ABSTRACT

Title of Document: ECOLOGY AND DEMOGRAPHY OF GOLDEN-HEADED LION TAMARINS (*Leontopithecus chrysomelas*) IN *CABRUCA* AGROFOREST, BAHIA STATE, BRAZIL.

Leonardo de Carvalho Oliveira, Doctor of Philoshophy, 2010

Directed By: Dr. James M. Dietz, Professor
Biology

Understanding how species use the matrix of habitat that surrounds forest fragments can contribute to conservation strategies in fragmented landscapes. In this dissertation, I evaluate the effects of habitat structure and resource availability on group characteristics, use of space, and predation risk for the endangered golden-headed-lion tamarins in shaded cocoa plantations locally known as *cabruca* agroforest. In the first chapter I present a list of tree species that provide key foods and sleeping sites used by lion tamarins. Families Myrtaceae and Sapotaceae are the most commonly used by lion tamarins for both food and sleeping sites. Fifty-five tree species were ranked as extremely valuable for the tamarins. *Cabruca* management that retains the species listed in this study may improve the long-term survival of lion tamarins. In the second chapter, I compare ecological and demographic data of lion tamarins in *cabruca* and other vegetation types. In contrast with my prediction that food resources would be scarce in *cabruca*, the exotic and invasive jackfruit (*Artocarpus heterophyllus*) was an abundant food resource for tamarins in *cabruca* while bromeliads were the favorite substrate for animal prey foraging. Group size and composition were similar in all vegetation types. Males in *cabruca* were heavier than those in primary forest. Density of lion tamarins in *cabruca* was the highest and home range size the smallest reported for the species. This is the first study to show that lion tamarins can live and reproduce exclusively in *cabruca* and has important implications for conservation of the species. In my third chapter, I test two hypotheses explaining the association between lion tamarins and Wied's marmoset (*Callithrix kuhlii*): foraging benefits and predation avoidance. I found no evidence to support the hypothesis that interspecific associations provide foraging benefits for lion tamarins. However, several findings support the predation avoidance hypothesis: associations occurred in areas where predation risk was higher, and during the part of the day in which predation risk was highest, and following birth events when the tamarins were more susceptible to predation. Despite the importance of *cabruca* to lion tamarins, they are more exposed to predation in this habitat.

ECOLOGY AND DEMOGRAPHY OF GOLDEN-HEADED LION TAMARINS (*Leontopithecus chrysomelas*) IN *CABRUCA* AGROFOREST,BAHIA STATE, BRAZIL

By

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Dissertation submitted to the Faculty of the Graduate School of the
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Preface

This dissertation contains a single introduction section and three chapters. Chapters I, II, and III are presented in manuscript form, with abstract, introduction, methods, results, and discussion, followed by tables, and figures. A single bibliography section occurs at the end for references cited throughout the dissertation.
Chapter I was published in *Animal Conservation* 13:60-70, in 2010

Dedication

This dissertation is dedicated to my wife Sylvia, whose love, friendship and encouragement gave me the strengths to finish this study (Bulli, te amo)

And to my family, whose love and support were always with me.

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Introduction

The “matrix” of modified habitat that surrounds existing habitat fragments (Gascon et al. 1999; Gascon et al. 2000; Laurance 1994; Pires et al. 2002) is an important component of a fragmented landscape and its characteristics affect population dynamics (Fahrig 2001; Ricketts 2001) as well as metapopulation dynamics (Moilanen & Hanski 1998; Vandermeer & Carvajal 2001). Understanding how species use and are affected by the matrix can enhance our understanding of wildlife population dynamics in human-altered landscapes and ultimately contribute to new conservation strategies (Anderson et al. 2007).

The focus of my research is to understand the relationship between an endangered primate species and an agroforest system that is the predominant matrix type in its geographic range. Agroforestry may be defined as practices that involve the integration of trees into agricultural systems through the conservation of existing trees, by planting new trees or by allowing recruitment of native tree species (Schroth et al. 2004). Agroforestry may provide a more sustainable economic activity than monocultures because, in addition to crop production it also provides ecological services (Pearce & Mourato 2004). At the same time, agroforests may support impressive levels of biodiversity of invertebrates (Johnson 2000; Mas & Dietsch 2004; Perfecto & Vandermeer 2002), vertebrates [amphibians and reptiles (Wanger 2009) birds (Bakermans et al. 2009; Faria et al. 2006) and mammals (Estrada et al. 2005; Faria et al. 2006; Pardini 2004; Vaughan et al. 2007)] as well as plant species (Boshier 2004; Saatchi et al. 2001).

Southern Bahia state is the cocoa production region of Brazil and the matrix that dominates the landscape is *cabruca* agroforest. *Cabruca* refers to cocoa plantations with native forest overstory. By the 1990's, *cabruca* covered almost 40% of the Atlantic Forest in southern Bahia whereas only 33% of the forest cover comprised of native forests (May & Rocha 1996). *Cabruca* has been considered an important habitat for conservation of Atlantic Forest biodiversity in southern Bahia state (Cassano et al. 2009; Rice & Greenberg 2000) for both plant (Sambuichi 2006; Sambuichi & Haridasan 2007) and animal species (Faria et al. 2006; Pardini 2004). However, the species assemblage supported by a given *cabruca* patch is related to its structural complexity and the proximity of intact forest fragments (Alves 1990; Faria et al. 2006; Faria et al. 2007). Southern Bahia is one of the richest Atlantic Forest regions in terms of plant communities (Amorim et al. 2005), plant endemism (Thomas et al. 1998) and density of tree species (Martini et al. 2007). Most of this species richness is found in a mosaic of forest fragments and *cabruca* agroforest.

Cabruca is the predominant habitat type throughout the eastern portion of the range of the golden-headed lion tamarin, *Leontopithecus chrysomelas* (Raboy et al. in press), one of four lion tamarin species endemic to the Atlantic forests of Brazil, all of which are either critically endangered or endangered (IUCN 2009). Lion tamarins are cooperative-breeding species in which groups are typically composed of one reproductive female, one to three adult males and their offspring (Dietz et al. 1994). The average group size is four to seven individuals, and group size ranges from two to 12 individuals (Becky Raboy, unpublished data). The home range size of golden-headed lion tamarins varies from 40 to 197 ha (Dietz et al. 1996; Rylands 1993) with an average of 53 ha (Dietz and Raboy, unpublished data). The home range size of lion tamarins is larger than expected based on its body mass (550 - 590 g), and is one of the largest per unit of group biomass for all New World primates (Dietz et al. 1997). The diet of lion tamarins consists of ripe fruits, flowers, nectar, insects, small vertebrates, and occasionally gums (Raboy & Dietz 2004). Lion tamarins typically sleep in tree holes, although vine tangles and palm leaves may also be used (Rylands 1989; Raboy et al. 2004). The golden-headed lion tamarin is endemic to the Atlantic forest of southern Bahia State and northern Minas Gerais state (Rylands et al. 2002) although most populations are found in the fragmented landscape of southern Bahia (Pinto & Tavares 1994). Estimates of the total wild population size ranges from 6,000 to 15,000 individuals in an area of 19,000 km^2 (Pinto & Rylands 1997), however, many small populations, mainly in the western portion of the distribution, may become extinct in the near future (Raboy et al. in press).

In 2005, a population and habitat viability analysis (PHVA) was conducted for lion tamarins. Results suggested that only one population of lion tamarins is viable and capable of preserving sufficient genetic variability for a period of 100 years. However, assuming a metapopulation scenario in which forested areas are connected by matrix habitat, in this case *cabruca*, suitable for dispersal by lion tamarins, their conservation in the wild is relatively secure (Holst et al. 2006). Since it was unknown if or how lion tamarins use the various types of *cabruca* agroforest, the evaluation of the use of *cabruca* by lion tamarins is recognized as a conservation priority for the species (Holst et al. 2006). Although lion tamarins were recorded using *cabruca* as part of their home range (Raboy et al. 2004), native forest associated with *cabruca* is more degraded and/or is found in association with fewer forest fragments in much of the species' geographic distribution (Faria et al. 2006).

Cabruca and the biodiversity it contains are now under threat in Brazil. A long-term economic crisis due to a decrease in the price of cocoa and the emergence of witches' broom (*Moniliophthora perniciosa*), a fungal disease that has been devastating Bahia's cocoa crops since 1989, is forcing landowners in southern Bahia to transform *cabruca* into other types of crops to increase their revenue. Furthermore, the long-term survival of native forest trees found in *cabruca* is at risk due to current management practices (Rolim & Chiarello 2004) and by the natural death of forest trees (Sambuichi 2006). Given the rapid degradation of Atlantic Forest in Bahia, the endangered status of the golden-headed lion tamarin and the rapid changes in *cabruca* management, a better understanding of the relationship between agroforest management and key resources found in *cabruca* emerges as an important conservation objective. The overall goal of this dissertation was to evaluate if or how golden-headed lion tamarins use *cabruca* agroforest, and to understand better the effects of habitat structure and resource availability on group characteristics (i.e. group size, weight and size of individuals), on their use of space (home range size and density) and the predation risk to lion tamarins.

In the first chapter my goal was to create a list of tree species and families that might be used in habitat recuperation and the creation of corridors, as well as in *cabruca* management protocols, that would favor the persistence of the lion tamarin populations in southern Bahia. I identified the tree species that provide key food resources (fruit, flower, nectar, gum and animal prey) and sleeping sites (mostly tree holes) for golden-headed lion tamarins and ranked them in terms of importance for the lion tamarins. I created a ranking index considering various components of a tree species' utility to the lion tamarins. I then evaluated the occurrence of these key species in *cabruca* plantations inventoried by the Executive Commission for Cacao Cultivation (Comissão Executiva do Plano da Lavoura Cacaueira – CEPLAC). Our list of key species comprised 155 tree species, 93 of them were used for food and 93 for sleeping sites. Fifty-five species were ranked as 'Extremely Valuable,' eight as 'Valuable' and 92 as 'Of Interest.' We observed a low congruence between our list of species and the list of tree species commonly found in *cabrucas*. Of 48 families, Myrtaceae and Sapotaceae were the most important for lion tamarins in both food and sleeping sites. Species in the Myrtaceae, Sapotaceae, Bromeliaceae, and Melastomataceae families are the most common in the lion tamarin diet (Catenacci 2008; Guidorizzi 2008; Raboy et al. in press) but their occurrence in *cabruca* is very rare or absent (Comissão Executiva do Plano de Lavoura Cacaueira-CEPLAC 1982). *Cabruca* management practices such as weeding may affect the recruitment of species in these families while replacement of native trees, after their natural death, is more likely to be by fast-growing exotics trees than by slower growing native trees from these families (Sambuichi & Haridasan 2007). We suggested that *cabruca* management activities favoring the species on our list would improve long term survival of lion tamarins.

In the second chapter, my goals were to determine whether golden-headed lion tamarins can live and reproduce entirely within *cabruca* agroforests, and to compare density, home range, group size, and body mass of tamarin populations in *cabruca* with those in other vegetation types. Due to the lower diversity and density of trees in *cabruca* (Alves 1990; Alvim & Peixoto 1972; Sambuichi 2006) and the rarity or absence of species from the families most used by lion tamarins (Sambuichi & Haridasan 2007; Vinha & Silva 1982), I expected to find differences in terms of food resource (lower in *cabruca*) and habitat structure in *cabruca* areas compared to other vegetation types. Because food resources may directly affect group and litter size, health, and weight of the animals (Chapman et al. 1990; Kirkwood 1983), density of populations (Hanya et al. 2005; Wauters & Lens 1995) daily movements and home range size (Clutton-Brock & Harvey 1977; McNab 1963), I expected to find smaller and lighter lion tamarins in *cabruca*. I also expected that home range sizes would be larger, group sizes smaller and density of tamarins lower in *cabruca*. I used data from three vegetation types: tamarin groups that lived exclusively in *cabruca* agroforest (N=3), groups that were captured in *cabruca* but that also used primary and secondary forest in their home range (mosaic groups, N=3) and groups that lived mostly in primary forest (N=3). Contrary to what I expected food resources in *cabruca* (predominantly the exotic and invasive jackfruit) were abundant and available throughout the year. Groups living in *cabruca* had smaller home range sizes and larger body sizes, higher reproductive rates and higher densities than other groups. My research was the first to show that lion tamarins can live and reproduce in *cabruca* agroforest not associated with native forest. The abundant and constantly fruiting jackfruit trees may be a keystone resource that allows tamarins in *cabruca* to live at densities higher than those in primary forest areas. This information will help to refine estimates of viability of lion tamarin populations in the wild.

My final chapter examines the relationship between habitat structure, predation risk and the interspecific association between the golden-headed-lion tamarins and the Wied's marmosets (*Callithrix kuhlli*). Predation is thought to be the main factor limiting group size and population size for primates (Stafford 1995) accounting for a large portion of deaths of individuals (Isbell 1990). Environmental characteristics can affect susceptibility of primates to predation (Franklin et al. 2007) and characteristics such as canopy complexity and connectivity and understory complexity are important components for protection of primates against aerial predators (Ferrari 2009; Isbell 1994). In *cabruca*, the canopy has lower connectivity and the understory has little complexity, which may expose tamarins to a higher risk of predation. Increasing group size is one of several strategies adopted by animals to avoid predation. A large group implies more eyes to detect predators, lower chance *per capita* for each individual to be taken by predators and the confusion of predators (Heymann & Buchanan-Smith 2000). However, large groups also have constraints linked to food competition and increase in travel distance to acquire necessary resources (Chapman et al. 1995; Terborgh & Janson 1986). Benefits of interspecific associations are generally related to improvement of foraging efficiency and improved predator detection and avoidance (Chapman & Chapman 2000b). The goal of this chapter was to evaluate if the association between the golden-headed-lion tamarins and the Wied's marmoset is explained by predation avoidance or foraging benefits. I measured predation risk by recording the number of encounters and alarm calls between the lion tamarins and potential predators from six to seven groups of lion tamarins living in *cabruca* or in mosaic forest (a mix of *cabruca*, primary and secondary forest). I also measured the number of associations between the two primates in both vegetation types in different scenarios of predation risk and foraging benefits. I observed that the tamarins are more exposed to predation in *cabruca* agroforest where they are also more often in association with marmosets. I did not observe any food related advantages for the lion tamarins associating with marmosets. On the other hand, I found evidence suggesting that lion tamarins and Wied's marmosets associated to decrease the risk of predation. Although lion tamarins can live and reproduce exclusively in *cabruca* they are exposed to higher predation risk in this modified habitat.

