Foraging Ecology and Use of Space in Wild Golden Lion Tamarins *(Leontopithecus rosalia)*

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In this paper we describe the use of space and feeding ecology of seven groups of golden lion tamarins observed for a total of 2,164 hr in Poço das Antas Reserve, Rio de Janeiro, Brazil. Relative to habitat availability in the home ranges of these groups, lion tamarins spent more time than expected in relatively undisturbed swamp forests and less time than expected in more degraded hillside and pasture habitats. Home range area was correlated with group biomass but not group size. Golden lion tamarins fed primarily on fruits and small animal prey, but relied heavily on floral nectar during seasonal periods of relatively low fruit availability. Compared to other New World monkeys, lion tamarins used larger home range areas and exhibited longer daily path lengths than would be predicted by group biomass alone. We suggest that this pattern of foraging and use of space may be explained by the relatively greater availability of cryptic prey and their microhabitats in forests that are flooded and/or have closed canopies than in forests that are in earlier stages of succession where prey may be more susceptible to desiccation during the dry season. Am. J. Primatol. 41:289–305, 1997.   © 1997 Wiley-Liss, Inc.

INTRODUCTION

Lion tamarins (genus *Leontopithecus*) are the largest members of the family Callitrichidae and are currently represented by four chromatic forms endemic to remaining fragments of the Atlantic coastal and semideciduous forests of southeastern Brazil. Most of the information available on this genus comes from studies of captive specimens, ranging from the descriptive analyses of food-sharing [Brown & Mack, 1978], scent-marking [Kleiman & Mack, 1977], and arch-displays [Rathbun, 1979] to theoretical investigations of parent–offspring conflict [Kleiman, 1979].

Pioneering work on the natural history of *Leontopithecus* conducted by Coimbra-Filho [1969, 1970, 1977; Coimbra-Filho & Mittermeier, 1973] has been augmented by field studies on golden *(L. rosalia),* golden-headed *(L. chrysomelas),* black *(L. chrysopygus)* and the recently described black-faced lion tamarin *(L. caissara)* [see reviews in Kleiman et al., 1986; Rylands, 1993]. These studies focused on patterns of paternal care and the evolution of mating systems [Baker et al., 1993; Dietz & Baker, 1993], the economics of resource defense [Peres, 1986, 1989a, 1991a], and the conservation of small populations [Valladares-Padua, 1993; Kierulff, 1993], whereas lion tamarin feeding ecology and ranging behavior remain largely undescribed [but see Peres, 1985, 1986; Keuroghlian, 1990; Rylands, 1990; Passos, 1992; Valladares-Padua, 1993; Dietz et al., 1994a].

Here we report the combined results of three concurrent studies on the behavioral ecology of free-ranging groups of golden lion tamarins within the largest remaining population of this species. We present data on group composition, biomass, use of space, movements, habitat use, and diet for seven study groups using a relic forest habitat mosaic within this species' former geographic range. We then compare the ecology of this species to that of other forms of lion tamarins, and smaller callitrichids.

It has been argued by other authors [e.g., Coimbra-Filho, 1976a; Rylands, 1993] that lion tamarins require intact primary forest and are unable to adapt to severely degraded forests, especially those lacking tree-hole shelters and animal prey foraging sites. The study site where we conducted our research is a patchwork of degraded forests and contains little if any primary forest. Yet, most forest in the study site is inhabited by reproductive groups of golden lion tamarins. In light of the fact that the original geographic distribution of golden lion tamarins has been almost entirely deforested and remaining forest is severely fragmented and degraded, an improved understanding of the ecological processes that shape the use of space in this species may be particularly important from a conservation perspective.

METHODS
Study Area and Subjects

This study was conducted in the Reserva Biológica de Poço das Antas (hereafter, RBPA), a remnant of the coastal Atlantic forest of Silva Jardim, Rio de Janeiro, Brazil (22° 30´–33´S, 42° 15´–19´W). The reserve contains a patchwork of vegetation types largely resulting from the interplay of human disturbance and habitat topography. By 1975, deforestation and fires had reduced the amount of habitat suitable for *L. rosalia* to approximately 40% of RBPA's current area of ca. 5,900 ha, and no large tracts of pristine forest remained [Green, unpublished data; Magnanini, 1977; Ferreira et al., 1981].

Data presented here represent a synthesis of three independent but largely concurrent studies on seven groups of wildborn golden lion tamarins using three distinct study areas of RBPA (locally known as Rodolfo, Aristides, and Portuense study areas). We defined six distinct habitat types [see Peres, 1986] within the home ranges of the study groups in the three study areas:

Hilltop forest. This consisted of tall, selectively logged mature forest on dry ridge-top soils. The upper canopy was discontinuous with emergent species reaching 32 m in height. Compared with other vegetation types, the understory was sparse and the midstory lacked discernible boundaries.

