwer	Lauraceae	Louro	Fr
<i>Parkia pendula</i> (Willd.) Benth.	Mimosaceae	Juerana-prego	Gu
<i>Passiflora quadrangularis</i> L.	Passifloraceae	Maracuja-acu	Fr
<i>Passiflora</i> sp.	Passifloraceae	Maracuja	Fr
<i>Philodendron willianisii</i> S.D. Hooker	Araceae	Imbé	Fr
<i>Pourouma</i> sp.	Moraceae	Tararanga	Fr
<i>Pourouma velutina</i> Miquel	Moraceae	Tararanga	Fr
<i>Pouteria ?bangii</i> (Rusby) Penn.	Sapotaceae	Bapeba	Fr
<i>Pradosia bahiensis</i> Teixeira	Sapotaceae	Jabute-de-cabóclo	Fr
<i>Psidium guajava</i> L.	Myrtaceae	Goiaba	Fr
<i>Rheedia</i> sp.	Clusiaceae	Bacupari	Fr
<i>Schoepfia af. obliquifolia</i> Turcz.	Olacaceae		Fr
<i>Simarouba amara</i> Aubl.	Simaroubaceae	Pau-paraiba	Fr
<i>Sprucella crassipedicellata</i> (Mart. & Endl.) Pires	Sapotaceae		Fr
<i>Stachyarrhena harley</i> Kirk.	Rubiaceae	Janipapo-bravo	Fr
<i>Symphonia globulifera</i> L.	Clusiaceae	Olandi	Ne
<i>Syzygium jambos</i> (L.) Alston	Myrtaceae	Jambo-branco	Fr
<i>Tabebuia elliptica</i> (DC.) Sandw	Bignoniaceae	Pau-d'arco/Ipê	Fr
<i>Talisia elephantipes</i> Sandw	Sapindaceae		Fr
<i>Tapirira guianensis</i> Aubl.	Anacardiaceae	Pau-pombo	Fr

Fr, fruit; Fl, flower; Ne, nectar; Gu, gum.

### Ranging Behavior

The groups traveled an average distance of  $1,753 \pm 211$  m/day (mean  $\pm$  SD). Home range size averaged 123.4 ha (130.4, 119.9, and 119.8 ha for PIA, ONÇ and ENT, respectively). The groups did not use their ranges evenly: PIA spent 50% of



TABLE III. Foraging Substrates Used\*

Foraging substrate	Group			
	PIA	ONÇ	ENT	Average ± SD
Bromeliads	86.9	66.1	35.1	76.5 ± 14.7
Tree bark and holes	9.6	16.3	31.9	19.2 ± 11.4
Palm fronds	1.8	12.8	29.6	14.7 ± 14.0
Dried leaves	1.5	3.8	2.9	2.7 ± 1.2
Other	0.2	1.0	0.5	0.6 ± 0.4

\*Numbers represent the percent of total scans in which an individual was documented foraging for animal prey in a particular substrate, averaged across individuals in a group.