Chapter 1: Key tree species for the golden-headed lion tamarin and implications for shade-cocoa management in southern Bahia, Brazil

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Abstract

The golden-headed lion tamarin *Leontopithecus chrysomelas* occurs in the Atlantic Forest of southern Bahia, Brazil, where shade-cocoa agroforestry (known as *cabruca*) predominates. The economic decline of the cocoa industry has caused many landowners to convert *cabruca* into cattle pasture or diversify their plantations with other crops. These and prior anthropogenic disturbances such as habitat fragmentation are threatening lion tamarin persistence. For some lion tamarin groups, *cabruca* comprises a large part of their home range. Considering these factors, the maintenance of the biological diversity in *cabruca* favorable to golden-headed lion tamarins is of considerable interest to their long-term survival. Here we identify plant species that provide food and sleeping sites for the lion tamarins and examine their occurrence in *cabruca* plantations, in order to investigate alternatives for conservation management practices that benefit both lion tamarins and *cabruca*. We determined the total number of trees and the frequency of individuals and species used for food and sleeping sites by lion tamarins in Una Biological Reserve, Bahia, from 1998 to 2006. We used this information to compare the richness and frequency of use across habitats (*cabruca*, mature and secondary forests) and to create a ranking index considering various components of a tree species' utility to the lion tamarins. Lion tamarins used 155 tree species, 93 for food and 93 for sleeping sites. Fifty-five species were ranked as 'Extremely Valuable,' eight as 'Valuable' and 92 as 'Of Interest.' Of 48 families, Myrtaceae and Sapotaceae were used the most. *Cabruca* contained fewer individual trees used by lion tamarins, but the highest frequency of use per tree compared with other habitats, indicating the large influence of single trees in these plantations. Using the key tree species identified in our study in the management of *cabruca* would be of considerable benefit to the long-term survival of lion tamarins

Keywords: *Leontopithecus chrysomelas*; diet; sleeping sites; agroforest; *cabruca* management; Atlantic forest.

Introduction

The golden-headed lion tamarin *Leontopithecus chrysomelas* is endemic to the Atlantic forest of southern Bahia. It is endangered due to its restricted geographic distribution and the loss, fragmentation and degradation of its forests (IUCN 2008; Rylands et al. 2002). Cacao (*Theobroma cacao*) cultivation is the predominant rural activity in the Atlantic forest of southern Bahia, and widespread in much of the eastern part of the lion tamarins range (Raboy et al.). Cacao plantations require shade, and traditionally this is provided by clearing the forest understory and thinning taller trees. This agroforestry system is called *cabruca*, and a number of studies have demonstrated its efficacy in maintaining a favorable habitat matrix for the conservation of Atlantic forest biodiversity (Cassano et al. 2009; Delabie et al. 2007; Faria & Baumgarten 2007; Faria et al. 2007; Pardini 2004; Rice & Greenberg 2000; Sambuichi 2002). In 1990, *cabruca* plantations comprised about 40% of the original extent of moist lowland Atlantic forest in southern Bahia, whereas only about 33% of the forest cover was intact native forest (May & Rocha 1996).

Unfortunately, the *cabruca* plantations are themselves now threatened. A collapse in cocoa prices in the early 1980s, and the emergence of witches' broom (*Moniliophthora perniciosa*) – a fungal disease that has been devastating Bahia's cocoa crops since 1989 – have resulted in landowners diversifying their crops (e.g. coffee *Coffea canephora* and oil palm *Elaeis guianeensis*) and transforming *cabruca* into cattle pasture so as to increase revenue. Furthermore, the practice of maintaining the understory clear means that older *cabrucas* are losing their native trees due to lack of replacement following tree death (Rolim & Chiarello 2004; Sambuichi 2006).

Although intact primary forest has been considered indispensable for lion tamarins (Rylands 1989; Rylands 1996), recent studies have shown that golden-headed lion tamarins are able to use degraded forests and *cabruca* (Alves 1990; Raboy et al. 2004). Given the rapid degradation of southern Bahia's forest including *cabruca* and the endangered status of *L. chrysomelas*, a better understanding of the relationship between lion tamarin resources and the management of *cabruca* is an important conservation objective (Holst et al. 2006).

In this study, we identify the tree species that provide key foods (fruit, flower, nectar, gum and animal prey) and sleeping sites (mostly tree holes) for golden-headed lion tamarins, characterize resource use across habitats and rank species according to their importance. We then examine their occurrence in the *cabruca* plantations as registered by inventories of the Executive Commission for Cacao Cultivation (Comissão Executiva do Plano de Lavoura Cacaueira-CEPLAC 1982). Based on our findings, we suggest tree species and families that might be used in habitat recuperation and the creation of corridors, as well as in *cabruca* management protocols, that would favor the persistence of the lion tamarin populations in southern Bahia.

Methods

Study area

The study was carried out in the Una Biological Reserve (18 500 ha) in southern Bahia, Brazil (15°06'–12'0S, 39°02'–12'0W). Here, the mature and regenerating forests are broadly characterized as lowland Atlantic rainforest (Mori 1989; Oliveira-

Filho & Fontes 2000). The annual temperatures in southern Bahia average 24–25° C. Rainfall is aseasonal, averaging *c*. 2000mm year^{-1} (Coimbra-Filho & Mittermeier 1973; Mori 1989; Oliveira-Filho & Fontes 2000).

Data collection

We examined the use of feeding trees (those in which the lion tamarins eat fruit, nectar, gum and flowers, and/or provided microhabitats for animal prey foraging) by three habituated groups, from March 1999 to December 2000. Records of the use of different tree species for sleeping sites were obtained in these and an additional five groups from June 1998 to September 2006. Data were collected as part of a long-term study of wild golden-headed lion tamarins in Una Biological Reserve (Raboy & Dietz 2004; Raboy et al. 2004). The data from the eight groups were obtained from both full and partial days of observation. On full days, groups were followed from morning sleeping site to afternoon sleeping site (n=331 days, range=4–91 days group^{-1}). On partial days, the groups were either followed from 11:00 h until they entered their sleeping site, or from when they left their sleeping site until 13:00 h (n=1181 days range=10–294 days group^{-1}). We marked each tree used for feeding or as a sleeping site, identifying them taxonomically whenever possible, and noted the habitat in which each was found (primary, secondary or *cabruca*).

Data analysis

General patterns of tree use

We calculated the number of species used (overall richness) by our study groups for all resource trees and broken down by resource type (feeding and sleeping). In addition, we determined richness by family. We also calculated the total number of trees used and the total number of visits to those trees, broken down by resource type and by family.

Characterizing resource trees by habitat

For each habitat, we determined the species richness, total number of individual trees, total number of visits to those trees and the average frequency of use of each species (the total number of visits to a particular species divided by the total number of individuals visited).We used randomization tests to examine the differences between habitat types for species richness and frequency of use, running separate analyses for feeding trees and sleeping sites. For species richness, we calculated the differences between habitats for the number of species present, and then randomly reassigned trees to habitat types, keeping the number of trees found in each habitat type consistent with the original data. We calculated the differences between habitats for each randomized dataset, and ran 10, 000 iterations of the randomization, counting the number of datasets that had differences more extreme (positive or negative) than the original dataset. A P-value was calculated by dividing the number of more extreme differences by 10,000. We followed the same procedure for frequency of use. Again, we constrained the number of trees classified in each habitat to match the original numbers. The P-value was calculated by determining the proportion of iterations out of 10,000 that had frequency differences more extreme than the original dataset. One sleeping tree (a *Ficus gomelleira* in secondary forest) was used 276 times during the study, an abnormally high frequency considering that the next most frequently used tree was slept in 47 times. We ran analyses with and without this *Ficus* to determine its effect on differences in the frequency of use.

We used Jaccard's coefficient of similarity (Magurran 1988) to evaluate the similarity of the plant species' composition used by the golden-headed lion tamarins as food and/or sleeping sites in the three different habitats. The Jaccard index (J) was calculated as J=s/(a+b+s), where s is the number of species shared across two habitats, a the number of species in the first habitat and b the number of species in the second.

Index of tree species' value

We used four criteria to create a numerical index of the relative value of each tree species for the lion tamarins:

(1) Versatility of function (maximum of six points): We reasoned that tree species providing both sleeping sites and food are of greater value to the lion tamarins than those used for only one purpose. Each species received three points for each type of use (sleeping or food).

(2) Attractiveness (maximum of six points): The more the groups using a particular species, the greater our confidence that it would be used broadly by the lion tamarins. Food and sleeping trees were assessed separately because the number of groups observed for each differed. For food trees, we assigned one point for each of the three groups using a species (maximum of three points). For sleeping sites, we added one point if one or two of the eight study groups used the tree species. If three groups

used the species, it received two points. If four or more groups used the species, it received three points.

(3) Prevalence in habitats (maximum of three points): The number of habitats in which a plant species used by the lion tamarins is found is another indication of its availability and importance as a resource. Each species received one point for each of the three habitat types where it could be found.

(4) Availability and use patterns (maximum of nine points): We reasoned that common and frequently used tree species are more valuable to tamarins than scarce and infrequently used species. We therefore assigned an availability and use score based on three variables: the number of individuals of each species, the number of visits per species and the frequency of use for each tree species as defined above. Specifically, we calculated the mean and standard error of the mean (SEM) for each variable and assigned one point when values were below the mean – SEM, two points when values were between the mean ± SEM and three points when the values were above the mean + SEM.

5) Final ranking: Based on these four criteria, the maximum score for any one species was 23. We summed the points for each species and analyzed the resulting totals following the same methods outlined for criterion 4 (availability and use), categorizing scores in relation to the overall mean and SEM. We considered a species receiving a final category of 3 as ‘Extremely Valuable,’ 2 as ‘Valuable’ and 1 as ‘Of Interest’ for the lion tamarins. Collectively, we refer to the species in these categories as ‘key.’

Comparison of key trees for lion tamarins and common shade trees

We compared data on the occurrence of trees commonly retained to provide shade in *cabruca* (Comissão Executiva do Plano de Lavoura Cacaueira-CEPLAC 1982) with our list of the key species for the lion tamarins. We calculated the percent of species common to both lists and listed the ‘Extremely Valuable’ species that did or did not appear on CEPLAC’s list of common *cabruca* shade trees.

Results

General patterns of tree use

The lion tamarins used 155 tree species in 49 families: 93 species for feeding (Table 1) and 93 as sleeping sites (Table 2). These totals were derived from 888 individual food trees used 1533 times, and 349 sleeping site trees used 1702 times. We were unable to identify the species of 47 of the trees. A number of unidentified species in two families Myrtaceae and Bromeliaceae were grouped into three functional units as follows: Myrtaceae gr. ‘araça’, Myrtaceae gr. ‘murta’ and Bromeliaceae gr. ‘Aechmea’ (hereafter referred to as Aechmea spp.). From the species used for feeding, 94% were used for fruit, 5% for nectar and 1% for gum. Bromeliads were used not only for fruit but also for animal prey foraging sites. Myrtaceae and Sapotaceae were the families with the greatest number of species (28 and 16, respectively) used by the lion tamarins. Twenty species of Myrtaceae and 13 of Sapotaceae were used for feeding and 13 Myrtaceae species and nine Sapotaceae species were used as sleeping sites. These two families also accounted for the highest numbers of individual trees used by the lion tamarins (171 and 179, respectively) and the highest numbers of total visits (347 and 400, respectively).

Resources trees by habitat: feeding

We obtained habitat information for 73 of the 93 species used for feeding. Based on Jaccard's index, there was a 47% similarity of food tree species between *cabruca* and primary forest, 36.5% between *cabruca* and secondary forest and 39% between secondary and primary forest. Twenty species were present in all three habitats. Overall, bromeliads (*Aechmea* spp.), *Henriettea succosa* and *Miconia mirabilis* were the taxa providing the greatest number of individuals used for food. In primary forest, Aechmea spp. were the most abundant species used (n=44), and *Anthodiscus amazonicus* was the species used most frequently (mean=3.4 visits individual tree^{-1}). *Aechmea* bromeliads were also the most abundant species used for food in *cabruca* (n=33), and *Diploon cuspidatum* was the species used most frequently (mean=2.4 visits individual tree^{-1}). In secondary forest, *H. succosa* was the species with the greatest number of individuals used (n=61), and *Artocarpus heterophyllus* was the species used most frequently (mean=2.4 visits individual^{-1}).

There was no significant difference in the species richness in *cabruca* versus primary forest (difference=3, P=0.98) nor in *cabruca* versus secondary forest (difference=10, P=0.074). The lion tamarins used significantly more species of food trees in primary forest, however, than in secondary forest (difference=13, P=0.038). We found no significant difference in the frequency of use between trees in primary forest and those in *cabruca* (difference=0.05, P=0.44). Secondary forest, however, had a significantly lower average frequency of use per tree than was found for primary forest (difference=0.29, P=0.001) or *cabruca* (difference=0.32, P=0.003).

Resource trees by habitat: sleeping sites

Of the 93 tree species used by the lion tamarins as sleeping sites, we have habitat information for 84. Based on Jaccard's index, we found a 31.6% similarity of tree species used for sleeping sites between *cabruca* and primary forest, 21.0% between *cabruca* and secondary forest and 16.4%, between secondary and primary forest. In contrast to results for food species, we found just eight species that were used as sleeping sites in all three habitats. Three were among the most commonly used by the lion tamarins in general: *E. guianeensis*, *Guapira opposita* and *Manilkara maxima* (Table 3). *Rinorea guianensis* was the species most commonly used in primary forest (n=15) while *G. opposita* was used most frequently (n=62, mean=5.4 visits tree^{-1}). In *cabruca*, *G. opposita* was the species with the most trees used by the lion tamarins (10 trees), and also the most frequently used 103 times (mean=10.3 visits tree^{-1}). In secondary forest, *E. guianeensis* was the most commonly used species (n=87 trees), and the most frequently used (231 times; mean-2.65 visits tree^{-1}).

There was no significant difference in the number of species used between *cabruca* and primary (difference=38, P=0.10) or secondary forest (difference=14, P=0.57). Despite this, the individual trees in *cabruca* were, on average, used more frequently than the individual trees in either primary forest (difference=4.08, P<0.001) or secondary forest (difference =4.38, P<0.001). There was no significant difference between primary and secondary forest in the average frequency of use of individual trees (difference=0.30, P=0.84), but more species were used in primary forest (difference=52, P<0.001).

Index of key tree species

The three grouped taxonomic units and a further 55 plant species were ranked as ‘Extremely Valuable’ for the golden-headed lion tamarins (overall score of 3). Eight species were ranked as ‘Valuable’ (score of 2), and the remaining 92 species were ranked as ‘Of Interest’ (score of 1) (Table 3).