Hillside forest. Disturbed forest occurring at elevations up to 120 m. A history of repeated clear-cutting exacerbated by soil instability resulted in a high

density of windfall gaps. Forest regeneration was probably retarded by steep terrain and water runoff. The undergrowth was denser than that of hilltop forest, and the forest stature was relatively low, with emergents reaching only 20 m.

Corridor. This was defined as a strip of lowland forest connecting hillside and swamp forests. The presence of exotic species, some of which were routinely used by tamarins (e.g., banana trees, *Musa* sp.), were clear signs of previous agricultural mosaics. Trees of up to 16 m were less common here than on hillside forests, and the undergrowth, consisting primarily of grasses and sedges, was less dense than that of inundated areas.

Swamp forest. This was characterized by continuous or seasonal standing water. The understory was denser than that of other vegetation types, usually with concentrations of arborescent palms (e.g., *Euterpe* and *Bactris*) and ferns. Large trees in these waterlogged areas supported heavy loads of lianas and epiphytes such as bromeliads and orchids.

Gingers (*Hedychium coronarium*, Zingiberaceae). These predominated in other poorly drained and water-saturated lowland areas, forming a continuous herbaceous layer of up to 2 m. The few scattered trees in these areas were heavily laden with epiphytes. Bromeliads were larger and more abundant here than in other plant communities.

Pasture. This was a vegetation type where only grasses and occasional shrubs were found. Previous conversion of forest to agricultural land and/or pasture resulted in this highly disturbed community, subsequently maintained by episodic wildfires [Oliveira, 1994].

The climate in Poço das Antas is seasonal with mean monthly precipitation ranging from less than 75 mm in June–July to over 250 mm in December–January. Yearly maximum temperatures of 39–41° occur in December–February, and minimum temperatures of 9–11° in June–August [Dietz et al., 1994a].

All tamarins in each of the study groups were captured, examined and individually marked with nyanzol dye [see Kleiman et al., 1986]. Transmitter collars were affixed to the heaviest member of each group. Members of the two groups in the Rodolfo study area (R1 and R2) and two groups in the Aristides study area (A1 and B) rapidly became habituated to observers, which enabled direct behavioral sampling. Data on three groups in the Portuense area (P10, P20 and P28) were limited to group locations and habitat use derived from triangulation, usually from distances less than 100 m.

Tamarins in the Rodolfo study area were observed for 914 hours between April–July 1984, and May–August 1985. Because of sampling discontinuity, changes in group composition, and a substantial shift in home range area, we consider these individuals as comprising two distinct groups (R1 and R2). The adult male and both juveniles in group R1 disappeared (i.e., emigrated or died) between the two years of study, and were replaced in R2 by two immigrant adult males [see Peres, 1986].

Two groups using the Aristides area were observed systematically for 1,001 hours between March and October 1984. Group A1 originally consisted of 8 individuals, but later split into two groups of four animals each. In December 1983, we captured a group of five tamarins (1 lactating female, 2 subadult males, and 2 infant females) in a small forest fragment adjacent to RBPA that was being converted to cattle pasture. We translocated these tamarins into an area with no resident groups in the center of the reserve. By April 1984, when observations on this group (hereafter, Group B) were initiated, the adult female and one of the subadult females had disappeared, and an adult male had joined the group. The remaining female produced two infants in March 1985 [see Pinder, 1986].

Finally, three groups in the Portuense area (P10, P20 and P28) were observed for a total of 249 hours between October 1983 and May 1985. Group P10 produced litters of two surviving males in April 1984, and of one surviving female in January 1985. The reproductive females of groups P20 and P28 bore twins in September and November 1984, respectively. Data on group size and composition are presented in Table I.

Procedure

Quantitative vegetation surveys were conducted along 2.7 km of existing trails in the Portuense and Rodolfo areas and in six 300 m^2 plots in the Aristides area. Each study area was divided into 0.25-ha quadrats which were assigned to a predominant vegetation category. A modified quadrant method (Cottam and Curtis, 1956] with sampling points at 15-m intervals along transects (Rodolfo and Portuense studies), or exhaustive sampling within 6 m × 50 m strips (Aristides study) was used to estimate the mean density, diversity, diameter (DBH) and height of trees (≥5 cm in DBH) and the dominant vegetation type in each quadrat. Species identifications of 350 and 1,345 trees occurring in the Rodolfo and Portuense sites, respectively, were conducted using reference collections at the Rio de Janeiro Botanical Garden.

In the Portuense area, we estimated the proportions of canopy cover and lianas using vertical sampling through monocular tubes of 2.5 cm diameter (N = 242 samples collected at 10 m intervals along transects). We used counts in 121 plots of 300 m^2 to estimate densities of bromeliads and tree holes potentially suitable for tamarins (an opening ≥7 cm × 10 cm) and we examined the reproductive phenology of 148 fruiting plants belonging to 20 species along 1.8 km of transects, determining the proportion of trees bearing ripe fruit on the first day of each month. Table II presents the results of the vegetation survey in the Portuense area. Results of vegetation studies in the Rodolfo and Aristides study areas have been presented elsewhere [Peres, 1985; Pinder, 1986]. The Aristides study areas differed from the others in that they did not contain mature hilltop forest and did contain about 30% "capoeira" (young secondary forest with 94% of trees with diameters of 5–15 cm, and tallest trees only 12–14 m in height) [Pinder, 1986].

