

The use of degraded and shade cocoa forests by Endangered golden-headed lion tamarins *Leontopithecus chrysomelas*

Becky E. Raboy, Mary C. Christman and James M. Dietz

Abstract Determining habitat requirements for threatened primates is critical to implementing conservation strategies, and plans incorporating metapopulation structure require understanding the potential of available habitats to serve as corridors. We examined how three groups of golden-headed lion tamarins *Leontopithecus chrysomelas* in Southern Bahia, Brazil, used mature, swamp, secondary and shade cocoa (*cabruca*) forests. Unlike callitrichids that show affinities for degraded forest, *Leontopithecus* species are presumed to depend on primary or mature forests for sleeping sites in tree holes and epiphytic bromeliads for animal prey. In this study we quantified resource availability within each habitat, compared the proportion of time spent in each habitat to that based on availability, investigated preferences for sleeping site selection, and determined how golden-headed lion tamarins allocated time to foraging behaviour in different habitats. Each group preferred to range in certain habitats during the day, yet patterns were not

consistent across groups. In contrast, all groups preferred to sleep in mature or *cabruca* forest. Golden-headed lion tamarins spent a greater proportion of time foraging and eating fruits, flowers and nectar in *cabruca* than in mature or secondary forests. Although the extent to which secondary and *cabruca* forests can completely sustain breeding groups is unresolved, we conclude that both habitats would make suitable corridors for the movement of tamarins between forest fragments, and that the large trees remaining in *cabruca* are important sources of food and sleeping sites. We suggest that management plans for golden-headed lion tamarins should focus on protecting areas that include access to tall forest, either as mature or *cabruca*, for the long-term conservation of the species.

Keywords Atlantic rainforest, Brazil, Callitrichidae, golden-headed lion tamarins, habitat use, *Leontopithecus chrysomelas*, shade cocoa, Southern Bahia.

Introduction

The dramatic increase in human populations has had a large negative impact on tropical forest (Turner *et al.*, 1990). As a result of shifting agriculture and logging practices, habitat loss, degradation, and fragmentation threaten the existence of many primate species (Johns, 1991). The ability of primates to use degraded forests varies widely and may depend on body size and the type and diversity of their diet (Johns & Skorupa, 1987). To the extent that the characteristics of forests may differ among primary, secondary, logged or agro- forests, so does a species' ability to exploit these environments.

Variation in the height of the forest, openness of the canopy, canopy connectivity and diversity, and abundance of resources can affect how a primate uses a particular habitat.

Many species of tamarins and marmosets (Callitrichidae), small New World primates, use disturbed and regenerating forests and are often considered 'edge-specialists' (Terborgh, 1983; Sussman & Kinzey, 1984; Rylands, 1986, 1996; Egler, 1992; Passamani & Rylands, 2000). Callitrichids eat fruit, insects, small vertebrates, and plant exudates, resources that vary in availability across habitats and in some cases may be abundant in degraded or secondary environments. In the relatively open canopy of secondary forests light penetrates easily, leading to a large quantity of fruit, flowers and foliage (Blake & Loiselle, 2001). The abundance of small fruits may explain why many migrating bird species frequently use secondary forest (Martin, 1985). However, it is not always clear that secondary forests have more fruit available than mature forest, and some suggest the opposite (Ferrari & Diego, 1995). Other key resources may influence the success with which callitrichids use secondary habitats. The thick undergrowth that is typical of regenerating forests may also provide protection from

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predators and structural support that facilitates travel (Rylands, 1996). Additionally some callitrichids, such as the genus *Callithrix*, have a specialized dental structure that enables them to easily consume gums obtained from trees and vines (Sussman & Kinzey, 1984). These specializations allow for efficient exploitation of disturbed forest when fruit is not available (Ferrari & Diego, 1995).