Comparison of key trees for lion tamarins and common shade trees

CEPLAC’s list of shade-tree species commonly found in *cabrucas* in southern Bahia totaled 144 (Comissão Executiva do Plano de Lavoura Cacaueira-CEPLAC 1982). Thirty-three per cent (48 either just genus and or species) were also registered in our study as being used by lion tamarins for feeding or as sleeping sites. Only 15 of the 55 species ranked as ‘Extremely Valuable’ for the lion tamarins were on the *cabruca* shade tree list. Members of the Myrtaceae, the family most exploited by lion tamarins for food and sleeping sites in our study, were entirely absent from the *cabruca* shade tree list.

Discussion

The number of species exploited for food by the three golden-headed lion tamarin groups in Una was higher than previously recorded for any lion tamarin study (Dietz et al. 1997; Lapenta et al. 2003; Passos 1999; Rylands 1993; Valladares-Padua

1993). This undoubtedly reflects the extraordinary diversity of tree species in the region (Thomas et al. 1998). Amorim et al. (2008) reported 947 flowering plant species in Una Biological Reserve, and more recent inventories have increased this number to around 1200 (A. M. Amorim, pers. comm.).

In our study, the most-used species for both food and sleeping sites by the lion tamarins belonged to the Sapotaceae and Myrtaceae families. Southern Bahia has a high diversity of Sapotaceae and Myrtaceae (Martini et al. 2007; Mori et al. 1983b), with the latter being dominant in many wet forests in terms of both the number of species and the number of individuals (Martini et al. 2007; Mori et al. 1983a). Therefore, the large number of species used by the golden-headed lion tamarins from these two families may be explained by preference and/or availability, but regardless, indicates the importance of these families as providing key resources for the lion tamarins.

When factoring the predominance of *cabruca* throughout the range of the golden-headed lion tamarin (Fig. 1) with findings indicating its usefulness to lion tamarins (Alves 1990; Raboy et al. 2004) and the endangered status of the species, we suggest that the *cabruca* agroforest has an important role in the survival of this primate in the long term. Lion tamarins not only foraged and slept in *cabruca*, but the richness of the food and sleeping-site resources used by lion tamarins in *cabruca* was similar to that found in other habitats. However, the similarity index between primary forest and *cabruca*, the habitats that had more species in common, did not exceed 50% for either food or sleeping sites.

One of our key findings was that single trees in *cabruca* can have a significant influence on the lion tamarins' patterns of resource use. Single trees were used more frequently in this habitat (sleeping sites in particular). Other researchers have documented fewer species and individuals, and a lower density of trees overall, in *cabruca* when compared with mature forest (Sambuichi 2002; Sambuichi 2006), and individual trees, therefore, may be used heavily by the lion tamarins out of necessity. Increased predation may be one of the costs of repeated use, especially in cases where predators have the capacity to learn the location of sleeping sites, as has been indicated previously for lion tamarins (Franklin et al. 2007).

Despite the fact that all habitats had similar levels of plant resource richness used by the lion tamarins, the species in each habitat were dissimilar. Only 16.5% of the species exploited were found in all three habitats. Large variations in the number of individuals per species across habitats may indicate habitat-specific adaptations of the use of different plant species. For example, of 84 *E. guianeensis* individuals, only one occurred in *cabruca* and one in primary forest, the remainder occurring in secondary forest. The golden-headed lion tamarin's use of tree species found in some habitats but not others supports prior suggestions that the lion tamarins may thrive in habitat mosaics of varied composition (Raboy et al. 2004), as long as necessary resources can be found in them.

Recommendations for conservation

We suggest that conservation measures on behalf of golden-headed lion tamarins in southern Bahia include the cultivation and conservation of the 55 resource trees that we have ranked as 'Extremely Valuable.' Most of these served both for food and sleeping sites, were available in multiple habitats and were used frequently. Additionally, individual trees (regardless of species) supporting large bromeliads should be retained wherever possible (Coimbra-Filho & Mittermeier 1973; Rylands 1989; Rylands 1993). Epiphytic bromeliads are an extremely important animal prey foraging site, and also supply fruits and sleeping sites for lion tamarins (Dietz et al. 1997; Prado 1999; Raboy et al. 2004).

The low congruence between our list of key golden-headed lion tamarin species and those commonly left standing as shade trees for cocoa plantations in southern Bahia is a concern, especially given the complete lack of Myrtaceae as a preferred shade tree. The plant families most frequently encountered in *cabruca* in southern Bahia were Anacardiaceae, Moraceae, Fabaceae, Caesalpiniaceae, Mimosaceae, Lecythidaceae, Euphorbiaceae, Lauraceae, Meliaceae and Annonaceae (Sambuichi & Haridasan 2007). Myrtaceae and Sapotaceae, the families most widely exploited by golden-headed lion tamarins in our study, are less commonly found in *cabruca*. Managers gradually replace trees of these families with exotic species supplying commercial fruit crops. Moreover, native tree seedlings of these families are slow growing and are consequently easily eliminated during periodic clearance of undergrowth (Sambuichi & Haridasan 2007).

A number of *cabruca* management practices can be identified that would improve the suitability of *cabruca* for lion tamarins. The first is the selective retention of key species listed in this study (those that provide food and sleeping sites to lion tamarins) to serve as shade trees in *cabruca*. Promoting the permanence of Myrtaceae and Sapotaceae species in *cabruca* would be particularly favorable to the lion tamarins. The second is increasing the overall density of trees in *cabruca*, again favoring the cultivation of those known to be propitious for lion tamarins. Increasing tree density will also support greater local diversity and act as an effective refuge for many tropical forest organisms (Delabie et al. 2007; Rice & Greenberg 2000; Vaughan et al. 2007; Williams-Guillen et al. 2006). These aforementioned actions require oversight when choosing the trees to be felled, selecting saplings for retention and in planting and fostering the successful growth of particular species. Economic incentives to plant and protect such 'eco-friendly' trees may be necessary (Acharya 2006; Ashley et al. 2006), given that agronomic recommendations for *cabruca* management tend toward decreasing rather than increasing plant density (Johns 1999) and prioritizing profits to the detriment of sustainability (Sambuichi & Haridasan 2007). Critical to the implementation of such measures is to promote an increased public awareness of the potential of *cabruca* to protect southern Bahia biodiversity.

We provide a template for using science-based findings on an endangered species as a way to guide agroforestry management choices. Our methods of ascertaining tree importance offer increased practical application for habitat conservation and recuperation by identifying the relative importance of plant resource species to a focal animal species based on a series of factors in relation to their use and function. *Cabruca* has a long history in southern Bahia, and in the face of the current crises including low cocoa prices and fungal disease, this agroforestry system is now undergoing much scrutiny and reform. Examples include assessment of tree spacing, examining solutions for natural tree death and of the use of commercially valuable exotics. In parallel with these efforts to improve the economic return from *cabruca*, we emphasize that management options exist to promote the persistence of endangered species.

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Tables

Table 1. Characteristics of plant resources used by golden-headed lion tamarins in each habitat. Variables include the number of species, number of individual trees, number of total visits by lion tamarins to those trees, and the average frequency of use of each species by three study groups.

Habitat	**No. of species**	**Individual trees**	**No. of visits**	**Frequency**
Mature forest	44	373	675	1.79
Cabruca	42	213	393	1.84
Secondary forest	31	303	466	1.52
Total	93	888	1533	1.71

Table 2. Characteristics of sleeping-site resources used by golden-headed lion tamarins in each habitat. Variables include the number of species, number of individual trees, number of total visits by lion tamarins to those trees, and the average frequency of use of each species by eight study groups. Numbers in parentheses are results of the analysis excluding one individual tree (OG50) that was used 276 times.

Habitat	**No. of species**	**Individual trees**	**No. of visits**	**Frequency**
Mature forest	72	179	603	3.50
Cabruca	34	60	455	7.58
Secondary forest	20	110 (109)	621 (345)	5.64 (3.2)
Total	93	349 (348)	1702 (1435)	4.88 (4.11)

Table 3. Species used for food and sleeping sites by golden-headed lion tamarins (*Leontopithecus chrysomelas*) at Una Biological Reserve. Abbreviations are as follows: Hab = habitat; Ind. = number of individual trees; Visit = total number of visits by lion tamarins; Freq= frequency of use; C = overall importance ranking category; SC= score; SS = sleeping site; F = fruit; N = nectar; G = gum; Sh = shrub, V = vine; P = primary forest; C = *cabruca* agroforest; S = secondary forest. Asterisks indicate cases where > one species in a family were used by lion tamarins but not identifiable to the species level, we grouped these as one taxonomic unit for the analyses.

Species	**Family**	**Use**	**Hab**	**SC**	**C**
*Myrtaceae group murta	Myrtaceae	Fr;SS	C,S,P	23	3
Manilkara maxima Penn.	Sapotaceae	Ne;SS	C,S,P	22	3
Rinorea guianensis Aubl.	Violaceae	Fr;SS	C,S,P	22	3
Ficus gomelleira Kunth & Bouché	Moraceae	Fr;SS	C,S,P	22	3
Guapira opposita (Vell.) Reitz	Nyctaginaceae	Fr;SS	C,P	21	3
Elaeis guianeensis Jacq.	Arecaceae	Fr;SS	C,S,P	21	3
Myrcia rostrata Berg.	Myrtaceae	Fr;SS	C,S,P	20	3
Tapirira guianensis Aubl.	Anacardiaceae	Fr;SS	C,S,P	20	3
*Myrtaceae group araça	Myrtaceae	Fr;SS	C,S,P	20	3
Inga nutans Mart.	Fabaceae	Fr;SS	C,S,P	20	3
Diplöon cuspidatum (Hoehne) Cronquist	Sapotaceae	Fr;SS	C,P	19	3
Symphonia globulifera L.	Clusiaceae	Ne;SS	S,P	19	3
Musa paradisiaca L.	Musaceae	Fr	C,S,P	18	3
Artocarpus heterophyllus Lamark	Moraceae	Fr;SS	S	17	3
Ocotea nitida (meissn.) Rohwer	Lauraceae	Fr;SS	P	17	3
Terminalia dichotoma G. Mey.	Combretaceae	SS	C,P	17	3
Pourouma velutina Miquel	Moraceae	Fr	C,S,P	16	3

Pourouma guianensis Aubl.	Moraceae	Fr	C,S,P	16	3
Micropholis guianensis (DC.) Pierre	Sapotaceae	Fr	C,S,P	16	3
Miconia mirabilis (Aubl.)L. Wms.	Melastomataceae	Fr	C,S,P	16	3
Henriettea succosa (Aubl.) DC.	Melastomataceae	Fr	C,S,P	16	3
Guatteria sp.1	Annonaceae	SS	C,S,P	16	3
Anthodiscus amazonicus GL & SM	Caryocaraceae	Fr	C,S,P	16	3
*Aechmea sp.	Bromeliaceae	Fr	C,S,P	16	3
Eschweilera ovata (Cambess.) Miers	Lecythidaceae	SS	C,P	16	3
Manilkara logifolia (DC.) Duband	Sapotaceae	Ne;SS	S,P	16	3
Hydrogaster trinerve Kuhlm.	Malvaceae	Fr;SS	C,P	15	3
Tibouchina elegans (Gardn.) Cogn.	Melastomataceae	SS	C,S,P	15	3
Rheedia macrophylla Mart.	Clusiaceae	Fr;SS	C,P	15	3
Licania sp.	Chrysobalanaceae	Fr;SS	C,P	15	3
Compamanesia guaviroba (DC.) Kiarer	Myrtaceae	Fr	C,S,P	15	3
Dialium guianense (Aubl.) Sandw.	Fabaceae	Fr;SS	S	15	3
Tocoyena bullata (Vell.) Mart.	Rubiaceae	SS	C,P	15	3
Manilkara sp.	Sapotaceae	Ne	C,P	15	3
Manilkara salzmannii (A.DC.) Lam.	Sapotaceae	Fr;SS	C,P	14	3
Psidium cattleyanum Sabine	Myrtaceae	Fr;SS	C,P	14	3
Chrysophyllum splendens Spreng.	Sapotaceae	Fr;SS	C,P	14	3
Philodendron willianisii S.D. Hooker	Araceae	Fr	C,S,P	14	3
Miconia sp.	Melastomataceae	Fr	C,S,P	14	3
Chrysophyllum sp.	Sapotaceae	Fr;SS	P	14	3
Emmotum nitens (Benth.) Miers	Icacinaceae	SS	C,P	14	3
Hortia arborea Engl.	Rutaceae	Fr;SS	P	13	3
Parkia pendula (Willd.) Benth.	Fabaceae	Gu;SS	C,P	13	3
Virola gardneri (A. DC.) Warb.	Myristicaceae	SS	C,P	13	3
Lacmellea aculeate (Ducke) Monach	Apocynaceae	Fr	S,P	13	3
Pradosia bahiensis Teixeira	Sapotaceae	Fr	C	13	3
Eugenia rostrata O.Berg	Myrtaceae	Fr;SS	P	13	3
Macrolobium latifolium Vog.	Fabaceae	Fr;SS	P	13	3
Gomidesia langsdorffii O. Berg.	Myrtaceae	SS	C,S,P	13	3