Behavioral data were collected on a total of 106 days (55 dawn to dusk) for the Rodolfo groups and 301 days (23 dawn to dusk) for the Aristides groups. Group locations were based on direct visual observations and radiotelemetry triangulations at close range, using a 100 × 100 m trial system for orientation.

TABLE I. Composition, Biomass and Home Range Area of Seven Groups of Wild Golden Lion Tamarins.

Study group	Group size and composition[a]	Group biomass(kg)	Home range size(ha)
R1	Am, Af, SAf, Jm, Jf	2.675	36.2
R2	2Am, 2Af, Jf	2.883	48.8
A1	2Am, Af, SAm, 2SAf, 2Jm	4.190	73.0
B	Am, Af, Jm, Jf	1.937	21.3
P10	2Am, 2Af, Jm, Jf, Im	3.329	44.2
P20	Am, Af, SAf	1.739	46.5
P28	2Am, 2Af, Jm, Jf	3.151	46.4
Mean ± S.D.	5.43 ± 1.72	2.843 ± 0.838	45.20 ± 15.50

[a]Age classes: A, adult; SA, subadult; J, juvenile; and I, infant. Sex classes: f, female; m, male.

TABLE II. Structural and Floristic Characteristics of Four Habitat Types Used by Golden Lion Tamarins in the Portuense Study Area of RBPA (represented by means ± SD)[a]

	Habitat types			
Habitat variables	Hilltop forest (Ht)	Hillside forest (Hs)	Corridor forest (C)	Swamp and gingers (Sg)
Tree height (m)	10.1 ± 4.7 >C, Sg, HS	7.4 ± 2.9 >C, Sg	6.3 ± 3.0	6.6 ± 3.1
Tree diameter (cm)	15.7 ± 8.9 >C, Sg, Hs	11.4 ± 6.5 >C	9.9 ± 8.5	11.0 ± 8.0
Tree density (No. trees/0.1 ha)	99.6 ± 60.0	154.3 ± 63.3 >Ht	216.7 ± 109.4 >Ht	151.7 ± 116.7
Liana density (scale of 1 to 10)	1.49 ± 1.30 >C	1.26 ± 0.61 >C	1.07 ± 0.37	1.69 ± 1.53 >C
Tree hole density (No./ha)	39.8 ± 65.0 >Hs	12.7 ± 38.6	67.9 ± 134.6 >Hs	49.5 ± 63.7 >Hs
Bromeliad density (No./0.1 ha)	11.8 ± 51.2	16.5 ± 44.0	619.7 ± 1041.7 >Ht, Hs	48.4 ± 980.9 >Ht, Hs
Canopy cover (scale of 1 to 10)	7.94 ± 1.83 >Hs	7.13 ± 2.28	8.17 ± 2.17	7.83 ± 2.12
Tree species richness Tree species/no. trees)	.431 ± .157 >C	.405 ± .101 >C	.345 ± .174	.350 ± .271

[a]T-tests are used for statistical comparisons (shown on succeeding lines if $P < 0.05$) involving heights or diameters of trees, and Mann-Whitney U tests for all other comparisons.

Locations were recorded every 15 minutes, which allowed a maximum of 43 locations per study group on any given day. Direct observations accounted for 83% of 3,655 locations of the Rodolfo group; the remainder for that group were based on radiotelemetric triangulation. We assumed independence among locations of a group in a day.

We used 0.25-ha quadrats to estimate home range size. In all cases, the cumulative number of new quadrats entered by the study groups, as a function of observation time, reached an asymptote well before termination of the study, suggesting that relatively few quadrats had been missed due to sampling error [Odum and Kuenzeler, 1955]. Group locations were plotted on a 1:5,000 scale map to calculate the differential use of 0.25-ha quadrats in different habitats. We then used a Bonferroni Z statistic [Miller, 1966] to compare observed use with that expected on the basis of habitat type availability [Neu et al., 1974].

Quantification of activity states was accomplished by instantaneous samples of all visible members of a group at intervals of 10 min (Rodolfo groups, N = 9,248 samples; Aristides groups N = 5,039 samples). An animal was considered feeding on plant material when it was observed handling or chewing food of plant origin. Lion tamarins were classified as foraging when they were manually searching for or eating animal prey items. Foraging maneuvers included probing woody crevices, reaching down between the leaf axils of bromeliads, sifting through dead leaves in palm crowns, ripping apart bark of trees and lianas, and grabbing, biting, and turning over rotting materials.