Lion tamarins (*Leontopithecus* spp.) are presumed to depend on mature forests for two principal resources that may be less abundant in secondary forests (Rylands, 1989, 1996). The first is tree holes for sleeping (Rylands, 1993). Although some species of *Callithrix* (Rylands, 1982, 1986) and tamarins from the genus *Saguinus* (Terborgh, 1983) occasionally sleep in tree holes, *Leontopithecus* spp. are the only callitrichids studied that habitually do so (Coimbra-Filho, 1978). Secondary forests are thought to have fewer tree holes of adequate size, especially in younger forests comprised of trees of small diameter (Coimbra-Filho, 1978; Rylands, 1993). The second resource is epiphytic bromeliads, sites where lion tamarins frequently forage for animal prey. Lion tamarins have long, slender hands, relative to other callitrichids, that aid in manipulative foraging (Rylands, 1993; Bicca-Marques, 1999). For three of the four species of *Leontopithecus*, bromeliads are a preferred foraging microhabitat for locating prey (Rylands, 1982; Peres, 1986; Prado, 1999; Raboy, 2002).

Irrespective of potential habitat preferences, lion tamarins are forced to use degraded forest because of the widespread destruction of mature forest (Rylands *et al.*, 1996). Lion tamarins are endemic to the Atlantic forest (Rylands *et al.*, 1996), one of the most threatened tropical forests in the world (Mittermeier *et al.*, 1982). This forest is now a mosaic of primary and secondary forest, and agricultural lands (Stallings & Robinson, 1991), with only 2–8% remaining forest (Mallinson, 2001; Saatchi *et al.*, 2001). *Leontopithecus* spp. are categorized as either Endangered (*Leontopithecus chrysomelas*) or Critically Endangered on the 2002 IUCN Red List (*L. rosalia*, *L. chrysopygus* and *L. caissara*; IUCN, 2002).

An understanding of the habitat requirements of lion tamarins is important for the design of conservation strategies. Plans incorporating metapopulation structure require discerning the potential of different habitats to serve as corridors for movement between larger tracts of forest (Lidicker & Koenig, 1996). Given the rapid degradation of Brazil's Atlantic forest, understanding how lion tamarins use regenerating forests and agricultural land is essential for prioritizing areas for conservation. For example, much of the eastern part of the range of golden-headed lion tamarins has been converted into agroforests known as *cabruca*. *Cabruca* is a system of shade cropping in which the middle and understory trees of intact forests are removed and replaced with cacao trees

Theobroma cacao. *Cabruca* has relatively few lianas and a reduced subcanopy, substrates that are commonly used by callitrichids. Prior to this study, it was not clear how successfully lion tamarins were able to use this habitat.

In this study we examine the extent to which golden-headed lion tamarins *L. chrysomelas* use available habitats. In particular, we determine resource density within each habitat and compare patterns of habitat use to availability, including whether golden-headed lion tamarins have preferences for the location of sleeping sites. In addition, we look at patterns of foraging behaviour in each of these habitats, consider the impact that *cabruca* and regenerating forest have on lion tamarin ecology, and highlight the importance of these habitats for successful conservation of the species.

Methods

We conducted our study in and near Una Biological Reserve in Southern Bahia, Brazil (Fig. 1). Points mapped with a global positioning system, ground surveys, historical records of land-use and aerial photographs were used to create a map outlining mature, secondary, swamp and *cabruca* forest. Swamps were classified as a distinct habitat type, regardless of whether they contained mature or secondary forest. Mature forest was characterized by a canopy at 25–35 m height, an abundance of epiphytes and vines and a relatively open understory. *Cabruca* had a similar height and presence

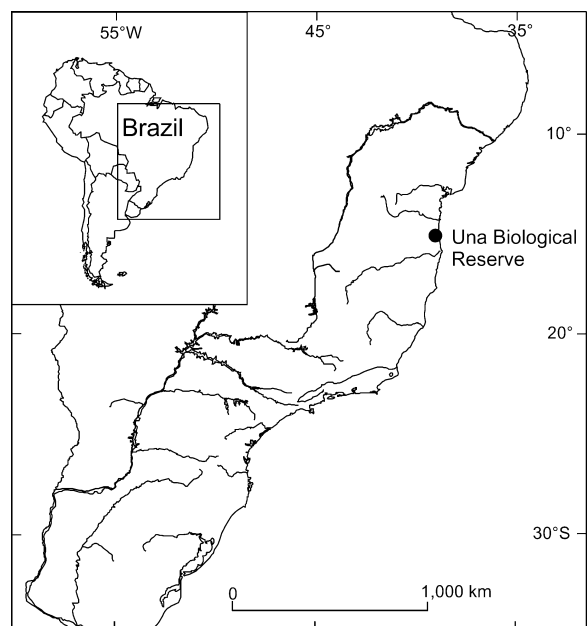


Fig. 1 The eastern coast of Brazil, indicating the location of Una Biological Reserve; the inset indicates the location of the main figure (map courtesy of Paulo de Cordeiro).