Diplotropis purpurea (L.C. Rich)Amshoff	Fabaceae	SS	P	13	3
Lecythis pisonis Cambess.	Lecythidaceae	SS	C,P	12	3
Sclerolobium densiflora Benth.	Fabaceae	SS	C,S,P	12	3
Protium heptaphyllum (Aubl.) Marchand	Burseraceae	Fr;SS	C	12	3
Passiflora quadrangularis L.	Passifloraceae	Fr	C,S	12	3
Compomanesia guazumifolia (Camb) O.Berg	Myrtaceae	SS	S	12	3
Pradosia lactescens (Vell.) Radlk.	Sapotaceae	SS	C,P	12	3
Couepia sp.	Chrysobalanaceae	SS	C	12	3
Albizia polycephalum (Benth) Killip ex Rec	Fabaceae	SS	S	12	3
Hyeromina alchorneoides Allemao	Euphorbiaceae	SS	C,S,P	11	2
Humiria balsamifera (Aubl.) J. St.-Hil.	Humiriaceae	SS	C,P	11	2
Rheedia sp.	Clusiaceae	Fr	C,P	11	2
Passiflora sp.	Passifloraceae	Fr	C,S,P	11	2
Lecythis lurida (Miers) Mori	Lecythidaceae	SS	P	11	2
Eriotheca sp.	Malvaceae	SS	P	11	2
Licania hypoleuca Benth.	Chrysobalanaceae	SS	C	11	2
Inga edulis Mart.	Fabaceae	Fr	S	11	2
Himatanthus bractethus (Vahl) Woodson	Apocynaceae	SS	C,P	10	1
Byrsonima laevigata (Poir) DC	Malpighiaceae	Fr	C,P	10	1
Nectandra sp.1	Lauraceae	SS	C,P	10	1
Randia armata (Sw.) DC.	Rubiaceae	SS	P	10	1
Pterodon emarginatus Vogel	Fabaceae	SS	P	10	1
Pterocarpus rhorii Vahl	Fabaceae	SS	P	10	1
Pouteria reticulata (Eichler) Eyma	Sapotaceae	SS	P	10	1
Parinari littoralis Prance	Chrysobalanaceae	SS	C	10	1
Myrcia thyrsoidea Berg.	Myrtaceae	Fr	P	10	1
Buchenavia grandis Ducke	Combretaceae	SS	C	10	1
Andira anthelmia (Vell.) J. F. Macbr.	Fabaceae	SS	P	10	1
Aegiphila sellowiana Cham.	Verbenaceae	SS	C	10	1
Aspidosperma polyneuron Muell. Arg.	Apocynaceae	SS	S,P	10	1
Terminalia brasiliensis (Camb. Ex A. St-Hil) Eichl.	Combretaceae	SS	P	10	1
Ficus insipida Willd.	Moraceae	SS	P	10	1

Attalea funifera Martius	Arecaceae	SS	S	10	1
Duguetia magnolioidea Maas	Annonaceae	Fr	C,S	9	1
Trichilia quadrijuga H.B.K.	Meliaceae	Fr	C,P	9	1
Psidium guajava L.	Myrtaceae	Fr	S,P	9	1
Tachigali multijuga Benth.	Fabaceae	SS	P	9	1
Miconia rimalis Naudin	Melastomataceae	Fr	P	9	1
Balizia pedicellaris (DC) Barneby & J. W. Grimes	Fabaceae	SS	P	9	1
Arapatiella psilophylla (Harms) R. S. Cowan	Fabaceae	SS	P	9	1
Tetrastylidium brasiliense Engl.	Olacaceae	SS	P	8	1
Eugenia mandioccencis Berg.	Myrtaceae	Fr	P	8	1
Maytenus sp.	Celastraceae	SS	P	8	1
Nectandra sp.	Lauraceae	Fr	C	8	1
Virola oficinalis (Mart.) Warb.	Myristicaceae	SS	C	8	1
Trichilia magnifoliola T. D. Penn.	Meliaceae	Fr	C	8	1
Tovomita sp.	Clusiaceae	SS	P	8	1
Stachyarrhena harleyi Kirk.	Rubiaceae	Fr	P	8	1
Sloanea sp.	Elaeocarpaceae	SS	P	8	1
Senefeldera multiflora (Mart.) Muell. Arg.	Euphorbiaceae	SS	P	8	1
Schoepfia cf. *obliquifolia* Turcz.	Olacaceae	Fr	P	8	1
Pouteria grandiflora (A. DC.) Baehni	Sapotaceae	SS	P	8	1
Pouteria bangii (Rusby) Penn.	Sapotaceae	Fr	P	8	1
Pogonophora schomburgkiana Miers ex Benth.	Euphorbiaceae	SS	P	8	1
Plinia sp.	Myrtaceae	SS	P	8	1
Peltogyne angustiflora Ducke	Fabaceae	SS	P	8	1
Ocotea sp.	Lauraceae	SS	C	8	1
Nectandra sp.2	Lauraceae	SS	P	8	1
Myrcia sp.1	Myrtaceae	SS	P	8	1
Myrcia sp.	Myrtaceae	SS	P	8	1
Micropholis venulosa (Mart. & Eichl.) Pier	Sapotaceae	Fr	C	8	1
Miconia hypoleuca (Benth.) Triana	Melastomataceae	Fr	P	8	1
Manilkara rufula (Miquel) Lam.	Sapotaceae	Ne	P	8	1
Mabea piriri Aubl.	Euphorbiaceae	Fr	C	8	1

Inga thibaudiana DC.	Fabaceae	Fr	C	8	1
Inga affinis Benth.	Fabaceae	Fr	C	8	1
Hymenaea coubaril L.	Fabaceae	SS	P	8	1
Guettarda platyphylla Muell. Arg.	Rubiaceae	Fr	P	8	1
Eugenia sp.	Myrtaceae	SS	P	8	1
Combretum sp.	Combretaceae	SS	P	8	1
Calyptanthes brasiliensis Spreng.	Myrtaceae	SS	P	8	1
Brosimum rubescens Taub.	Moraceae	Fr	P	8	1
Brosimum guianense (Aubl.) Huber	Moraceae	SS	P	8	1
Annona salzmannii A.DC.	Annonaceae	Fr	C	8	1
Couepia grandiflora (Mart.& Zuc.) Ben. Ex Hook.	Chrysobalanaceae	SS	P	8	1
Trichilia pleena (A. Juss.) C. CD.	Meliaceae	SS	P	8	1
Terminalia sp.	Combretaceae	SS	P	8	1
Theobroma cacao L.	Sterculiaceae	Fr	C	8	1
Talisia elephantipes Sandw	Sapindaceae	Fr		8	1
Syzygium jambos (L.) Alston	Myrtaceae	Fr		8	1
Sprucella crassipedicellata (Mart.& Endl.) Pires	Sapotaceae	Fr		8	1
Simarouba amara Aubl.	Simaroubaceae	Fr	S	8	1
Ocote insignis Mes	Lauraceae	SS	S	8	1
Neomitranthes sp.	Myrtaceae	Fr		8	1
Neea floribunda Poepp. & Endl.	Nyctaginaceae	Fr	S	8	1
Myrciaria sp.	Myrtaceae	Fr		8	1
Myrcia cf. bergiana Berg.	Myrtaceae	Fr		8	1
Myrcia cauliflora (C.Mart.) O.Berg.	Myrtaceae	Fr		8	1
Myrcia acuminatissima Berg.	Myrtaceae	Fr		8	1
Mendoncia blanchetiana Prof.	Mendonciaceae	Fr		8	1
Marlierea obversa Legrand	Myrtaceae	Fr		8	1
Marlierea cf. claussemiana (Gardner) Kiaerskou	Myrtaceae	Fr		8	1
Macoubea guianensis Aublet	Apocynaceae	Fr		8	1
Gurania sp.	Cucurbitaceae	Fr		8	1
Guapira cf. *obtusata* (Jacq.) Little	Nyctaginaceae	Fr	S	8	1
Gomidesia sp.	Myrtaceae	Fr		8	1

Ficus sp.1	Moraceae	Fr	S	8	1
Ficus sp.	Moraceae	Fr	S	8	1
Eugenia sp.1.	Myrtaceae	Fr		8	1
Eugenia cerasiflora Miquel	Myrtaceae	Fr		8	1
Dyopyros cf. *miltonii* P. Cavalcante	Ebenaceae	Fr		8	1
Croton macrobotrys Baill.	Euphorbiaceae	Fr		8	1
Cordia magnoliaefolia Cham.	Boraginaceae	Fr		8	1
Coccoloba sp.	Polygonaceae	Fr		8	1
Bowdichia virgilioides Kunth	Fabaceae	SS		8	1
Guarea macrophylla Vahl	Meliaceae	SS		8	1
Margaritaria nobilis L. f.	Euphorbiaceae	SS		8	1
Myrcia falax (Rich.)DC.	Myrtaceae	SS		8	1
Tabebuia obtusifolia (Cham.) Bureau	Bignoniaceae	SS		8	1

Figures

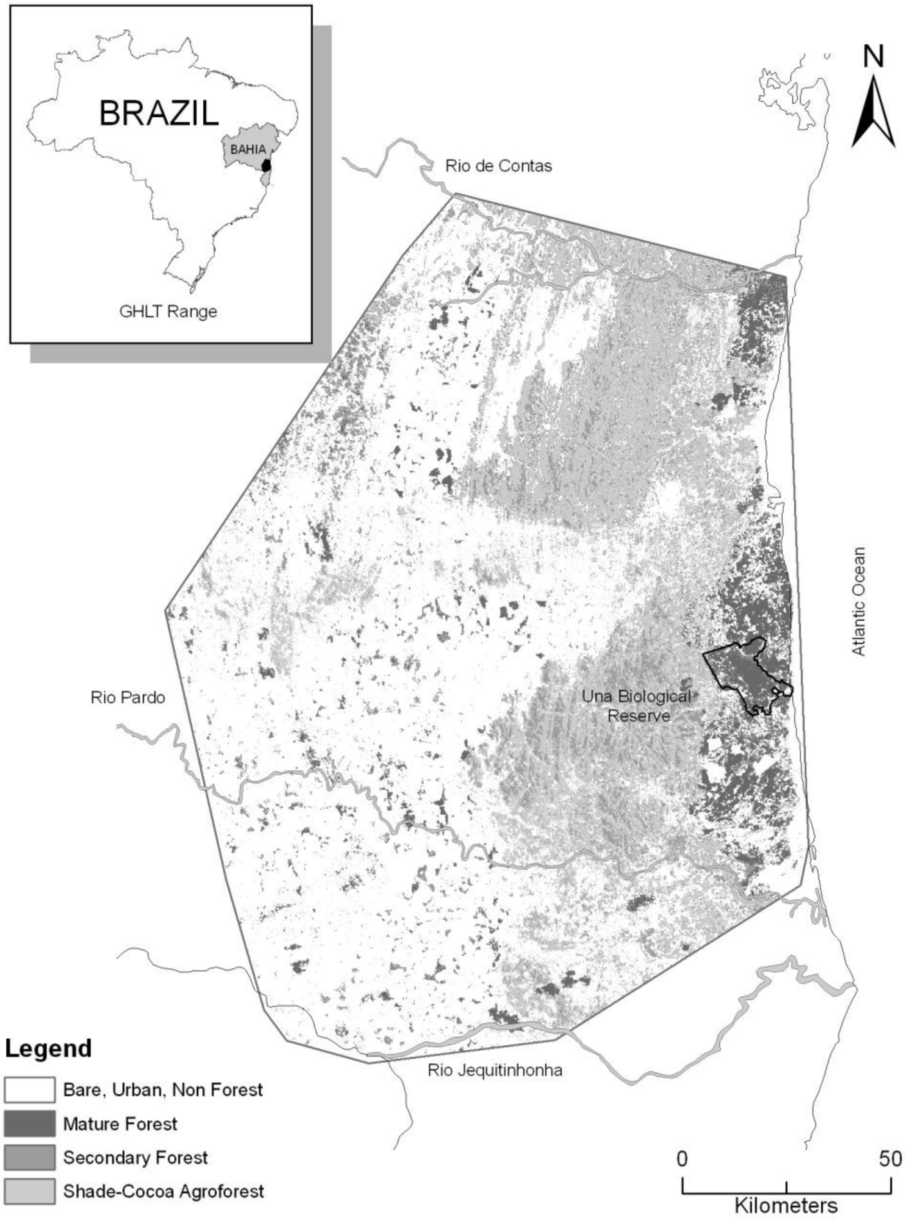

Figure 1. Geographic distribution of golden-headed lion tamarins in southern Bahia state, Brazil and location of the study site of the current study. Map created by Becky Raboy based on a reclassification of land cover at 30m resolution published in (Landau et al. 2003) from 1996-1997 Landsat data."

Chapter 2: Abundance of jackfruit (*Artocarpus heterophyllus*) affects group characteristics and use of space by golden-headed lion tamarins (*Leontopithecus chrysomelas*) in *cabruca* agroforest.

Abstract

Cabruca is an agroforest of cocoa trees shaded by native forest trees and it is now the predominant vegetation type throughout the range of golden-headed lion tamarins, *Leontopithecus chrysomelas,* an endangered primate endemic to Atlantic Forest of southern Bahia state, Brazil. Understanding how lion tamarins use this agroforest is a conservation priority. To address this question, we documented the home range size, group sizes and composition, and density of lion tamarins living in *cabruca*, primary forest, and in mosaic forest (mix of *cabruca*, primary and secondary forest). We also recorded the number of litters per reproductive season and the body condition of lion tamarins in these habitats. Diet was recorded for *cabruca* and mosaic forest groups. Lion tamarins used 43 plant species for food, 26 of them in *cabruca*. The jackfruit, *Artocarpus heterophyllus*, an exotic and invasive species, was the most important species used by lion tamarins in *cabruca* and was widely available throughout the year. Bromeliads were the most-used substrate for animal prey foraging in cabruca. In cabruca, home range size was the smallest (22-28 ha) and density of lion tamarins was the highest (1.7 ind/hectare) reported for the species, and both parameters were significantly different from groups in primary forest. Group size averaged 7.4 individuals (3-15 individuals), and was not significantly different among the three vegetation types. Groups produced one or two litters a year, and all with twins, in both *cabruca* and in mosaic forest. Adult males in *cabruca* were significantly heavier than males in primary forest (averaging 668g and 584g, respectively). Our study is the first to demonstrate that breeding groups of golden-headed lion tamarins can survive and reproduce entirely within *cabruca* agroforest. These findings have conservation implications as they will affect the estimates of habitat available for the species, number of individuals in the wild, and the likelihood that *cabruca* can be used for dispersal among forest fragments. Jackfruit proved to be a keystone resource for lion tamarins in *cabruca*, and bromeliads were important as an animal prey foraging microhabitat. If *cabruca* contains concentrated resources, such as jackfruit and bromeliads, as well as suitable sleeping sites, lion tamarins may not only survive and reproduce but may fare better than in other forest types, at least in terms of body condition and reproduction.

Key words: *Cabruca*, Agroforest, *Leontopithecus chrysomelas*, Endangered species, Jackfruit, Bromeliads, Conservation

Introduction

In a fragmented landscape, the persistence of an animal population depends on the ability of individuals to use the "matrix", the various habitats that surround isolated forest patches in a landscape (Gascon et al. 1999), and to disperse among fragments (Gascon et al. 2000; Laurance 1994; Pires et al. 2002). The matrix is an important component of the landscape (Fahrig 2001; Gascon et al. 1999; Gascon et al. 2000), as it affects within-fragment population dynamics (Fahrig 2001; Ricketts 2001) as well as metapopulation dynamics (Moilanen & Hanski 1998; Vandermeer & Carvajal 2001). The harshness of the matrix for a given species will depend on its composition and complexity. The matrix may vary from open fields such as cattle pastures that are unsuitable for an arboreal mammal, for example, to a more complex matrix resembling the original habitat that may be suitable for many species (Schroth et al. 2004).