Vouchers of plant food items were identified to species or genus at the Rio de Janeiro Botanical Gardens. Prey items, on the other hand, could rarely be identified because these were often small and rapidly ingested. Tamarins manually captured the majority of their animal prey items from small, discrete microhabitats. Thus, we noted the frequency of prey capture attempts, and in cases of

successful captures, the type of microhabitat (bromeliads, other epiphytes, palm crowns, palm leaf sheaths, woody crevices, lianas, vine tangles, tree bark, dead bamboo, rotten logs, and leaf litter on the ground).

RESULTS

Use of Space and Movements

Range locations for the Rodolfo groups shifted southward between the 1984 and 1985 study periods: 74.6% of the 1984 range overlapped with that for 1985; 55.4% of the 1985 range overlapped with that for 1984. Certain areas of intensive use were maintained by both groups between years of study, however, and no shifts in home range boundaries were noted for other study groups.

Home range size varied from 21.3 to 73 ha, and averaged 45.2 ± 15.5 ha (N = 7). The correlation between group size and home range size was not statistically significant (r_s = 0.65, P = 0.11, N = 7). However, there was a significant correlation between group biomass and home range (r_s = 0.76, P = 0.048, N = 7). The mean path length of complete days for the Rodolfo groups was 1,339 ± 256 m (N = 15) in 1984 and 1,553 ± 406 m (N = 40) in 1985. Longer path lengths in 1985 were consistent with the larger range size in that year.

The percent of time the Rodolfo and Aristides groups spent traveling ranged from 21.3 to 42.9 and averaged 33.5 ± 9.0 (Table III). Regular travel routes were typical between long-lasting, superabundant resources (e.g., *Symphonia* trees in flower), but were not discernible when animals exploited smaller food patches such as fruit trees producing small, ephemeral fruit crops (e.g., *Pouteria* and *Randia*) and microhabitats used for manipulative foraging. Rate of travel was highly variable. For example, the standard deviation of straight line distances traveled by the Rodolfo groups during 15-minute intervals was greater than the mean in 1984 (47.1 ± 55.6 m, N = 863) and 1985 (42.3 ± 51.1 m, N = 1,690).

Sleeping sites of *L. rosalia* consisted primarily of tree holes and occasionally of tangles of vines, palm crowns, and bamboo thickets. Maximum straight line distances between different consecutive sleeping sites for the Rodolfo group averaged 179 ± 193 m (N = 26) in 1984, and 210 ± 170 m (N = 49) in 1985.

TABLE III. Percent of Scan Samples in Nine Activity Classes for Four Groups of Wild Golden Lion Tamarins

Activity	Study group			
	R 1	R 2	A 1	B
Travel	42.9	34.7	21.3	35.2
Rest	24.7	19.4	18.8	7.4
Forage	9.2	13.2	30.3	26.1
Feed	15.3	21.6	nd[a]	nd
Feed on fruits	nd	nd	17.9	29.1
Long call	2.3	2.0	nd	nd
Intergroup interactions	nd	nd	11.6	2.2
Scent mark	2.5	2.1	nd	nd
Other	3.1	7.0	nd	nd
Number of scan samples	3,358	5,890	3,646	1,393

[a]Data not collected on this group for this activity category.

Habitat Selection

Tamarins used their ranges unevenly. For instance, the Rodolfo groups spent 90% of their time in 53% (1984) and 65% (1985) of their range areas. Use of habitat types by tamarins differed significantly from that expected based on habitat availability in the three study areas (Table IV). All study groups used swamp forest more frequently than expected. Hillside forest and pasture was used less frequently than expected. Tamarins spent most of daylight hours at lower elevations within their ranges. For instance, 86% of the diurnal locations for the Portuense groups were at elevations of less than 35 m above sea level (ca. 20 m above the level of standing water), a significantly greater proportion than that expected on the basis of availability (chi square = 23.85, $P < 0.001$).

Vegetative Diet

We identified 64 plant species in 23 families fed on by the tamarins of the Rodolfo and Aristides groups between April and October of 1984 and 1985 (Appendix). Fruit availability was highest at the beginning (40–41%) and the end of the wet season (36–38%), and lowest at the end of the dry season (25%), a pattern similar to that observed in most other Neotropical forests [e.g., Foster, 1982; Sabatier, 1985; Peres, 1994]. There were marked seasonal shifts in the use of ripe fruits and nectar, the two plant food categories most often consumed by tamarins. During the dry season, when ripe fruit availability was lowest, tamarins relied heavily on nectar from a few common plant species (e.g., *Symphonia globulifera*), whereas exudates, unripe fruits, and flowers were consumed less frequently. Tamarins occasionally fed on exposed exudates from trees and woody lianas, particularly in the dry season.