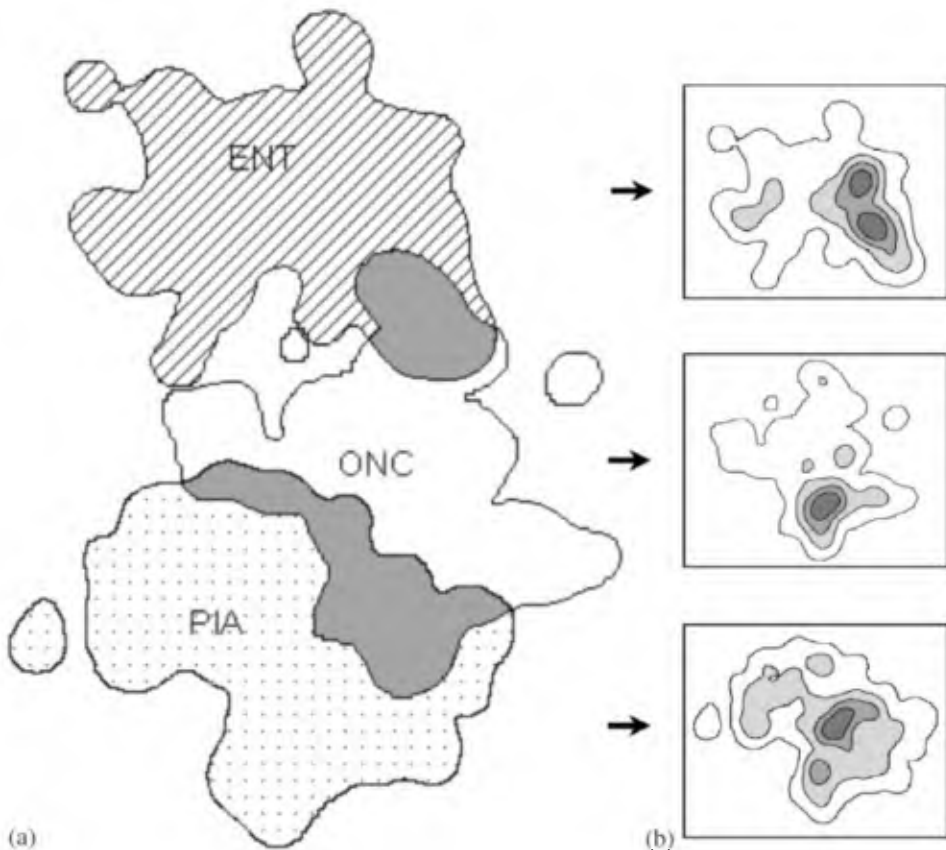


Fig. 3. a: Home ranges of the principal study groups. Gray areas represent overlap between groups. b: Home ranges showing the 25%, 50%, 75%, and 95% contours. The darkest areas represent the areas used most intensely (high use), and the lightest areas represent the areas used least intensely (low use). The “islands” seen in the PIA and ONÇ home ranges are created as a result of the methodology used to calculate home range size (see Materials and Methods for an explanation of the kernel density estimator).

the time in 9.6% of its range, ONÇ in 7.3%, and ENT in 15.6% (Fig. 3). All of the groups appeared to use the edges of their home ranges less frequently than other areas, although high-use areas were not necessarily centrally located. The overlaps between home ranges were 15.6 ha between PIA and ONÇ, and

12.0 ha between ENT and ONÇ. The home ranges of ENT and PIA did not overlap (Fig. 3).

Four groups (study and extrastudy) surrounded the ONÇ group, while PIA and ENT were surrounded by at least three groups each. Encounter rates with neighboring groups of GHLTs were 0.028, 0.025, and 0.012 encounters per hour of observation for PIA, ONÇ, and ENT, respectively. These rates included encounters with nonfocal groups, but did not include interactions with solitary individuals that were likely to disperse. The average encounter rate for all groups was 0.022 encounters per hour of observation, corresponding to two encounters every 9 days. Encounters were always aggressive, and included intensive bouts of long-calling [Ruiz-Miranda et al., 2002], chases, and fights between individuals of opposing groups.

## DISCUSSION

### Activity Patterns

The GHLTs spent most of the day traveling ( $33\% \pm 1.2\%$  of the time budget) and foraging and feeding ( $30\% \pm 3.3\%$ ), a pattern similar to those described for populations of lion tamarins at other sites [reviewed in Kierulff et al., 2002]. The investigation of daily activity cycles indicated that the GHLTs traveled and searched for and ate fruit, flowers, nectar, and animal prey throughout the day. Although there was a large degree of diurnal behavioral variation, the proportion of time the GHLTs allocated to particular behaviors showed a tendency to peak at different times during the day. The tendency of GHLTs to forage for fruits and flowers at higher rates during the first hour of the day is similar to that of many species of omnivorous primates that require easily digestible energy after the night fast [Oates, 1987], and has been documented in other lion tamarins [Peres, 1989; Rylands, 1982].

The high rates of traveling during the earliest and latest hours of the day suggest that the ranging behaviors of the GHLTs in Una may be constrained by limited choices of sleeping sites. GHLTs use a small number of sleeping sites on a regular basis—usually in tree cavities [Raboy, 2002]—and their locations are likely to influence ranging patterns early and late in the day. The GHLTs left their morning sleeping sites and usually moved rapidly to fruiting or flowering trees that were not necessarily located near their sleeping sites. Similarly, we saw GHLTs moving rapidly at the end of the day, over long distances, to reach sleeping sites.