Agroforest can be defined as a dynamic and ecologically based natural resource management practice in which trees and other tall woody plants are integrated with farms and agricultural landscape to diversify production for increased social, economic and environmental benefits (ICRAF 2000). Agroforests may provide biodiversity conservation benefits not present in deforested areas. Agroforestry may reduce the need for deforestation of new areas by offering a more sustainable economic activity than monocultures, which are more susceptible to pests (Schroth et al. 2000). Agroforest can also provide habitat and resources for forest-dependent species that would not survive in a purely agricultural landscape, or may permit species dispersal in a fragmented landscape (Schroth et al. 2004). In the Atlantic

Forest of southern Bahia, northeastern Brazil, the matrix that dominates the landscape is composed mainly of an agroforestry system locally known as *cabruca*, i.e. cacao plantations shaded by native trees. In the 1990s, *cabruca* comprised almost 40% of the Atlantic Forest of southern Bahia, and only 33% of the forest cover was composed of native vegetation (May & Rocha 1996). *Cabruca* has been considered as an important habitat for conserving the Atlantic Forest's biodiversity (Rice & Greenberg 2000; Saatchi et al. 2001), for both plants (Sambuichi 2002; Sambuichi 2006; Sambuichi & Haridasan 2007) and animals (Cassano et al. 2009; Delabie et al. 2007; Faria & Baumgarten 2007; Faria et al. 2007; Pardini 2004; Rice & Greenberg 2000; Sambuichi 2002).

Cabruca is the predominant habitat type throughout the eastern portion of the range of the golden-headed lion tamarin, *Leontopithecus chrysomelas* (Raboy et al. in press), an endangered primate (IUCN 2008) endemic to the Brazilian Atlantic Forest (Rylands 1989). The diet of lion tamarins consists mostly of ripe fruits, flowers, nectar, insects, small vertebrates, and occasionally gums (Rylands 1989; Raboy & Dietz 2004). They use tree holes as their main source of sleeping sites although vine tangles and palm leaves may also be used (Rylands 1989; Raboy et al. 2004). The estimated wild population [6,000 to 15,000] lives in a fragmented landscape (Pinto & Tavares 1994) with very few patches of forest large enough to support a genetically viable population of this species (Zeigler et al. 2010).

Assessing how lion tamarins use this agroforest is crucial for the conservation of this species (Holst et al. 2006). Important conservation questions include whether lion tamarins live and reproduce in *cabruca*, use *cabruca* for dispersal, and whether population density is similar in *cabruca* and in native forest habitats. Other studies showed that the number of trees per hectare in *cabruca* affects the availability and use of resources by lion tamarins (Oliveira et al. 2010; Raboy 2002), and may consequently affect their biology (weight and reproduction) and ecology (home range size and habitat use).

The objectives of this study were to determine whether golden-headed lion tamarins can live and reproduce entirely within *cabruca* agroforests, and to compare density, home range, group size, and body mass of lion tamarin populations in *cabruca* and in other vegetation types. As the density and richness of trees are lower in *cabruca* than in other types of forest (Alves 1990; Sambuichi 2002; Sambuichi & Haridasan 2007), we expected the abundance of food and sleeping sites to be lower in *cabruca*. Thus, we predicted that home ranges would be larger in *cabruca*, assuming that home range size is affected by availability of food resources (Clutton-Brock & Harvey 1977; McNab 1963) and has to be large enough to provide the amount of resources necessary to meet energetic and nutritional requirements for survival and reproduction (Chapman 1990). We expected that the density of lion tamarins would be lower in *cabruca* than in other vegetation types, as population density typically is proportional to food resource availability (Hanya et al. 2005; Wauters & Lens 1995). We also expected groups to be smaller and individuals to weigh less in *cabruca* than in other vegetation types as food availability affects group size and individual weight (Chapman et al. 1990; Kirkwood 1983).

Methods

Study sites

This study was carried out in the cacao-growing region of southern Bahia, northeastern Brazil, in the municipalities of Ilhéus, Jussari, Camacan, Arataca and Una. Study sites (Fig. 1) included one public protected area (Una Biological Reserve; 18,500 ha), four private areas (Almada, Riachuelo, Santa Rita and São José farms), two private reserves (Ararauna and Teimoso) and one rural settlement (Bem Te Vi).

Data collection

We captured ten lion tamarin groups in the study areas using Tomahawk live traps (48.3 x 15,2 x 15,2 cm) baited with banana and placed on platforms 1.5 meters above ground (Dietz et al. 1996). During capture and examination of the animals we recorded for each individual: weight, knee to heel and wrist to elbow lengths, reproductive condition, and group size and composition (age and sex of individuals in the group). We adjusted the group size and composition to include any individuals seen outside the traps. Lion tamarins are cooperative breeders that live in cohesive family groups (Dietz et al. 1994) and thus we assumed that individuals that remained in the vicinity of captured individuals were members of the same group. We used tooth wear to estimate the age of adult animals and tooth wear, body weight and dental composition to estimate ages of younger members of groups (Bales et al. 2001; Dietz et al. 2000).

We affixed radio-collars to one or two individuals from each group to facilitate location and monitoring. We followed the lion tamarins during full days (from when the group left its sleeping site in the morning until when they entered a sleeping site in the evening), or partial days (either from the time they left the sleeping site until noon, or from noon until when they entered a sleeping site).

Groups were categorized *post hoc* according to the types and combinations of habitat occurring within their home ranges: primary forests (Una Biological Reserve: Portão 2, Jeremy and Piavelha groups); *cabruca* (municipality of Ilhéus: Almada, Bomfim and Santa Rita groups), and a mosaic of *cabruca*, primary and secondary forests (municipalities of Una, Arataca, Camaca and Jussari: Ararauna, Bem te vi, São José and Teimoso groups, respectively) hereafter referred to as mosaic groups. For two of the primary forest groups (Jeremy and Piavelha), we used information about group size and composition, and home range size and density from Dietz et al. (1996). We defined vegetation types used by the lion tamarins using categories adapted from (Catenacci et al. 2009):

Primary forest: forest with little or no signs of past human disturbance, a closed canopy, trees in general at least 20 m high with large diameters, many bromeliads in a wide range of sizes and an extensive layer of vines.

Secondary forest: forest with visible signs of previous human disturbance, which has been subjected to either ‘general’ (recovering from complete deforestation) or ‘selective’ logging (recovering from the cutting of selected species).

Cabruca: forest in which the undergrowth has been cut and replaced by cacao trees.

Mosaic forest: tamarin home ranges that included the previous three vegetation types.

Groups that lived mostly in primary forests were studied during three periods: from August 1992 to June 1994 (Piavelha), from September 1994 to July 1995 (Jeremy), and from March 2005 to April 2006 (Portão 2). All groups in *cabruca* and mosaic forests were studied from April 2008 to September 2009. For the mosaic groups, we recorded vegetation type (primary, secondary, or *cabruca*) and group location at 20-min intervals using maps with marked trails (groups Jeremy, Piavelha and Portão 2) or GPS (all others). For both *cabruca* and mosaic groups, we also collected information about use and location of feeding trees. Whenever possible we identified feeding trees to the species level. Group size and the presence of infants were recorded daily. Whenever possible we also collected information on size, location and composition of non-focal groups observed while following focal groups or during encounters with conspecifics.

Data analysis

Diet

Habituation to human observers varied from high (*cabruca* groups) to medium or low (mosaic groups) which made it difficult to record feeding activities of mosaic groups. Thus our data on feeding come mainly from *cabruca* groups. We calculated the number of feeding tree species (overall richness) used by the study groups living in *cabruca* and in mosaic forest. We also calculated the total number of visits to feeding trees. We recorded the type of substrate used by the lion tamarins when foraging for animal prey and the time spent in this activity.

We used Jaccard's coefficient of similarity (Magurran, 1988) to evaluate the similarity of food-plant species used by lion tamarins in *cabruca* groups and in mosaic groups. We also compared the plant species consumed by these above-mentioned groups with the list of plant species consumed by lion tamarins in *cabruca* reported in (Oliveira et al. 2010), first chapter of this dissertation. The Jaccard index (J) was calculated as J=s/(a+b+s), where **s** is the number of species shared across two areas, **a** is the number of species found exclusively in the first area and **b** is the number of species found exclusively in the second. We estimated mean and standard error of the mean (SEM) for the total number of individual trees used by the lion tamarins. We considered species for which the number of individuals was higher than the mean + SEM to be the most important species for the lion tamarins in *cabruca* (as in (Oliveira et al. 2010). We recorded the geographic location of all individual food trees used by lion tamarins as well as the month when each individual tree was used.

Home range

We excluded the São José group from all analyses except size and condition, because it was composed of two dispersing adult males and thus was not a breeding group. We estimated home range size using the minimum convex polygon method (Mohr 1947). Home range sizes were compared using one way ANOVA followed by least squares mean t-tests for multiple comparisons using a significance level of $p < 0.05$.

Density

We estimated tamarin density by dividing the number of individuals in each group by the group's home range size. We considered only exclusive home ranges (with no overlap among group home ranges) in the calculation of density. We compared densities among all vegetation types using one-way ANOVA followed by least squares mean comparisons using a significance level of $p < 0.05$.

Group sizes and composition

Group size and composition varied over the study period. Thus, we estimated the sizes of each group considering the average of group size recorded on each day of observation. We evaluated differences in group size among the three different vegetation types using one-way ANOVA.

Size and condition of the lion tamarins

We compared the mean weights of adult individuals in each group using one way ANOVA followed by least squares mean comparisons using a significance level of $p < 0.05$. We evaluated the condition of individual males and females by analyzing residuals of a regression (Packard & Boardman 1988) between individual weight and knee-heel length. We selected the residuals and used one way ANOVA to compare the means of the residuals followed by least square means t-tests for multiple comparisons using a significance level $p < 0.05$. For those analyses we considered only adult individuals, categorized according to tooth wear.

Results

Diet

Overall, our study groups used 43 plant species from 24 families (Table 1). *Cabruca* groups used 26 plant species while mosaic groups used 23 species. We identified 35 taxa of trees at least to genus level. From these, 22 (12 in *cabruca* and 17 in mosaic forest) were also represented in the list of key tree species identified in

Oliveira et al. (2010). We were unable to identify 19 individual feeding trees (15 from mosaic groups and four from *cabruca* groups). In *cabruca,* the families Bromeliaceae, Mimosaceae and Moraceae were dominant in number of species and number of individuals. The three species used most frequently belonged to the Moraceae and Mimosaceae families. We recorded only two species belonging to the Myrtaceae and Sapotaceae families.

There was a 35% similarity of food-tree species between *cabruca* and mosaic, 32% between mosaic and the *cabruca* species listed in (Oliveira et al. 2010) and 15% between the species used by *cabruca* groups and the list of *cabruca* species used by the lion tamarins in (Oliveira et al. 2010). Seven species were present in the diet of the groups from both *cabruca* and mosaic forest.

Species composition and dominance in food-tree species varied between groups that lived in *cabruca* and in mosaic forest (Fig. 2 a and b). Jackfruit (*Artocarpus hetrophyllus*) was the dominant species in the diet of individuals in both habitats combined (33.5% of total food tree individuals used) as well as in *cabruca* and mosaic habitats (37.5% and 21.3%, respectively). *Ficus gomelleira*, (10.4%) and *Inga affinis* (9.3%) were the second and third most-used plant species, respectively. Fruits of the two most-used plant species were available throughout the year (Table 2). The level of dominance of *A. heterophyllus* in the diet of lion tamarins varied among study groups in *cabruca* comprising 55%, 33% and 25% of the fruits consumed by Almada, Bomfim and Santa Rita groups, respectively. For mosaic groups, *A. heterophyllus* comprised 60%, 52%, 14.3% and 2.1% (Bem te Vi, São José, Teimoso and Ararauna groups, respectively). In the latter groups, it was consumed mostly in *cabruca* and to a lesser extent in secondary forest. However, differences in sample size, degree of habituation of the groups and changes in home range may have affected the results obtained in mosaic forest. For example, we recorded only five individual trees used by the Bem te Vi mosaic group (three of them were *A. heterophyllus*); the São José mosaic group shifted its home range to a *cabruca* area with an abundance of jackfruit trees.

In *cabruca*, the three most important plant species represented 79%, 76% and 54.5% of the fruits consumed by the Almada, Bomfim and Santa Rita groups, respectively, and were widespread inside the home ranges of these groups (Fig 3 a, b and c). The number of plant species in the diet of *cabruca* groups varied from nine to at least 21 species (Fig. 4 a, b and c). Bromeliads were the most common foraging sites for animal prey in both *cabruca* (96.7%) and mosaic forest (80.6%) followed by tree bark (Table 3). For some groups, bromeliads were the only substrate used for foraging for animal prey. The lion tamarins spent up to 220 minutes a day foraging for animal prey in *cabruca* areas and up to 98 minutes a day in mosaic forest areas. Considering the time that lion tamarins spent in feeding behavior (both fruits and animal prey foraging) they spent 61 ± 11.1 % foraging in bromeliads in *cabruca* and 35.7 ±12.6% in mosaic forest.

Home ranges

The average home range size for all study groups was 83 ha, ranging from 22 ha to 197 ha (Table 4). We observed a significant difference in home range size in the three vegetation types (F=5.70, df=8, P=0.0410). The average home range size for groups that used *cabruca* exclusively (average 45ha) was significantly smaller (P=

0.018) compared to groups from primary forests (average 140 ha), but not different (P=0.525) from mosaic groups (average 65 ha). Home range size also differed between mosaic groups and primary forest groups (P=0.044). The smallest home range sizes reported for the species (22 and 28 ha) occurred in two of the three *cabruca* groups. We observed that 80% of the home range of one group (Bomfim) overlapped the home range of another group (Almada), both living in *cabruca*.

Density

The overall mean density in our study was 0.12 individuals per hectare, a value in the range of densities reported for the species in other studies (Table 5). The average density of tamarins in *cabruca* areas was 0.17 individuals/ha (range: 0.1-0.21 individuals/ha), the highest density recorded for the species. The average density in mosaic groups was 0.13 individuals/ha (range: 0.08 - 1.8 individuals/ha) and 0.06 individuals/ha in primary forest (range: 0.04 - 0.11 individuals/ha). Although those ranges suggest a difference in lion tamarin densities in the three vegetation types, the differences were not statistically significant (F= 4.36, df= 8; P = 0.067). However, the density recorded in *cabruca* was significantly higher than the density recorded in primary forest groups (P= 0.0267).