of epiphytes, but was distinguished from mature forest by the presence of cacao and banana trees, a sparser understory and mid-canopy, and an absence of vines. Secondary forests at our study site generally had canopies at 5–10 m, and occasionally at 15 m, with trees of small diameter and dense, scrubby understory. Secondary forests also included small areas of newly regenerating fields with few trees and mainly bushes and grasses. Swamp was characterized by muddy ground or standing water, usually in stream valleys, and had the densest understory.

To census lion tamarin resources we sampled along eight 5 * 100 m transects in each of the four habitats. The locations of transects in mature, secondary and cabruca forest were determined randomly. Swamp habitats were found in few locations and were chosen non-randomly. We counted the total number of trees in each transect using four size classes based on diameter at breast height (10–20, 20–30, 30–40 and >40 cm). We counted all bromeliads in each of three size classes (0–20, 20–40 and >40 cm), determined by estimating the basal diameter. The number of *piçava* palms *Attalea funifera*, *dendê* palms *Elaeis guineensis*, and rotting-wood sites, all common foraging microhabitats for lion tamarins, were also counted. Every 10 m along the transect all visible tree holes within a 2.5 m radius of the midline of the transect were recorded. Each 5 * 10 m quadrat within a transect was classified as having a presence or absence of vines connecting trees.

We studied three groups, named Piaçava, Onça, and Entulho, consisting of eight, nine and six individuals respectively, between 1998–2000. Each group used mature, secondary and swamp forests. Piaçava and Onça also used cabruca but this habitat was not available in the home range of Entulho. We followed methods from Dietz *et al.* (1996) to capture and habituate individuals to the presence of human observers. Systematic observations were taken on groups Piaçava, Onça and Entulho on 92, 70 and 45 complete days, respectively, from the time they left their sleeping sites in the morning to the time they returned in the late afternoon. Every 20 minutes we conducted scan sampling (Altmann, 1974). The identity and behaviour of all visible group members were recorded at the first instance they were observed during a 4-minute scanning period.

In order to characterize the groups' preferred habitats, we required information about each group's home range and the distribution of habitats within that home range. Home ranges were determined by recording the location of the group's centre, estimated by using a map and marked trails as reference, every 2 hours. We used the fixed-kernel method (Worton, 1986, 1989) to calculate the area of the range, using the Animal Movement Analysis

Extension (Hooge & Eichenlaub, 1997) for ArcView software, version 3.2 (Environmental Systems Research Institute, Inc., Redlands, USA). We overlaid the home range and habitat maps to determine the amount of each habitat in the home range of each group.

We conducted a weighted multivariate analysis of variance on the transect data to determine if overall differences in resource availability existed between habitats. The total numbers of trees, bromeliads, alternative foraging sites, and tree holes were used as the dependent variables. To test for differences in density of resources between particular habitats, we conducted multiple comparisons using the Tukey-Kramer procedure for three of the four variables. We used a logistic regression to test for variation in the probability that transects would contain lianas as a function of habitat, and conducted contrasts between all habitats using the Bonferroni method to control for experiment-wise type 1 error (Sokal & Rohlf, 1995).

χ^2 goodness of fit tests were used to determine habitat preferences for each group. We compared the number of scans collected in each habitat with the number expected based on availability. We used the Bonferroni *z* statistic (Neu *et al.*, 1974) to test whether particular habitats were used significantly more or less than expected (Dietz *et al.*, 1997). To test the relationship between sleeping site selection and availability of habitat types, we conducted a χ^2 goodness of fit test for group Onça and an exact test for groups Entulho and Piaçava. The distinction was necessary because of restrictions due to small sample sizes for the latter groups. Monte Carlo simulations were run to obtain an approximation of the exact distribution of the χ^2 statistic.