In 1984, the Rodolfo R1 group consumed ripe fruit pulp during 78.4% of the 608 observations in which it was observed feeding. The remaining foods used by the group consisted of animal prey (13.6%), unripe fruits (5.6%), plant exudates (1.5%), and fluids of unripe *Astrocaryum* palm nuts (0.9%). In 1985, floral nectar of *Symphonia globulifera* was heavily used, accounting for 43.4% of 1,271 feeding records. Other sources of nectar included *Combretum fruticosum* vines and *Monstera* sp. epiphytes, but these were relatively rare and ephemeral, and only occasionally taken. The remaining feeding records during this year of study on

TABLE IV. Habitat Selection by Six Groups of Golden Lion Tamarins, Comparing Observed Use of Habitat Types With That Expected Based on Habitat Availability

Habitat type	Study area and number of groups sampled								
	Rodolfo (2 groups)			Aristides (1 group)			Portuense(3 groups)		
	Obs.	Exp.	Dev.[a]	Obs.	Exp.	Dev.	Obs.	Exp.	Dev.
Hilltop	39	25	+	nd[b]	nd		6	14	—
Hillside	17	34	—	38	58	—	19	28	—
Corridor	25	24		nd	nd		29	17	+
Swamp	14	7	+	52	25	+	44	33	+
Gingers	5	7	—	8	6		nd	nd	
Pasture	1	3	—	0	5	—	2	7	—

[a]Significant deviation of the percent of observations in the habitat type from that expected based on its availability in the group's home range (chi–square test in which $\propto < 0.05$ and confidence intervals for estimating the simultaneous use of five habitats were adjusted using the Bonferroni z statistic [Neu et al. 1974]).
[b]No data available.

the Rodolfo group consisted of ripe fruit pulp (31.8%), unripe fruits (6.5%), animal prey (16.1%), plant exudates (1.3%), and flowers (0.4%).

Fruits used by tamarins were typically small, soft, and sweet, such as the berries of *Miconia candolleana* (ca. 4–8 mm diameter) and fruits of *Ficus* (ca. 10 mm). Larger fruits (e.g., *Genipa americana,* ca. 9 cm) were consumed occasionally. Whole seeds up to 1.5 cm in length, such as those of *Abuta sellowiana* vines, were almost invariably swallowed whole and later defecated. Fruits from two genera of trees in the Melastomataceae, *Clidemia* and *Miconia,* were the food items most frequently used by the Rodolfo group in 1984, particularly during the dry season, and by the two Aristides groups. Species of *Miconia* were widely distributed in hilltop forests and corridors, but were replaced on more humid soils at lower elevations by *Clidemia* shrubs, particularly in corridors. *Inga* and banana trees, located primarily along corridors, were used heavily by all study groups. Unripe fruits of *Euterpe edulis,* an arborescent palm common in swamp forests, were also used frequently in the dry season.

Tamarins appeared able to take advantage of a wide variety of fruits, many of which were patchily distributed and ephemeral in their fruiting pattern. For example, during the month of April, *Symphonia* was not consumed and *Miconia candolleana* accounted for 67% of feeding records of one Aristides group. In May, during the peak of flowering of *Symphonia,* consumption of *Miconia* dropped to 30% and *Symphonia* accounted for 30% of feeding records. In June, following the period of flowering of *Symphonia,* consumption of that species dropped to 0% of feeding records for the group. In contrast, *Miconia candolleana* and *Symphonia* were rare in the range of the other Aristides group and these species accounted for 0% and 2% of feeding records, respectively. The Aristides groups were observed feeding on a total of 40 species of plants and 80% of their vegetative diet was comprised of 13 species. The Rodolfo groups fed on at least 45 plant species. Six species accounted for 80% of their plant diet in 1984 and eight species in 1985.

Animal Prey

Small vertebrates (e.g., frogs *Hyla berthalutzae* and *Dendrophryniscus brevipollicatus* and small lizards and snakes), arthropods and occasional snails and nestling birds appeared to comprise the majority of animal prey items taken by study animals. Captures of mobile prey such as katydids or other orthopterans directly exposed on the foliage, or flying insects were relatively rare. In contrast, embedded and often cryptic prey items comprised over 98% of 317 observed captures by the Rodolfo groups. Insects accounted for the bulk of these prey items, and included adult orthopterans, and larvae of Coleoptera and Lepidoptera. Tamarins often fed on young and adult spiders plucked from web colonies in palm crowns and bamboo culms, but were rarely observed capturing and ingesting millipedes, centipedes, or aposematic hemipterans, despite their relative abundance. Occasional bouts of extensive salivation and/or vomiting followed captures of animal prey, suggesting that unpalatable and noxious arthropods had been ingested.

Typically, lion tamarins used their long fingers to manipulate substrates when searching for embedded prey. Microhabitats frequently searched included dead leaves, epiphytic growth, overhanging palm leaf sheaths, tree bark, vine tangles, hollow bamboo, and the humid debris accumulated in the funnel-like apical regions of *Euterpe* palms.

Bromeliads and palms, the microhabitats most frequently searched for animal prey, occurred primarily in lowland habitats and attained their highest den-

sities in swamp forest and ginger patches. *Astrocaryum* palms, the crowns of which were frequently used for foraging, were extremely common in hillside and hilltop forest. *Euterpe* palms, although also occurring on well-drained soils, were most abundant in waterlogged habitats.