Based on differences in size and composition, we estimated that the range of each of our study groups was bordered by one to six neighboring groups. *Cabruca* groups were bordered by the highest number of neighbors (3-6), while in two of the mosaic groups (Teimoso and São José) we observed no neighbor groups (i.e. no observed encounters with conspecifics) and for one group (Bem te Vi) we observed only one encounter with conspecifics. We observed encounters with at least three different groups of lion tamarins inside the overlap area of the groups Almada and Bomfim (Fig. 5a). Most encounters with conspecifics in *cabruca* occurred near the center of the group's home range, while for mosaic groups they occurred on the edge of the group's home range (Figs.5a to 5c).

Group sizes and composition

Group size varied from 3 to 15 individuals (Table 6) and averaged 7.4. There was no difference in group size among the three vegetation types (F=0.51, df =8, P= 0.6238). The average size of groups in *cabruca* (this study) was similar to reports for groups of lion tamarins (Table 7). We observed that all groups but one contained at least one reproductive female, one to four adult males and other individuals (subadults, juveniles and infants) probably related to them (Table 8). Two reproductive females were recorded in one group (Ararauna) at the first capture, and no reproductive females were observed in the Santa Rita group, although one adult female joined the group a few weeks after the capture.

We observed individuals of all age classes, including newborn infants (born within the study period), in all study groups. We recorded the birth of 14 litters (26 infants) of nine reproductive females during the study (Table 9). Groups in both *cabruca* and mosaic forest produced one litter per reproductive season and in all birth events the reproductive female gave birth to twins. The Ararauna group, with two reproductive females, produced litters of twins one week apart. Group from primary forest produced twins just in 50% of litters and 0.4 litters per reproductive season.

Size and condition of the lion tamarins

The average weight of adult individuals was 653g for *cabruca* groups, 614g for mosaic groups and 586g for primary forest groups. We found significant differences in the weights of adult males living in the three vegetation types (F=4.54, df=24, P=0.023). Males from *cabruca* were heavier than males from primary forest (P= 0.0131) and mosaic (P= 0.0263); however, males from primary forest and mosaic forest did not differ significantly (P= 0.573). We found no difference in the weights of adult females in the three vegetation types (F=0.07, df=12, P= 0.929). The regression between weight and knee-heel length, performed in order to evaluate the body condition of the lion tamarins was significant for males (R^2= 0.35, $F_{1, 28}$, P=0.0006) but not for females (R^2= 0.005, $F_{1, 14}$, P=0.79). The residuals of the regression were not significantly different for females among the different vegetation types (F=2.17, df=16, P= 0.153). However, the residuals of the regression were significantly different for males (F=5.37; df= 30, P=0.010). Males from *cabruca* and primary forest were significantly different (P= 0.003) although neither males from *cabruca* and mosaic forest nor from mosaic and primary forest were different (P= 0.132 and P= 0.119, respectively).

Discussion

Our study is the first to demonstrate that breeding groups of golden-headed lion tamarins can survive and reproduce in home ranges entirely within *cabruca* agroforests. This observation is important for the conservation of this species for two reasons. First, it increases the estimated total amount of habitat that may be used by the species, and thus the estimated number of individuals in nature. Second, it suggests that lion tamarins can use *cabruca* for dispersal among forest patches previously considered as isolated. For both these reasons, populations may be less vulnerable to the negative genetic and demographic effects of habitat fragmentation in areas where *cabruca* connects native forests.

Shaded agroforest systems are important for arboreal mammals, especially for primates, functioning as a refuge, and feeding and breeding areas (Estrada et al. 2005; Vaughan et al. 2007). Primate species have been recorded living and reproducing in shaded agroforest systems in other places [the mantled howler monkey, *Alouatta palliata* in shaded coffee plantations, (McCann et al. 2003; Munoz et al. 2006); *Alouatta palliata* in shaded cocoa (Munoz et al. 2006); *Alouatta palliata* (Williams-Guillen et al. 2006); *Alouatta palliata* and the Geoffroy's spider monkey, *Ateles geoffroyi* in shaded cocoa and shaded coffee (Estrada & Coates-Estrada 1996)].

Diet

The diet of groups that lived exclusively in *cabruca* comprised few plant species from the Myrtaceae and Sapotaceae families. The species from these two families are the most important in the diet of the lion tamarins (Oliveira et al. 2010), Chapter 1, this dissertation). These two families are usually rare or absent in *cabruca* (Vinha & Silva 1982) probably because the majority of Myrtaceae and Sapotaceae species are slow-growing climax species typically found in low density and thus the probability of these seedlings being eliminated by weeding in *cabruca* is very high (Sambuichi & Haridasan 2007). In contrast, the three tree species most frequently used by lion tamarins in *cabruca* are typically abundant in this agroforest. Both *A. heterophyllus* and *Ficus* spp. have been reported as very abundant if not the dominant species in *cabruca* areas (Hummel 1995; Sambuichi 2002; Sambuichi 2006; Sambuichi & Haridasan 2007). Species of the genus *Inga* are also common in *cabruca* (Sambuichi 2002; Vinha & Silva 1982) and because they are fast-growing they are planted by agroforest owners when they need to improve shade in *cabruca* areas (Sambuichi & Haridasan 2007).

A. heterophyllus was the only species present in the diet of all study groups in mosaic and *cabruca* forest. Jackfruit is an exotic species introduced into cacao plantations of southern Bahia and its edible fruits are widely used by local people (Correia 1975). Each jackfruit tree may produce up to 100 fruits a year, with individual fruits weighing up to 40 kg (Correia 1975). This species has high recruitment rates, is the dominant species in number of individuals and biomass in many areas (Abreu 2008; Cunha et al. 2006) and has been considered an invasive species in some regions of Brazil (Abreu 2008; Horus 2010). The distribution pattern of *A. heterophyllus* may be either equally spaced or clumped (Boni et al. 2009), and we observed both patterns in our *cabruca* study areas. In our study areas, *A. heterophyllus* fruits were available all year. In the Amazon, higher fruit production is expected from January to March and July to September (Falcão et al. 2001).

In contrast with our assumption that *cabruca* would contain fewer resources than other vegetation types, we found that jackfruit provides a superabundant and reliable food source for tamarins. We believe that jackfruit is a keystone resource in *cabruca* in which it occurs, providing the food resources necessary to sustain breeding groups of golden-headed lion tamarins.

Bromeliads were also an important resource for lion tamarins in *cabruca*. In *cabruca* areas bromeliads comprised 96.8% of all lion tamarin animal foraging sites. Previous studies also reported bromeliads as the principal foraging substrate for animal prey but with lower percentage of use, 50% of the records in (Rylands 1989), 76.6% in (Raboy & Dietz 2004), 81.7% in (Catenacci 2008) and 86% in (Guidorizzi 2008) than in this study. However, contrary to other studies (Catenacci 2008; Guidorizzi 2008; Oliveira et al. 2010; Raboy & Dietz 2004), fruits of bromeliads were not consumed frequently by lion tamarins in our study. Guidorizzi (2008) correlated the high consumption of fruits from bromeliads to a lower abundance and availability of food resources in his study area. Fruits of bromeliads are rich in carbohydrates and poor in protein and minerals (Catenacci 2008) as are most fruits (Rode et al. 2006). It is possible that the low consumption of bromeliads in our study is related to high abundance of jackfruit that is very rich in carbohydrates. We believe that lion tamarins gained energy mainly from the temporally and spatially abundant jackfruit, which allowed them to spend more time foraging in bromeliads to obtain fat and protein from animal prey (Erbesdobler 2003).

Home range sizes and density

Contrary to what we expected, home range sizes were smaller and the density of lion tamarins was larger in *cabruca* compared to other vegetation types. Previously reported home range sizes for lion tamarins range from 40 to 130 ha (Raboy & Dietz 2004; Rylands et al. 1989) and up to 200 ha in one study (Dietz et al. 1996). Many factors can affect estimates of home range size including the methods to estimate home ranges, duration of observation, and biological characteristics such as individual body size, group size and composition and biomass (Benson et al. 2006; Chapman 1990; Clutton-Brock & Harvey 1977; Dietz et al. 1997; Lehmann & Boesch 2003; Milton & May 1976; Terborgh 1983). However, none of these seem to be a reasonable explanation for differences in home range sizes reported in our study. Group sizes and composition were similar in our study groups living in different vegetation types. Duration of observation was in the range for those reported in other studies, and we used methods similar to those of other authors to estimate home range sizes.

Food availability and density of animals can also affect home range size. Although we did not quantify the availability of food resources in *cabruca*, we observed high spatial and temporal abundance of jackfruit, which probably affected the size of home ranges of the *cabruca* groups. Home range size has been reported to be negatively correlated with food availability (Herfindal et al. 2005; Litvaitis et al. 1986; Mares et al. 1982). As availability of food resources increases, individuals can acquire sufficient resources for survival and reproduction within a smaller area (Benson et al. 2006). Boutin (1990) experimentally tested this hypothesis and observed a decrease in home range for terrestrial mammals with an increase in resources abundance. This may explain the smaller home range sizes of *cabruca* and mosaic groups, in which three of four groups used jackfruit as the main fruit resource. However, the relationship between food availability and home range size is difficult to demonstrate because food supply and population density are often positively correlated (Hanya et al. 2005; Heydon & Bullon 1997; Wauters & Lens 1995). As availability of food resources increases, more individuals are able to exploit them for survival and reproduction. Thus, abundance of jackfruit in *cabruca* may affect home range size directly (individuals need to travel less distance to find adequate food) or indirectly, by permitting increased density of lion tamarins in the area. High population densities, in general, result in smaller home range sizes (Forsyth & Smith 1973; Maza et al. 1973) as shown for lion tamarins (Dietz et al. 1996; Holst et al. 2006; Kierulff et al. 2002) and in our study.

Our study groups in *cabruca* had the highest densities reported for the species. This affirmation is supported by the observed overlap of home ranges (almost 80%) of two groups (Almada and Bomfim), and the high number of encounters with different groups of conspecifics inside this overlap area. We also observed a high number of encounters on the exclusive parts of the home range of these two groups and higher numbers of encounters in *cabruca* groups compared to mosaic groups.

Group sizes and composition

In contrast with what we expected, group sizes were similar across vegetation types. Changes in group size may be affected by many factors. For example, Pinto (1994) suggested that human activities in unprotected areas might have caused the smaller group sizes found in his study. On the other hand, Chapman (1990) proposed that patch characteristics (e.g. size, density and distribution) may limit group size. Patch size would limit the number of individuals that could exploit such a patch, while patch density would affect group feeding efficiency, and patch distribution would affect the distance that animals must travel to find food (Chapman 1990). Spatial distribution of resources will affect path length (the distance groups must travel each day) which may also act to constrain group size (Chapman et al. 1995; Chapman & Chapman 2000b; Janson & Goldsmith 1995; Wrangham et al. 1993). However, the results of our study did not support either hypothesis. We found no correlation between group size and degree of protection. The group sizes were similar in private reserves and productive farms. Also, despite the high availability of food resources (specifically jackfruit) found in *cabruca*, groups that lived there were no larger than those in other types of vegetation. One possible constraint on lion tamarin group size in *cabruca* is the limited number of suitable sleeping sites. As tamarins in a group sleep together, mainly in tree holes (Dietz et al. 1996; Raboy & Dietz 2004; Rylands 1989), it would be necessary to have trees with DBH large enough to support large groups of tamarins. Another possible explanation is that group sizes in *cabruca* may be limited by predation (Stanford 1995), especially in *cabruca*, where predation risk is high (Chapter 3 of this dissertation).

The reproductive success of lion tamarins in *cabruca* is greater than the average reported for the species in other areas. In *cabruca* groups all litters consisted of twins in every reproductive season. Reproductive female lion tamarins may produce 1-2 offspring per litter, and up to two litters per year (Dietz et al. 1994; Holst et al. 2006). Holst et al. (2006) reported females having four offspring a year (two litters of twins) in just 8% of years, although higher values were reported by others. Dietz et al. (1996) observed 13 litters (20 infants) from seven reproductive females in which 54% were twins and 46% singletons. Similarly, Bach et al. (2001) reported two litters per year for only 27% of reproductive females. The high availability of food in *cabruca* may affect the number of litters and offspring produced by lion tamarins in *cabruca*, as has been shown for other species elsewhere (Chapman et al. 1990; Epple 1970; Kirkwood 1983) and for lion tamarins (Kleiman 1983). The presence of groups with offspring of several consecutive litters in *cabruca*, and with similar or higher number of litters and offspring per year than in other vegetation types indicates that golden-headed lion tamarins can live and reproduce in this agroforest.

Size and condition of the lion tamarins

The lion tamarins in *cabruca* were larger and heavier compared to other vegetation types. Availability and quality of food may affect primate weight and population biomass (Brugiere 2002; Kirkwood 1983; Knott 1998), including callitrichid primates (Epple 1970). In our study, most of the fruit consumed by lion tamarins living in *cabruca* consisted of jackfruit. These fruits are rich in carbohydrates and were available year round in *cabruca*. In addition, lion tamarins spent a large amount of time foraging for animal prey, which are sources of protein and fat, as mentioned before. Diets rich in carbohydrates and protein may result in increased weights and sizes of lion tamarins using these agroforests. Another possible explanation for the heavier weight of lion tamarins in *cabruca* may be the effect of the density of tamarins in these areas. Scheffer (1955), using data from a variety of mammal species, suggested that an increase in aggressive contact among individuals in a high density environment might result in selection for larger and stronger individuals. In our study, the heaviest and largest tamarins were in *cabruca* areas, where the density was highest. In those areas we observed frequent aggressive encounters, as expected due to higher densities of tamarins. However, we don't have enough information to address this hypothesis.

In contrast with reports by other authors (Alves 1990; Coimbra-Filho & Mittermeier 1973), we found that lion tamarins can live in *cabruca* agroforest that is not associated with native forest. If *cabruca* agroforests contain a concentrated food source, such as jackfruit, and bromeliads, lion tamarins may not only survive and reproduce but may fare better than in other forest types, at least in terms of body condition and reproduction.