To test whether or not the proportion of time allocated to foraging behaviours varied with habitat type, we used a mixed model repeated measures analysis of variance. Denominator degrees of freedom were adjusted using the Kenwood-Rodgers method. To test for differences between particular habitats, we conducted multiple comparisons using the Tukey-Kramer procedure. We excluded from analyses those individuals for which we had < 30 scans in each habitat type. The alpha level was set at 0.05 for all statistical tests. Further details on the methods and analyses are outlined in Raboy (2002). All analyses were performed using SAS software (SAS Institute, Cary, USA).

Results

Analyses of transect surveys revealed differences in resource density among the four habitats ($P = 0.002$). Total tree density and the density of alternative foraging sites differed significantly among the four habitats. The

difference in number of bromeliads was close to statistical significance ($P = 0.054$) and pairwise comparisons revealed that secondary forests had fewer bromeliads than any other habitat. Pairwise comparisons also revealed that mature forests had higher densities of trees than cabruca and secondary forests and that cabruca had fewer alternative foraging sites than mature or swamp forests (Table 1). The presence or absence of lianas was significantly different among habitats ($P < 0.001$). Fewer lianas were found in cabruca than in other forest types ($P < 0.001$ for all contrasts between cabruca and the other habitats, $\alpha = 0.0083$).

Lion tamarin groups used all habitats available in their home ranges, but did not use them in relation to their availability (Table 2). Although each group showed preferences, these were not consistent among groups. Entulho did not have cabruca within their home range and instead used secondary forest preferentially. Onça had all four habitats available and preferentially used mature forest and swamp. Use of secondary forests by Onça was much less than expected. In contrast, Piaçava used most habitats in proportion to their availability with the exception of mature forest, which was used less than expected.

Piaçava, Onça and Entulho were observed to sleep in 54, 65 and 38 different distinct sleeping sites respectively,

averaging 1.6, 2.5 and 2.1 different locations per week. Piaçava and Onça slept only in tree holes whereas 31.6% of the sites chosen by Entulho were vine tangles located in secondary forest. Each group used sleeping sites in most habitats, but did not choose them in relation to the proportion of habitats in their home range. Sites were selected in mature or cabruca forest more often than expected based on availability of those habitats. Piaçava preferred cabruca for sleeping sites but Onça and Entulho preferred mature forests in the sense that they used those habitats for sleeping more than expected (Table 3). Each group used a few sleeping sites repeatedly (Fig. 2). Piaçava went to five sites, Onça nine and Entulho only three on 50% of the evenings they were observed. For Piaçava and Onça the locations of these most commonly used sites were in mature forest or cabruca, and never in secondary forest. In contrast, the most commonly used sleeping sites for Entulho were in secondary forest.

The proportion of the time budget that individuals foraged for animals in different habitats was not significantly different ($P = 0.061$; Fig. 3a). Conversely, the proportion of the time budget that individuals foraged for and ate fruits, flowers, and nectar varied among habitats ($P < 0.001$; Fig. 3b). Multiple comparisons revealed that lion tamarins spent a greater proportion of time foraging

Table 1 Structural characteristics of four habitat types used by golden-headed lion tamarins. Unless otherwise indicated, numbers represent the mean per ha \pm SD. A MANOVA indicated that resources varied among the four habitats (Wilks' $\Lambda = 0.3091$; $F_{12, 63.79} = 2.97$). Univariate ANOVAs also revealed differences among total trees ($F_{3,28} = 3.35$; $P = 0.034$), total bromeliads ($F_{3,28} = 2.89$; $P = 0.054$) and total foraging sites ($F_{3,28} = 9.98$; $P < 0.001$), but not between total number of tree holes ($F_{3,28} = 1.39$; $P = 0.266$). Significant differences in pairwise comparisons of habitat variables between habitats are indicated by values that do not share a common letter in the upper right corner.