### Diet

The GHLTs in Una ate a large variety of plants, even more than lion tamarins at other sites (Table IV). The forests of southern Bahia are known for their high levels of plant diversity [Thomas & Carvalho, 1997], and thus there may be more choices available for GHLTs. However, differences in the duration of studies may also contribute to the differences observed in the diversity of plant items consumed. The short durations of previous field studies may have resulted in underestimates of the number of plant species eaten, due to incomplete sampling. The number of plant species consumed correlated to study length across seven lion tamarin studies (Spearman's rank correlation,  $r = 0.821$ ,  $P = 0.023$ ).

*Myrtaceae* and *Sapotaceae* were the families of plants most commonly eaten by the GHLTs at Una, based on the numbers of different species consumed.

TABLE IV. Number of Different Plant Species Eaten by *Leontopithecus* spp.

Lion tamarin species	Plant species	Study	Study length	Number of lion tamarin groups studied
<i>L. caissara</i>	30	Prado [1999]	9 mo	1
<i>L. chrysopygus</i>	47	Passos [1999]	1 yr, 3 mo	1
<i>L. chrysopygus</i>	53	Valladares-Padua [1993]	2 yr, 2 mo	4
<i>L. chrysomelas</i>	79	Raboy and Dietz <sup>a</sup>	2 yr, 6 mo	3
<i>L. chrysomelas</i>	13	Rylands [1989]	3 mo	1
<i>L. rosalia</i>	64	Dietz et al. [1997]	1 yr, 7 mo	7
<i>L. rosalia</i>	54	Miller [2002]	1 yr	8

<sup>a</sup>Current study.

Previous studies also reported that *L. chrysopygus* [Valladares-Padua, 1993] and *L. caissara* [Prado, 1999] predominantly consumed plants from the *Myrtaceae* family, in terms of both frequency and number of species consumed. *Melastomataceae* is the preferred family for *L. rosalia* in Poço das Antas [Dietz et al., 1997], where most of the habitat is regenerating from previous deforestation [Coimbra-Filho & Mittermeier, 1977]. *Melastomataceae* was also abundant in the degraded and edge habitats of Una Reserve, but rare in mature habitats. Groups of GHLTs that ranged in more degraded areas frequently consumed fruits of this family, as well as *Tapirira guianensis* (Anacardiaceae), another prominent species in degraded areas.

Two of the three GHLT groups showed preferences for foraging for animal prey in bromeliads (Table III). When they are available, bromeliads are also the favored foraging substrates for GHLTs in Lemos Maia [Rylands, 1989], as well as for other species of lion tamarins [Dietz et al., 1997; Prado, 1999]. The bromeliads, or clusters of bromeliads at Una were up to 1.5 m in diameter, and contained an abundance of insects and small vertebrates nested among the bases of the leaf axils. Bromeliads were abundant in the mature forest of Una Reserve, but nearly absent in young secondary forests [Raboy et al., 2004]. In contrast to the other two groups, there were few bromeliads in the home range of ENT [Raboy et al., 2004]. This explains the elevated levels of searching for prey in bark, tree hollows, and in palm trees observed in the ENT group.

Lion tamarins are known to consume gum or fungi when fruit, flowers, and nectar are scarce. This was not the case for the GHLTs in Una Reserve. The consumption of gums by the GHLTs in Una was minimal compared to that observed for *L. chrysopygus* in Morro do Diabo Sate Park and Caetetus Ecological Station [Passos, 1999; Peres, 1989a; Valladares-Padua, 1993]. Gum represents up to 55% of the diet of *L. chrysopygus* in Caetetus, and is most commonly eaten in the dry season [Passos, 1999]. *L. chrysopygus* is the only lion tamarin that has been studied in semideciduous tropical forests. The pronounced seasonality in these forests [Rylands, 1993] may explain the greater use of gum resources by this species. *L. rosalia* in Poço das Antas was observed biting lianas to elicit the flow of exudates during a very dry period [Peres, 1989a]. In Superagui, *L. caissara* ate gums infrequently, but did eat fungal sporocarps, which were the most common item in the diet for 3 months of the dry season [Prado, 1999]. This pattern was not observed for GHLTs. The infrequent use of gum, a relatively low-quality dietary resource for tamarins [Power, 1996], by the GHLTs in Una may indicate that seasonal shortages of fruit flowers and nectar are less common at Una Reserve.

The GHLTs were observed eating fruits, flowers, and nectar all year long. Phenological studies are required in order to resolve this issue.