We found a significant positive relationship between the frequency of foraging in specific microhabitats and the number of prey captures (Rodolfo's group in 1984: $r^2 = 0.69$, F = 26.5, P = 0.001; Rodolfo's groups in 1985: $r^2 = 0.75$, F = 36.5, P = 0.001). Mean capture success per microhabitat type was significantly higher for the R1 group in 1984 than the R2 group in 1985 (from 10.2% to 19.0%; t = 3.47, P = 0.004). However, there was no year-to-year variation in capture success derived from any given microhabitat (Wilcoxon signed-ranks test, T = 29, P > 0.05) or in the average number of captures per foraging bout (1984: 33.0%, 1985: 27.7%; t = 0.64, P > 0.05).

DISCUSSION

Leontopithecus and other large-bodied callitrichids, such as tamarins of the genus *Saguinus,* use the largest home ranges per unit of group biomass of all New World primates [e.g., Grant et al., 1992]. Range sizes of golden lion tamarins are considerably larger than those of *Cebuella* and *Callithrix,* comparable to those of *Saguinus* [Sussman & Kinzey, 1984; Snowdon & Soini, 1988], and smaller than those of other species of *Leontopithecus*. Black lion tamarins *(L. chrysopygus)* use home ranges of 100–200 ha [Carvalho & Carvalho, 1989; Keuroghlian, 1990; Valladares-Padua, 1993; Valladares-Padua & Cullen, 1994]. Golden-headed lion tamarins *(L. chrysomelas)* use home ranges of 40 ha at Lemos Maia Station [Rylands, 1990] and 66–93 ha at Una Biological Reserve [Dietz et al., 1994b, 1997], which are intermediate in size between those of *L. rosalia* and *L. chrysopygus.*

Range size estimates for mixed-species groups of tamarins *(S. fuscicollis avilapiresi* and *S. mystax pileatus)* in relatively uniform Amazonian terra firme forests also range between 150 and 200 ha [Peres, 1991b]. The similarity of spatial requirements between tamarins and lion tamarins may be attributed not only to their large body size and group biomass [Milton & May, 1976], but also to their convergent feeding ecology. Saddle-back tamarins *(Saguinus fuscicollis),* a species which exhibits a manipulative prey foraging pattern similar to that of lion tamarins [Peres, 1992], also uses comparably sized home ranges per unit of group mass, whether or not they occur in mixed-species groups [Snowdon & Soini, 1988; Peres, 1991b].

The distribution of animal prey available to lion tamarins is largely dependent upon the distribution of foraging microhabitats, which in turn is a function of microclimatic conditions and floristic composition. Within a group's home range in RBPA, discontinuous portions of permanently inundated swamp forest support the highest densities of foraging microhabitats and animal prey [Domingues et al., 1989], elevations at which tamarins concentrated much of their foraging for animal prey. As is the case with cottontop tamarins [*Saguinus oedipus*: Neyman, 1977], the long daily path lengths and large ranges of golden lion tamarins may result from foraging on animal prey that are locally abundant but patchily distributed. Indeed, recent habitat analysis taking into account a large number of *L. rosalia* groups indicates that size of a given home range is negatively correlated with the proportion of swamp forest occurring within it [Dietz & Baker, 1993].

Densities and distribution of keystone plant resources are also thought to regulate the size, habitat composition, and temporal stability of tamarin territories. Terborgh and Stern [1987] showed that the number of flowering *Combretum*

assimile vines, a species that occurs in floodplain forest and is a critical source of nectar for many frugivores during food-stressed times of the year, remain relatively constant across home ranges of saddle-back tamarin groups. In RBPA, the dry season role of *Combretum* nectar appears to be replaced by *Symphonia globulifera,* a common tree species in swamp forest. Nectar of the considerably rarer *Combretum fruticosum* vines is also taken by lion tamarins.

Callitrichids are markedly variable in their use of secondary or human-disturbed habitats. While a number of species of different genera are reported to favor forest edges [e.g., Dawson, 1976; Castro & Soini, 1977; Mittermeier & Coimbra-Filho, 1977], this tendency is more pronounced in *Cebuella* and *Callithrix* than in *Saguinus* and *Leontopithecus* [Peres, 1985, 1993b]. Indeed, some authors [e.g., Coimbra-Filho, 1976a; Rylands, 1993] suggest that lion tamarins require intact primary forest and are unable to adapt to severely degraded forests. For example, *L. chrysomelas* uses secondary growth only in proportion to its availability [Rylands, 1990] and *L. chrysopygus* apparently prefers mature forest on hills and seasonally flooded lowlands [Valladares-Padua, personal communication].