Habitat variable	Habitat types			
	Mature	Secondary	Swamp	Cabruca
No. of trees				
Total	9.80 \pm 3.24 ^a	5.28 \pm 1.49 ^{bc}	7.10 \pm 1.56 ^{ab}	4.08 \pm 0.95 ^{cd}
10–20 DBH ¹	6.20 \pm 2.92	4.03 \pm 1.29	4.08 \pm 1.49	1.29 \pm 0.62
20–30 DBH	2.18 \pm 0.54	1.03 \pm 0.51	1.95 \pm 1.06	1.19 \pm 0.33
30–40 DBH	1.05 \pm 0.83	0.13 \pm 0.15	0.90 \pm 0.67	0.98 \pm 0.67
>40 DBH	0.38 \pm 0.20	0.10 \pm 0.15	0.18 \pm 0.13	0.62 \pm 0.30
No. of bromeliads				
Total	3.62 \pm 2.90 ^a	0.08 \pm 0.21 ^b	1.98 \pm 1.08 ^a	1.26 \pm 1.0 ^a
Small	2.67 \pm 2.60	0.00	0.95 \pm 0.55	0.64 \pm 0.87
Medium	0.66 \pm 0.38	0.08 \pm 0.21	0.73 \pm 0.59	0.29 \pm 0.25
Large	0.30 \pm 0.39	0.00	0.30 \pm 0.19	0.33 \pm 0.25
No. of alternative foraging sites				
Total	2.40 \pm 0.67 ^a	1.43 \pm 1.03 ^{bc}	2.20 \pm 1.32 ^a	0.82 \pm 0.38 ^{bc}
Rotting wood	2.05 \pm 0.80	1.00 \pm 1.09	2.15 \pm 1.20	0.82 \pm 0.38
Piaçava palm	0.35 \pm 0.38	0.00	0.05 \pm 0.14	0.00
Dendê palm	0.00	0.50 \pm 0.59	0.00	0.00
No. of tree holes				
	0.38 \pm 0.53	0.00	0.38 \pm 0.53	0.31 \pm 0.54
Presence or absence of lianas ²				
	0.83 \pm 0.17	0.69 \pm 0.31	0.56 \pm 0.25	0.08 \pm 0.15

¹DBH, diameter at breast height

²Proportion of quadrats within a transect that contained lianas

Table 2 Habitat selection by three groups of golden-headed lion tamarins, comparing the observed number of scans in each habitat with that expected if groups were using habitats in relation to their availability.

Habitat	Group								
	Piaçava ¹			Onça ¹			Entulho ²		
	Obs.	Exp.	Dev. ³	Obs.	Exp.	Dev.	Obs.	Exp.	Dev.
Mature	176	218	–	145	118	+	8	8	
Secondary	39	37		116	207	–	160	145	+
Swamp	51	36		55	38	+	4	19	–
Cabruca	200	175		43	31		NA	NA	

¹ $\chi^2 P < 0.001$

² $\chi^2 P < 0.01$

³Significant deviation (+ or –) is based on confidence intervals following techniques from Neu *et al.* (1974)

Table 3 A comparison of the number of sleeping sites (tree holes and vine tangles) selected in each habitat to that expected if groups of golden-headed lion tamarins chose sleeping sites in proportion to the amount of each type of habitat available in their home range.

Habitat Type	Group					
	Piaçava*		Onça**		Entulho***	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Mature	20	25.3	44	19.8	11	1.7
Secondary	4	4.3	8	34.6	27	32.0
Swamp	0	4.1	5	6.4	0	4.2
Cabruca	30	20.3	9	5.2	NA ¹	NA

*P < 0.05, **P < 0.001, ***P < 0.0001

¹Not applicable

for and eating fruits, flowers, and nectar in cabruca than in mature ($t_{42} = 7.22$, $P < 0.001$) or secondary forests ($t_{42} = 4.96$, $P < 0.001$), and in swamp than in mature forests ($t_{42} = -4.70$, $P < 0.001$).

Discussion

Our data suggest that golden-headed lion tamarins select tall forest for sleeping at night. Relative to the amount of available habitat, all groups tended to use sleeping sites in mature forest or cabruca and avoided sleeping in swamp or secondary forests. We were unable to distinguish whether groups did so because they prefer sleeping in these habitats or because more sleeping sites were available. This was in part because our method of sampling for tree holes underestimated their actual availability in secondary forest. Although we did not record any tree holes in secondary forest during our transect surveys, golden-headed lion tamarins that we followed did sleep in tree holes in this habitat. In particular, Entulho used sleeping sites in secondary forest more

frequently than the other groups; however, the group's home range was located almost entirely within that habitat type. Interestingly, this group was also the only group to sleep in vine tangles, which were also present in mature habitat, but never used. Vine tangles clearly represent an alternative resource when tree holes are less abundant.