Conclusion and recommendations

Our results show that lion tamarins can live and reproduce in some types of *cabruca* agroforest, with demographic and ecological aspects apparently similar to groups that live in native forest habitats. However, *cabruca* areas, even those close to each other, vary in richness and density of overstory trees (Sambuichi & Haridasan 2007) and consequently in forest structure. Understanding how or whether lion tamarins use the range of available *cabruca* types would help to refine estimates of the number of lion tamarins in the wild [6,000-15,000 (Pinto & Rylands 1997)]. *Cabruca* was not considered in this estimation. The precision of these estimates is critical in modeling estimates of species viability and in making management recommendations (Lacy 2000).

Our results show that the conservation and appropriate management of *cabruca* agroforest can contribute to the conservation of golden-headed lion tamarins and probably to that of many other endangered species as well. Based on our results, we suggest that changes in management of native forest and *cabruca* would improve the conservation status of this endangered primate. First, the retention of all native forest fragments within the geographic distribution of lion tamarins would positively affect the long-term conservation of lion tamarins. At the local scale, tamarins in *cabruca* would benefit from retention or planting of tree species known to be important as sleeping sites or for foraging, and by increasing the density of these trees in *cabruca* (Oliveira et al. 2010). Cocoa farmers should be encouraged to cultivate organic cocoa, which brings a better price and consequently would decrease the pressure to remove cocoa in favor of more profitable types of crops. Economic incentives should be given to farmers that adopt a tamarin-friendly management of *cabruca*. This could be accomplished by creating a certification of tamarin-friendly cocoa, which also might result in a better market price. Finally, independent of any management strategy, retention of traditional *cabruca* should be favored over clear-cutting for conversion to any agricultural monocultures or to cattle pasture.

Tables

Table 1: Plant species used for food by lion tamarins in *cabruca* and mosaic forest with the total number of individuals of each tree species used and the total number of visits to each tree species.

Scientific name	Family	Ind		N of visits	
		C	M	C	M
**Artocarpus heterophyllus* Lamark	Moraceae	106	17	227	27
**Ficus gomelleira* Kunth & Bouché	Moraceae	38	0	83	0
**Inga affinis* Benth.	Mimosaceae	28	6	37	6
**Duguetia magnolioidea* Maas	Annonaceae	20	1	27	1
Celtis glycycarpa Mart. ex Miq.	Ulmaceae	16	1	39	1
**Musa paradisiaca L.*	Musacae	8	6	8	6
Sarcaulus brasiliensis (A.DC.) Eyma.JPG	Sapotaceae	11	0	26	0
Hohenbergia blanchetii (Baker) EM ex Mez	Bromelidae	9	0	9	0
Hohenbergia disjuncta L.B.Sm	Bromelidae	8	0	10	0
Cecropia hololeuca Miq.	Cecropiaceae	8	0	9	0
**Miconia mirabilis* (Aubl.)L. Wms.	Melastomataceae	0	6	0	6
**Symphonia globulifera* L.	Clusiaceae	3	3	4	4
Spondias venulosa Mart. Ex Engl.	Anacardiaceae	5	0	5	0
**Tapirira guianensis* Aublet	Anacardiaceae	5	0	13	0
**Macoubea guianensis* Aublet	Apocynaceae	0	4	0	5
**Theobroma cacao* L.	Sterculiaceae	3	1	3	1
**Aechmaea* sp	Bromeliaceae	0	2	0	3
Carica papaya L.	Caricaceae	2	0	2	0
Chondrodendron microphyllum (Eichl)Mol	Menispermaceae	0	2	0	3
**Eugenia cauliflora* DC.	Myrtaceae	0	2	0	4
**Lacmellea aculeate* (Ducke) Monach	Apocynaceae	0	2	0	2
Myrtaceae sp1	Myrtaceae	0	2	0	2

Myrtaceae sp3	Myrtaceae	0	2	0	2
***Protium sp*	Burseraceae	0	2	0	2
Syngonium sp	Araceae	2	0	2	0
Ampelocera glabra Kuhlm	Ulmaceae	0	0	0	0
Anacardiaceae sp1	Anacardiaceae	0	1	0	2
Bactris ferruginea Burret	Arecaceae	0	1	0	1
***Aechmea lingulata* (Linnaeus) Baker	Bromelidae	1	0	1	0
Coffea Arabica L.	Rubiaceae	1	0	1	0
***Cordia nodosa* Lam	Boraginaceae	1	0	5	0
**Elaeis guianeensis* Jacq.	Arecaceae	1	0	1	0
**Ficus* sp	Moraceae	0	1	0	3
**Inga edulis* Mart.	Mimosaceae	1	0	1	0
***Micropholis gardneriana* (ADC)Pier JPG	Sapotaceae	0	1	0	2
Myrtaceae sp2	Myrtaceae	1	0	1	0
Passiflora haematostigma Mart exMart.JPG	Passifloraceae	0	1	0	1
Persea Americana Mill.	Lauraceae	1	0	1	0
**Pourouma velutina* Miq.	Moraceae	0	1	0	1
**Protium heptaphyllum* (Aubl.) Marchand	Burseraceae	0	1	0	5
Quararibea turbinata Pohl.	Bombacaceae	1	0	5	0
Sapotaceae sp1	Sapotaceae	1	0	1	0
Soroceae sp	Moraceae	0	1	0	1
Unknown	*Unknown*	4	15	4	20
TOTAL		285	82	523	109

Veg, vegetation type; Ind, N of individuals; Freq, Frequency of use; %, relative abundance; C, *cabruca*; M, mosaic. * Species also recorded on the list of key species for the lion tamarins presented in chapter 1. ** Genus also recorded in the list of key species for the lion tamarins presented in chapter 1

Table 2. Percentage of each plant-food species used by the three groups of golden-headed- lion tamarin in *cabruca* agroforest over the period of study (May 2008 to November 2009), with the total number of individuals and species used per month. In parentheses is the sample effort in days of observation for each month.

Species	2008								2009								
	M (2)	J (5)	J (6)	A (4)	S (6)	O (3)	N (3)	D (4)	J (4)	F (6)	M (7)	A (11)	M (5)	J (7)	J (7)	A (3)	S (6)
Artocarpus heterophyllus	67	40	64	62	60	67	88	92	71	38	29	14	15	23	60	60	68
Ficus gomelleira		27	7	10	33	33			29	44	18	2	10	19	20	20	19
Inga affinis											14	18	20	8			
Duguetia magnolioidea		13									2	14	20	15			
Bromeliaceae		7	7	5						19	10	8		4			
Celtis glycycarpa											4	16	5				
Sarcaulus brasiliensis												10	25	12			
Musa paradisiaca				5	3						2	1				20	13
Cecropia hololeuca	33							8			6	4					
Spondias venulosa				5							4	3					
Tapirira guianensis			7								2	3			10		
Symphonia globulifera			7								2	3			10		
Syngonium sp				10													
Carica papaya		7												4			
Inga fogifolia												2					

Myrtaceae sp1											2	1					
Elaeis guianeensis							13										
Quararibea turbinata															10		
Cordia nodosa													1				
Persea americana					3												
Inga edulis		7															
Ficus sp											2						
Myrtaceae sp2											2						
Coffea arabica														4			
Theobroma cacao				5													
Unknown			7								2	2	5	4			
Total individuals	3	15	14	21	30	6	8	12	7	16	49	93	20	26	10	5	31
Total species consumed	2	6	6	7	4	2	2	2	2	2	14	15	7	10	4	3	3

Table 3. Foraging substrates used by the lion tamarin groups for animal prey. Numbers represent the total number of observations and in parenthesis is the percentage that each substrate used.

Substrate	*Cabruca*			Mosaic		
	Almada	Bomfim	Santa Rita	Ararauna	Teimoso	São José
Bromeliads	159 (93%)	127 (100%)	290 (97.3%)	55 (100%)	25 (69.4%)	3 (75%)
Tree bark	10 (5.8 %)	-	4(1.3%)	-	7 (19.4%)	1 (25%)
Palm	1 (0.6%)	-	2 (0.7%)	-	3 (8.3%)	-
Leaves	-	-	2 (0.7%)	-	1 (2.8%)	-
Other	1 (0.6%)	-	-	-	-	-

Table 4. Home range sizes, vegetation type and sample effort for the study groups. Home range size was estimated using minimum convex polygon methods. Sample effort included full and partial days of observation.

Group	Vegetation type	Home Range size (in hectares)	Number of days of observation
Almada	*Cabruca*	84	64
Bomfim	*Cabruca*	22	24
Santa Rita	*Cabruca*	28	66
Ararauna	Mosaic	65	32
Bem te Vi	Mosaic	65	15
Teimoso	Mosaic	64	60
Jeremy	Primary	129	48
Piavelha	Primary	93	61
Portão 2	Primary	197	62

Table 5: Density expressed as number of individual of lion tamarin per hectare in this and other studies.

Density	N of groups	Source
0.07	2	Rylands 1989
0.08	4	Dietz et al. 1994
0.05	4	Dietz et al. 1996
0.10	8	Holst et al. 2006
0.11	3	Holst et al. 2006
0.07	2	Guidorizzi 2008
0.12	9	This study

Table 6. Range and average number of individuals in each study group of lion tamarin in the three vegetation types.

Group	Vegetation type	Range of individuals per group	Average group size
Almada	*Cabruca*	5-12	8.3
Bomfim	*Cabruca*	3-5	4.7
Santa Rita	*Cabruca*	3-6	5.3
Ararauna	Mosaic	8-15	11.8
Bem te Vi	Mosaic	7-8	7.7
Teimoso	Mosaic	2-7	5.2
Jeremy	Primary	4-7	5.1
Piavelha	Primary	9-12	9.8
Portão 2	Primary	6-9	7.3

Table 7. Average group sizes for lion tamarins in this and other studies with the number of studied groups of each study.

Average group size	N of groups	Source
5.0	2	Rylands 1989
4.5	26	Pinto 1994
5.2	4	Dietz et al. 1994
5.0	4	Dietz et al. 1996
5.3	3	Raboy and Dietz 2004
5.0	3	Holst et al. 2006
4.7	5	Guidorizzi 2008
7.4	9	This study

Table 8. Composition of the study groups at first capture. Composition was estimated by summing individuals captured plus those individuals observed outside the traps.

Group	Alm	Bom	Sta	Ara	BTV	Tei	Jer	Pia	Por
Reproductive ♀	1	1	-	2	1	1	1	1	1
Adult ♀	1	-	-	-	-	1	1	1	1
Adult ♂	4	3	2	4	3	1	1	3	2
Sub adult ♀	1	1	-	1	1	-	-	-	-
Sub adult ♂	1	-	2	1	1	-	1	2	1
Juveniles	-	-	1	2	2	2	2	2	-
Infants	2	-	-	-	-	-	-	-	-
Total	10	5	5	10	8	5	6	9	5

Alm=Almada; Bom= Bofim; Sta= Santa Rita; Ara= Ararauna; BTV= Bem te Vi; Tei= Teimoso; Jer= Jeremy; Pia= Piavelha; Por= Portao 2

Table 9: Number of litters and offspring for each reproductive female in each study group over the period of study. Reproductive seasons from February to March and October to December (Bach et al. 2001)

Group	Habitat type	Number of reproductive seasons	Number of litters	Number of offspring
Almada	*Cabruca*	2	2	4
Bomfim	*Cabruca*	1	1	2
Santa Rita	*Cabruca*	2	2	4
*Ararauna	Mosaic	1	2	4
Bem te Vi	Mosaic	1	1	2
Teimoso	Mosaic	2	2	4
**Jeremy	Primary	2	-	-
Piavelha	Primary	4	2	3
Portao 2	Primary	3	2	3
Total			14	26

*The group had two reproductive females that both had twins with a week between birth events.

** No available information about litter size.

Figures

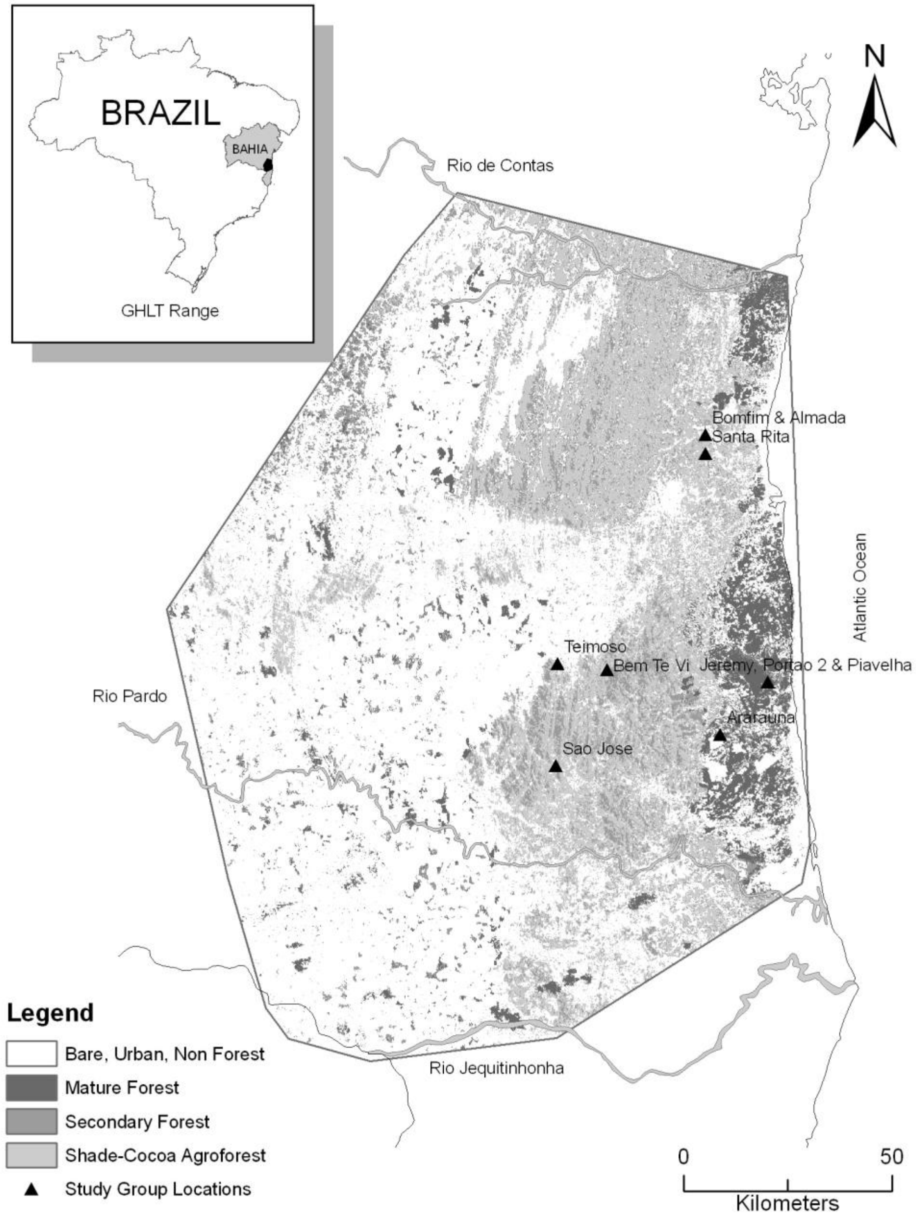

Figure 1. Geographic distribution of golden-headed lion tamarins in southern Bahia state, Brazil and the location of the study sites. Map created by Becky Raboy based on a reclassification of land cover at 30m resolution published in (Landau et al. 2003) from 1996-1997 Landsat data."