However in our study areas, virtually all forest was previously degraded and was occupied by reproductive groups of lion tamarins, demonstrating that primary or undisturbed forest is not an ecological necessity for *L. rosalia*. Further, all our study groups favored swamp forest and avoided hillside forest within their highly heterogeneous home ranges. Although the stature of hilltop and hillside forest was greater than that of swamp forest, the latter was rich in specific microhabitats used for foraging (e.g., bromeliads) and in animal prey [Domingues et al., 1989].

We suggest that the open and often discontinuous canopies of upland secondary forest, as rich as they are in fruit resources, retain insufficient humidity levels to support continuous high densities of embedded animal prey inherently susceptible to desiccation. Lowland forests on the other hand, provide high densities of appropriate microhabitats and high humidity levels essential for the year-round survival of small animal prey. Thus, it is the presence or absence of these ecological characteristics that regulates tamarins' use of space. Although Poço das Antas Reserve does not contain large tracts of primary forest, it is likely that their closed canopies would also offer high densities of foraging microhabitat and animal prey.

Unlike *Saguinus oedipus* which sleeps in tree crowns or in dense masses of vines [Neyman, 1977; Dawson, 1979], the almost exclusive use of tree cavities by *L. rosalia* [Coimbra-Filho, 1977; Peres, 1986] may further restrict their use of disturbed secondary forest [and see Rylands, 1993]. Use of tree cavities is also a consistent trait in *L. chrysomelas* in southern Bahian hyleae, where such cavities tend to be located in relatively tall primary forest [Rylands, 1990]. Although our estimates of tree hole density were lower in hillside forests regenerating from logging than in other forest types, we found no clear relationship between tree height or diameter and the presence of tree holes. For example, although hillside forests contained trees of larger diameter and height than those of corridor forests, hillside forest had a lower density of tree holes. Whether or not lion tamarins use nest holes in proportion to their abundance remains unknown.

Feeding Ecology

Previous studies of the diet of *Leontopithecus* [Coimbra-Filho, 1976b, 1981; Coimbra-Filho & Mittermeier, 1973] described lion tamarins as frugivore-faunivores specializing on relatively large-bodied prey items. In RBPA, bouts of

feeding on plants (as defined by visits to fruit trees) occurred less often than bouts of manipulative foraging (as defined by foraging maneuvers occurring in specific microhabitats). However, plant feeding bouts were of greater duration than those on animal prey, and supplied the majority of food volume.

With the exception of the smaller marmosets, which tend to specialize on exudates [e.g., *Callithrix* and *Cebuella:* Coimbra-Filho & Mittermeier, 1976; *Cebuella pygmaea:* Soini, 1982; *C. penicillata:* Lacher et al., 1984], fruits comprise the bulk of food items consumed by callitrichids. Exudates appear to represent an important, albeit supplementary, proportion of the diet of several tamarins [e.g., *Saguinus o. geoffroyi:* Garber 1984a; *S. nigricollis:* Izawa, 1978; *S. fuscicollis:* Izawa, 1975; Peres, 1993a; *S. imperator:* Terborgh, 1983; *Callimico goeldii:* Pook & Pook, 1981]. *L. chrysomelas* feeds on the gum exuded from the seed pods of *Parkia pendula* [Rylands, 1982]. Both *L. chrysopygus* and *L. rosalia* bite and lick liana exudates [Peres, 1989b; Passos, 1992; Valladares-Padua, 1993]. Unlike marmosets, however, tamarins tend to feed only opportunistically on exudates. Indeed, gouging while clinging vertically on tree trunks, a feeding pattern typical of "short-tusked" callitrichids [Coimbra-Filho & Mittermeier, 1977], was never observed in *L. rosalia* [cf. Peres, 1989b]. Although tamarins and lion tamarins are equipped with the specialized claw-like nails found in all callitrichids, they do not have the modified scraping dentition characteristic of true exudate feeders, such as certain prosimians [Charles-Dominique & Petter, 1980] and marmosets [Hershkovitz, 1977]. The greater concentration of what appears to be a more predictable and less seasonal resource base may explain the relatively smaller home range of areas of marmosets, compared to those of tamarins [reviewed by Ferrari & Lopes Ferrari, 1989].

Although primates are relatively inefficient nectar-feeders [Sussman & Raven, 1978], this resource provides an important seasonal source of sugars for callitrichids, particularly when fruits are most scarce. During the dry season of 1985 in which *Symphonia* trees flowered heavily and in synchrony, the Rodolfo group spent 44% of its feeding time in swamp forests consuming nectar of this species. *S. imperator* and *L. chrysomelas* have been observed licking inflorescences which produce copious amounts of nectar [Janson et al., 1981; Rylands, 1982]. Although Amazonian *S. globulifera* trees supply nectar to *S. fuscicollis* and *S. mystax* for only 1–3 months of the year [Rio Blanco, Peru: Garber, 1988; Urucu, Brazil: Peres, 1993a], lion tamarins used *Symphonia* nectar for 3–5 months in Southern Bahia, Brazil and at RBPA [Rylands, 1982; this study].