Golden-headed lion tamarins did not show overall preferences for secondary forest, contrary to what has been suggested for other callitrichid genera. Two of the three groups used secondary forests less than or in relation to its availability, and secondary forests were not used more than other habitats to search for insects or fruits and flowers. From transect sampling we determined that secondary forests contained fewer bromeliads than other habitats, indicating that secondary forest may not represent the most profitable habitat for locating animal prey. In studies of birds, insectivorous species were more diverse and common in old-growth forests than in young secondary forests (Blake & Loiselle, 2001). We do not have evidence for whether or not there is a greater abundance of fruit in secondary forests. In our study, only one group, Entulho, preferentially used secondary forest. However, the home range of that group contained no cabruca, and only relatively small areas of other habitats.

Cabruca appeared to offer more adequate resources to the tamarins than were available in secondary forests. Golden-headed lion tamarins did not avoid cabruca when it was available, and occasionally would spend entire days within this forest type (pers. obs.). Although much of the understory in cabruca has been removed to plant cacao trees, the habitat represented an important source of fruit and flowers, animal prey and sleeping sites. The percentage of time spent foraging for insects was similar in cabruca and other habitats, and the percentage of time spent foraging and eating fruits, flowers, and nectar was higher in cabruca than in mature or secondary forests. Cabruca did not have as many alternative prey foraging sites relative to mature or swamp forests but seemed to have equal densities of large bromeliads. Large bromeliads are rich patches of invertebrate and vertebrate prey (Domingues *et al.*, 1989). Although cabruca had fewer total trees than mature forest, it did have equal densities of the largest tree class size (>40 cm diameter at breast height). Despite the potential foraging advantages of cabruca, golden-headed lion tamarins may still suffer costs while travelling within this habitat. Cabruca had very few connecting vines between trees relative to other habitats, potentially inhibiting locomotion and escape from predators.

Golden-headed lion tamarins in Una Reserve did not select swamp over other available habitats, in contrast to the findings of Dietz *et al.* (1997) for *L. rosalia* in Poço das