### Ranging Behavior

The home ranges of the GHLTs in Una are intermediate in size compared to other lion tamarin species [reviewed in Kierulff et al., 2002], but variation is also found within species. Rylands [1989] reported a home range size for one group of GHLTs in Lemos Maia of 36 ha, a considerably smaller area than that documented in the current study. Group size did not differ greatly between the two studies. The study group at Lemos Maia consisted of five individuals [Rylands, 1989], and the average group size at Una Reserve was 5.3 individuals [Raboy, 2002]. The forest structure of the two sites differed significantly (personal observation), and in contrast to groups at Una, the GHLT group in Lemos Maia ranged in a patch of forest that was almost entirely discontinuous from the neighboring forest [Rylands, 1982, 1996]. Differences in home range sizes may also result from variation in the age of the forests, or the availability and distribution of resources [Kierulff et al., 2002].

The GHLTs in our study used specific areas of their home ranges more frequently than others. Valladares-Padua [1993], Passos [1997], Peres [1989b], and Dietz et al. [1997] also noted location preferences for *L. chrysopygus* in Morro do Diabo State Park and Caetetus Ecological Station, and for *L. rosalia* in Poço das Antas Reserve. However, the relative location of preferred areas in home ranges varied across studies. All study groups at Una used core areas that were either in the center of the home range or shifted to one side. The preferential use of certain areas may be related to variation in habitat quality and resource density in these areas; however, this was not measured in the current study. *L. rosalia* in Poço das Antas used the periphery of its home range more than the center [Peres, 1989b]. However, even though *L. rosalia* spent more time in peripheral areas of their home range, they had less foraging success at the periphery than in their range center [Peres, 1989b]. Peres suggested that the frequent use of borders by *L. rosalia* was a form of interference and exploitative competition. The case of *L. rosalia* in Poço das Antas may be unique because the population density is high compared to other lion tamarins [Kierulff et al., 2002]. Competition for food resources and mating opportunities may be more intense for *L. rosalia* in areas of overlap, drawing groups to spend more time at their borders. However, the pattern observed for *L. rosalia* in Poço das Antas was based on only one study group [Peres, 1989], and thus it may not be indicative of the entire population.

Although the function of intergroup encounters in lion tamarins is not fully understood, it is likely that resource defense plays a large role [Peres, 2000]. The frequency of territorial encounters in *L. rosalia* documented by Peres [1989b] was approximately twice that documented for the GHLTs in the current study. In addition, Miller [2002] reported that eight groups of *L. rosalia* spent an average of 17% of their time engaged in encounters with neighboring groups—nearly four times the value for GHLT groups at Una. Encounter rates are not available for the other two *Leontopithecus* species. Differences in encounter rates and durations may be a function of population density and group composition, or they may reflect differences in home range sizes and patterns of resource distribution and defense.

Large home ranges may make it impractical for GHLTs to engage in defensive behaviors to the same extent as *L. rosalia*, which maintain much smaller home ranges. Interestingly, despite the marked difference in home range

size, group sizes are similar between the two species. Following Mitani and Rodman [1979], we calculated an index of defendability (daily path length  $\div$  diameter of the home range) for GHLTs in Una to be 1.40, and that of *L. rosalia* in Poço das Antas to be 1.76–2.05 (based on data from Dietz et al. [1997]). According to these measures, the home ranges of *L. rosalia* are more defendable than those of the GHLTs, which may explain why encounters occurred more frequently in *L. rosalia*. Although GHLTs travel approximately 30% (300 m) farther each day than *L. rosalia*, the GHLT territories are 175% larger. The chances a group of GHLTs would encounter a neighboring group are less than for *L. rosalia*. GHLTs do not allocate more time to resource defense relative to *L. rosalia*, as would be necessary to maintain similar levels of defense. The travel costs incurred by the GHLTs are likely to outweigh any benefits derived from more frequent resource-defense behaviors.

In conclusion, our results suggest that the need to search for food resources in relatively large home ranges, and the reliance on a limited number of sleeping sites are the main factors that shape GHLT ranging patterns at Una, more so than resource defense. Groups traveled extensively throughout their home ranges in search of animal prey, ripe fruit, flowers, and nectar. In contrast to many other callitrichid species, the GHLTs rarely consumed gum resources. Within larger home ranges, the GHLTs showed strong affinities for smaller core areas. Large home ranges may prohibit GHLTs from engaging in defensive behaviors to the same extent as lion tamarin species with smaller home ranges.

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