Saddle-back tamarins *(S. fuscicollis)* in southern Peru may also allocate as much as 78% of their dry season feeding time to *Combretum* vines [Terborgh & Sterm 1987]. *Combretum fruticosum* was ephemeral and at low density in RBPA, thus comprising a smaller proportion of the tamarins' diet than appears to be the case for primates elsewhere [Janson et al., 1981; Torres de Assumpção, 1981].

CONCLUSIONS

1. For seven groups of tamarins, group size, biomass and home range area averaged 5.43 individuals, 2.32 kg and 45.20 ha, respectively. Home range size was correlated with group biomass but not group size. Mean daily path length for two groups was 1,339 m and 1,553 m.

2. All forest in the Reserve was recovering from selective logging or clear cutting and all forest was inhabited by tamarins. Relative to availability of habitat types within home ranges, study groups used swamp forest more than expected and degraded hillside forests less than expected.

3. Animal prey taken by tamarins consisted largely of anthropods and small vertebrates. Nearly all animal prey captured by tamarins were cryptic and/or embedded in microhabitats such as tree bark, palm leaves or clusters of bromeliads.

4. Tamarins fed on a large variety of typically small, soft and sweet fruits and foraged heavily on nectar from a few tree species during the dry season, when ripe fruits were relatively scarce.

5. Tree hole cavities potentially available to tamarins as sleeping sites were significantly more abundant in swamps and relatively undisturbed upland habitat than in hillside forests recovering from logging.

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APPENDIX. Plant Species in the Diet of Two Groups of Golden Lion Tamarins Between April and October 1984 and 1985.

Family[a]	Species[b]	Item[c]
Cyclanthaceae	*Thoracocarpus bissectus*	Rf
Melastomataceae	*Clidemia bulbosa*	Rf
	Clidemia biserrata	Rf, Fw
	Miconia candolleana	Rf
	Miconia hypoleuca	Rf
	Miconia ibaguensis	Rf
	Miconia clavescens	Rf
	Henriettea saldanhai	Rf
Guttiferae	*Symphonia globulifera*	Nc
	Tovomita sp.	Rf
Leg. Mimosoideae	*Inga edulis*	Rf
	Inga leptantha	Rf
	Inga thibaudiana	Rf
	Inga fagifolia	Rf
	Inga leptandra	Rf
	Liana 1	Ex
Moraceae	*Cecropia lyratifolia*	Rf
	Cecropia hololeuca	Rf
	Ficus obtusiuscula	
	Ficus cluseaefolia	Rf
Musaceae	*Musa paradisiaca*	Rf
	M. rosaceae	Rf
Rubiaceae	*Genipa americana*	Rf
	Randia spinosa	Rf
	Sabicea cinerea	Rf
	Coussarea sp.	Rf
	Rubiaceae 1	Rf
Palmae	*Euterpe edulis*	Uf
	Bactris sp.	Rf
	Astrocaryum airi	Uf
	Geonoma gracilis	Rf
	Palmae 1	Rf
	Palmae 2	F1
Menispermaceae	*Abuta sellowiana*	Rf
Sapotaceae	*Chrysophyllum* sp.	Rf
	Pouteria parviflora	Rf
	Pouteria sp. 1	Rf
	Pouteria sp. 2	Rf
	Pradosia latescens	Rf
	Mimusops sp.	Rf
Myrtaceae	*Eugenia glomerata*	Rf
	Eugenia fusca	Rf
	Eugenia sp.	Rf
	Psidium guineense	Rf
	Psidium sp.	Rf
	Syzygium jambos	Rf
	Marliera racemosa	Rf
	Marlierea edulis	Rf
	Myrcia sp.	Rf
	Campomanesia sp.	Rf
	Myrtaceae 1	Rf
Boraginaceae	*Cordia sellowiana*	Rf

(continued)

APPENDIX (*continued*).

Family[a]	Species[b]	Item[c]
	Cordia sp.	Rf
Ebenaceae	*Diospyros hispida*	Rf
Leg. Papilionaceae	*Machaerium* sp.	Ex
Combretaceae	*Combretum fruticosum*	Nc
Araceae	*Monstera* sp.	Nc, Rf
Caricaceae	*Jacaratia dodecaphylla*	Rf
Vitaceae	*Cissus* sp.	Rf
Verbenaceae	*Vitex polygama*	Rf
Myristicaceae	*Myristicia theidora*	Rf
Ulmaceae	*Celtis* sp.	Rf
Sapindaceae	*Paullinia carpopodea*	Rf
Monimiaceae	*Siparuna guianensis*	Rf

[a]Families are ranked according to their frequency of use in the diet of the two Rodolfo study groups of tamarins between April and October, 1984–1985.
[b]Plants which could only be identified to the family level are indicated by numbers.
[c]Plant items: Rf, ripe fruit; Uf, unripe fruit; Fw, flowers; Nc, nectar; Ex, exudates; Fl, fluids.