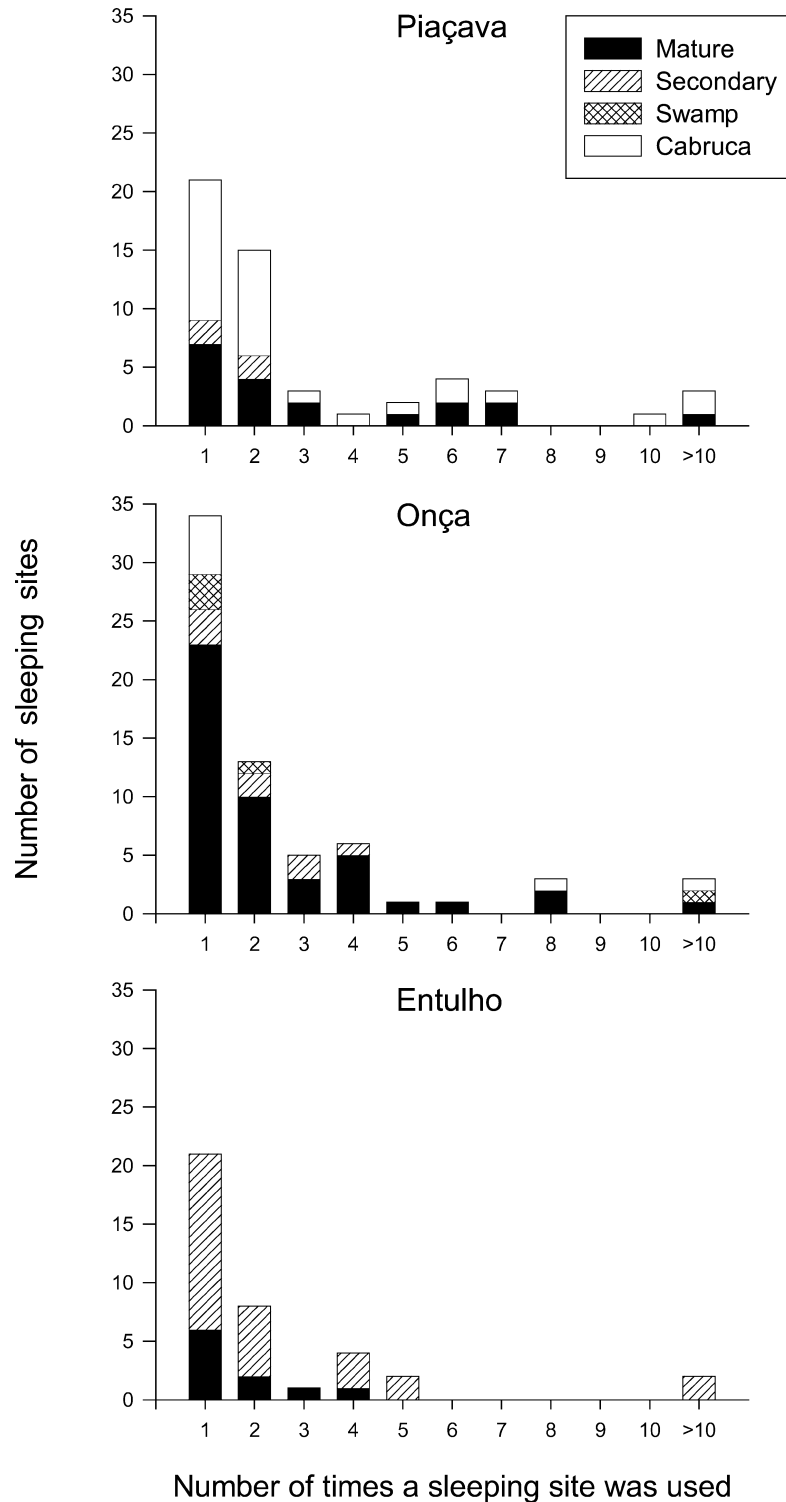


Fig. 2 Repeated use of sleeping sites in mature, secondary, swamp and cabruca forest. $N = 54$, 65 and 38 sleeping sites for Piaçava, Onça and Entulho respectively.

Antas Biological Reserve. Dietz *et al.* (1997) suggested the tamarins' preference for swamp was due to more humid microclimates, favourable in terms of the abundance of animal prey during the dry season. The eastern part of the golden-headed lion tamarins' range, including our

study site, does not have any seasonality in its rainfall (Rylands, 1993). Although the extent of fluctuations in food resources is unknown, the lack of a distinct dry season at Una may provide more stable prey resources throughout the year.

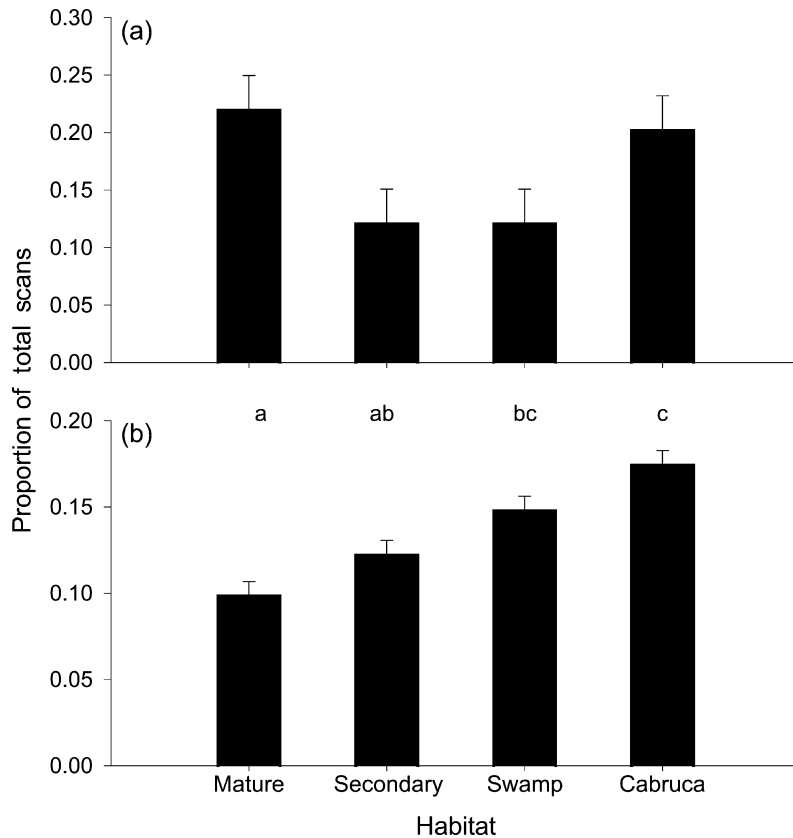


Fig. 3 The average proportion of the time budget \pm SEM spent by individuals a) foraging for animals and b) foraging and eating plants in each habitat. ANOVAs revealed there were no significant differences in the percentage of time spent foraging for animals ($F_{3,29} = 8.27$, $P = 0.062$) but there were for the percentage of time spent foraging or eating fruit, flowers and nectar ($F_{3,42} = 19.37$, $P < 0.001$). Significant differences from pairwise comparisons are indicated by bars that do not share a common letter.

Given the rapid rate of habitat loss in southern Bahia, the fact that golden-headed lion tamarins preferentially selected sleeping sites in habitats with tall forest and/or that more sleeping sites were available in tall forest raises additional concerns about conservation of the species. The use of poorly protected sleeping sites (e.g. exposed sites such as hollow tree stumps and sites near to the ground or on branches) in the degraded forests of Poço das Antas Reserve may explain the recent occurrences of predation on complete groups of *L. rosalia* in that reserve (Dietz & Baker, unpub. data). Our results suggest that lion tamarins will sleep in degraded areas when faced with limited options, but frequently select tall forest habitats when available.

The forest structure of cabruca is similar to shade-coffee plantations, a habitat that has been documented to have high diversity of birds and has been a focus of conservation concern throughout the tropics (Sherry, 2000). Many rainforest species are likely to suffer population declines if landowners continue to convert their shade-coffee or cabruca forests into monoculture crops or cattle ranches. In the past 14 years cocoa production in Southern Bahia has faced severe problems, including the rapid spread of a fungal disease, witches' broom (Alger & Caldas, 1994; Saatchi *et al.*, 2001). As the price of cocoa falls, farmers are forced to seek alternative

sources of income by converting cabruca and forests into cattle pasture (Nobre, 1998; Saatchi *et al.*, 2001). In so doing, they are eliminating habitat for many threatened species. A recent study of biodiversity in the Una region indicated that cabruca forests maintained at least 70% of the terrestrial frog and lizard, small mammal and bat species that are found in neighbouring intact forests (Dixo, 2001; Pardini, 2001; Faria, 2002).

Golden-headed lion tamarins did not preferentially use degraded and regenerating habitats, but neither did they avoid them. We suggest that regenerating secondary forests and cabruca forests may be considered as suitable habitat for corridors facilitating the movement of the tamarins between larger tracts of intact forest. The majority of the secondary forest at our study site was approximately 30 years old at the time of the study. We do not know the full extent to which golden-headed lion tamarins use younger forests, although we have tracked tamarins passing through fields and newly regenerating forests < 10 years old.

In this study we showed that golden-headed lion tamarins used all forested habitats that were available. Home ranges with heterogeneous habitat structure may offer more resources, or more flexible access to resources, than home ranges containing only one habitat type. Habitat heterogeneity has been shown to be positively

correlated with primate abundance and species richness (Stallings & Robinson, 1991) and may decrease the probability of local extinctions. Thomas (1991) suggested that secondary forests in Zaire supply important lower quality resources to *Cercopithecus* monkeys to supplement the seasonal productivity in primary forest in drier periods, and found the highest densities of *Cercopithecus* in areas that had such habitat mosaics. Mosaics of old and young forest have also been suggested to be important in maintaining high levels of bird diversity at La Selva Biological Station in Costa Rica (Blake & Loiselle, 2001). Similarly, we suggest that habitat mosaics containing tall forest, either mature or cabruca, will be important to long-term conservation of golden-headed lion tamarins.

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