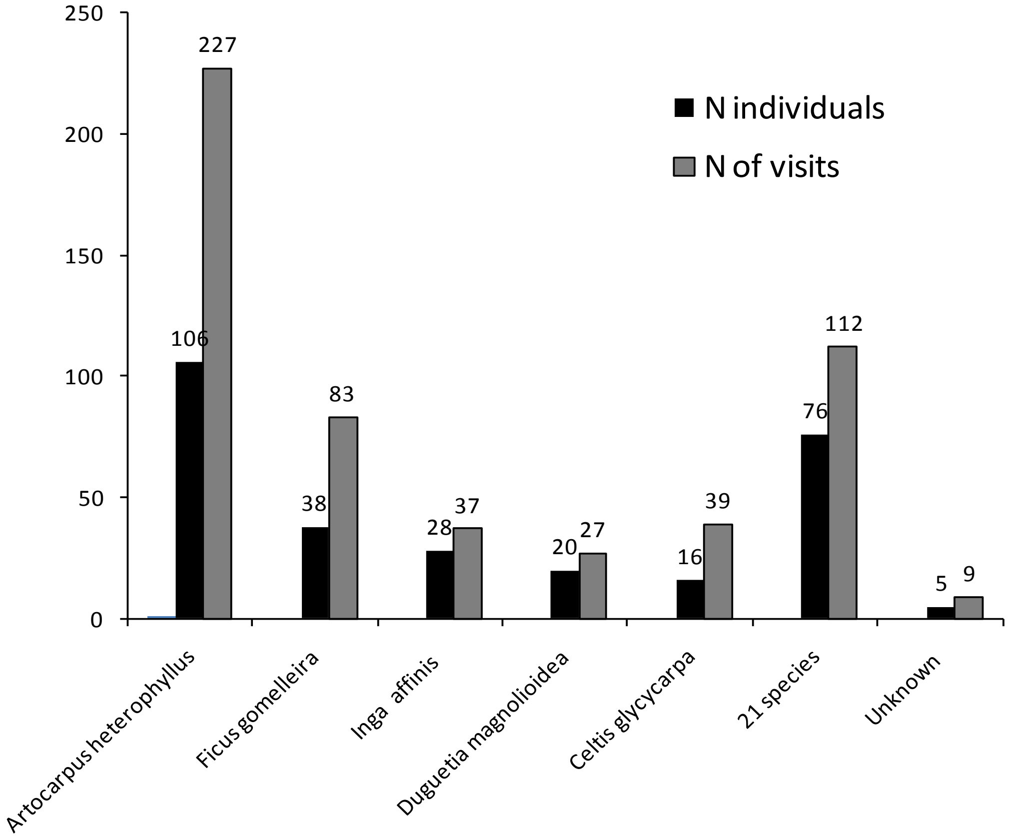

Figure 2a. Number of individuals and number of visits to the five most-used food-tree species compared to 21 infrequently used food-tree species and unidentified food-tree species used by *cabruca* groups.

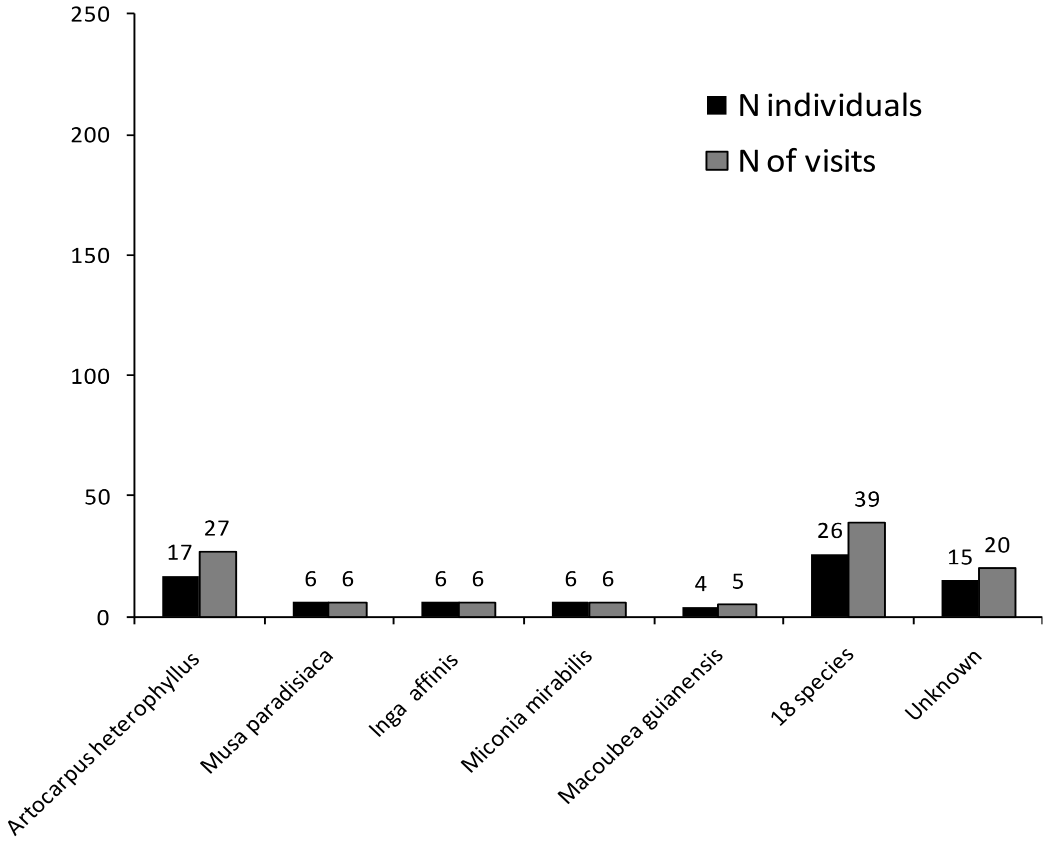

Figure 2b. Number of individuals and number of visits to the five most-used food-tree species compared to 18 infrequently used food-tree species and unidentified food-tree species used by mosaic groups.

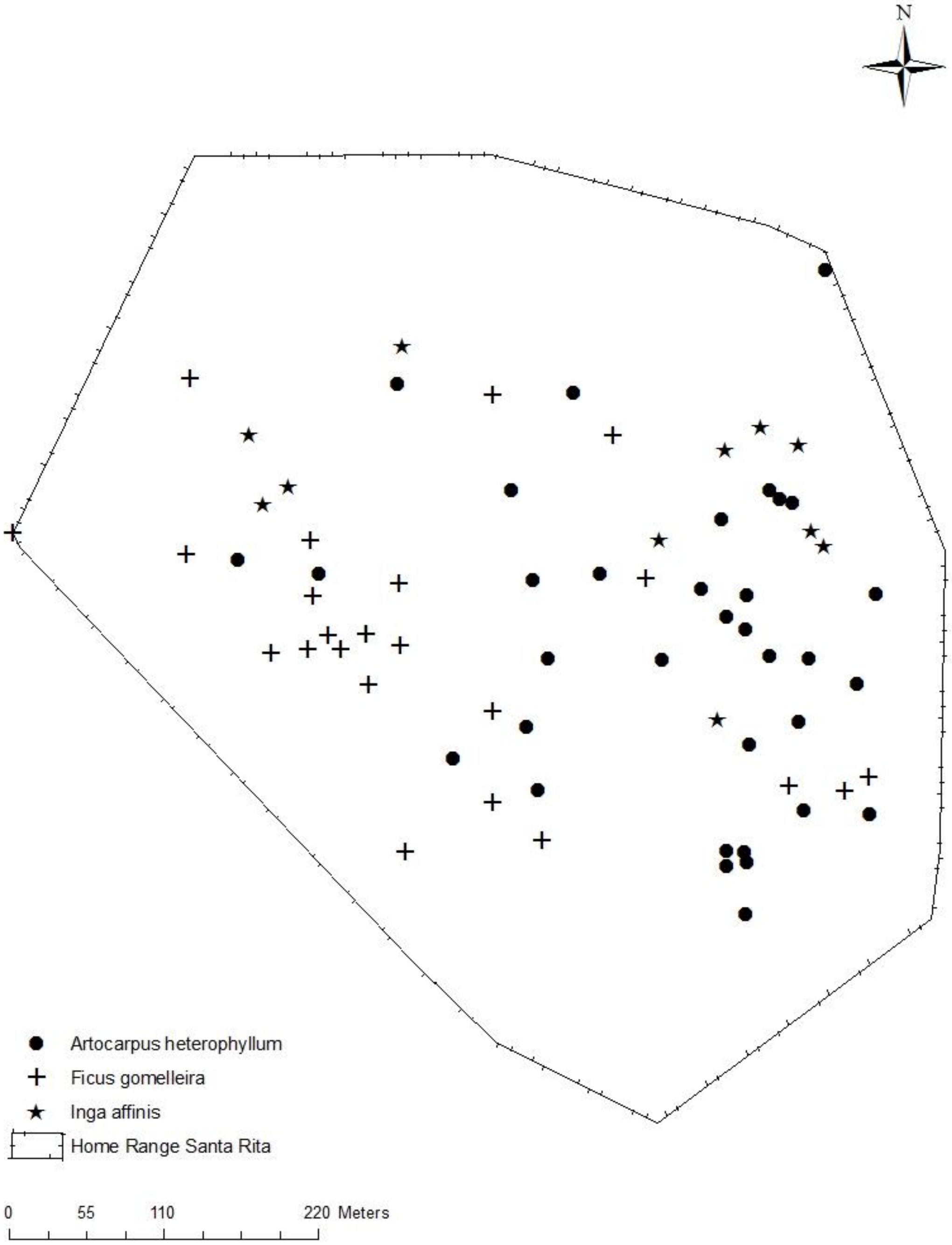

Figure 3a. Distribution of the three most used plant species inside the home range of the Santa Rita *cabruca* group.

Figure 3b. Distribution of the three most used plant species inside the home range of the Almada *cabruca* group.

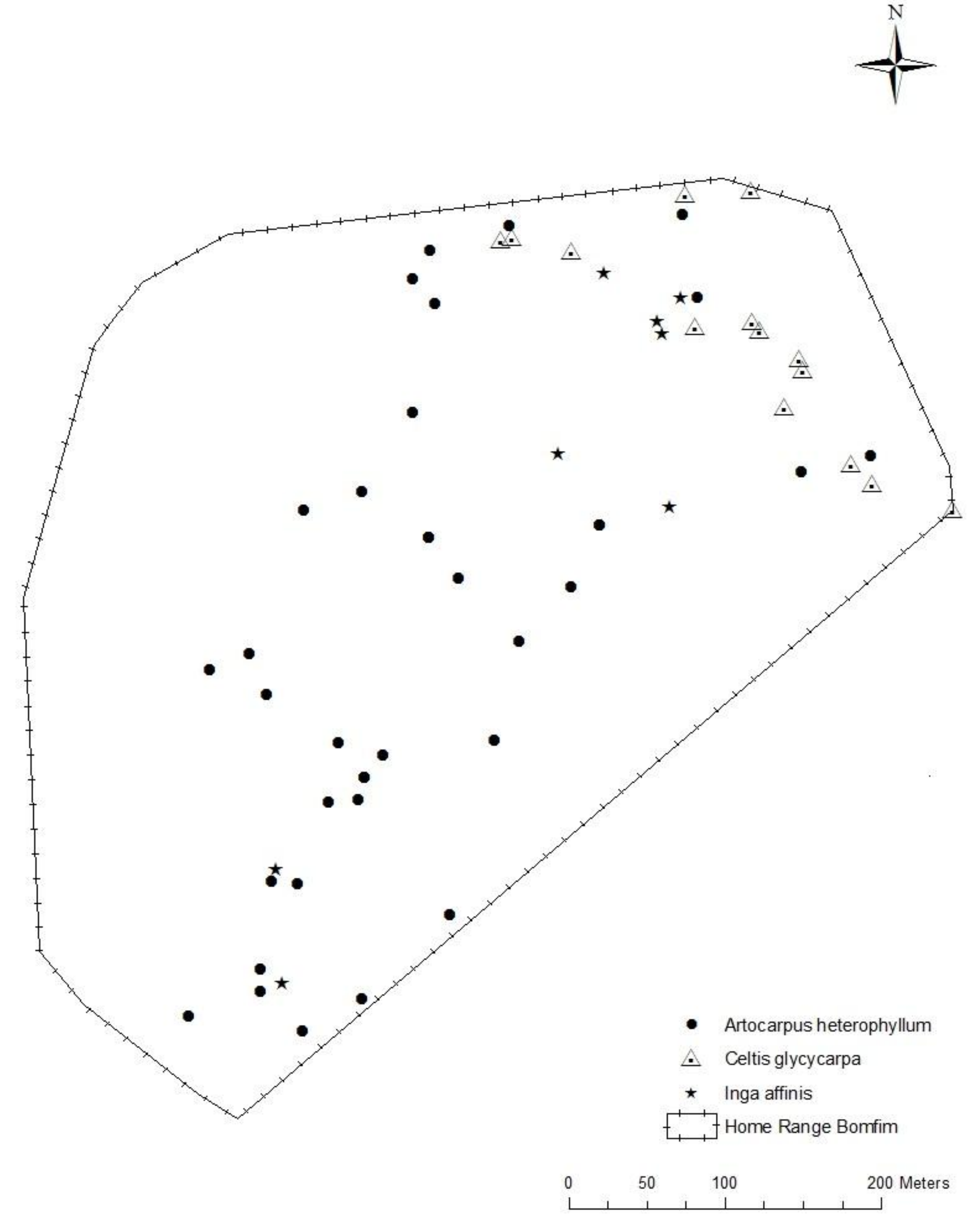

Figure 3c. Distribution of the three most used plant species inside the home range of the Bomfim *cabruca* group.

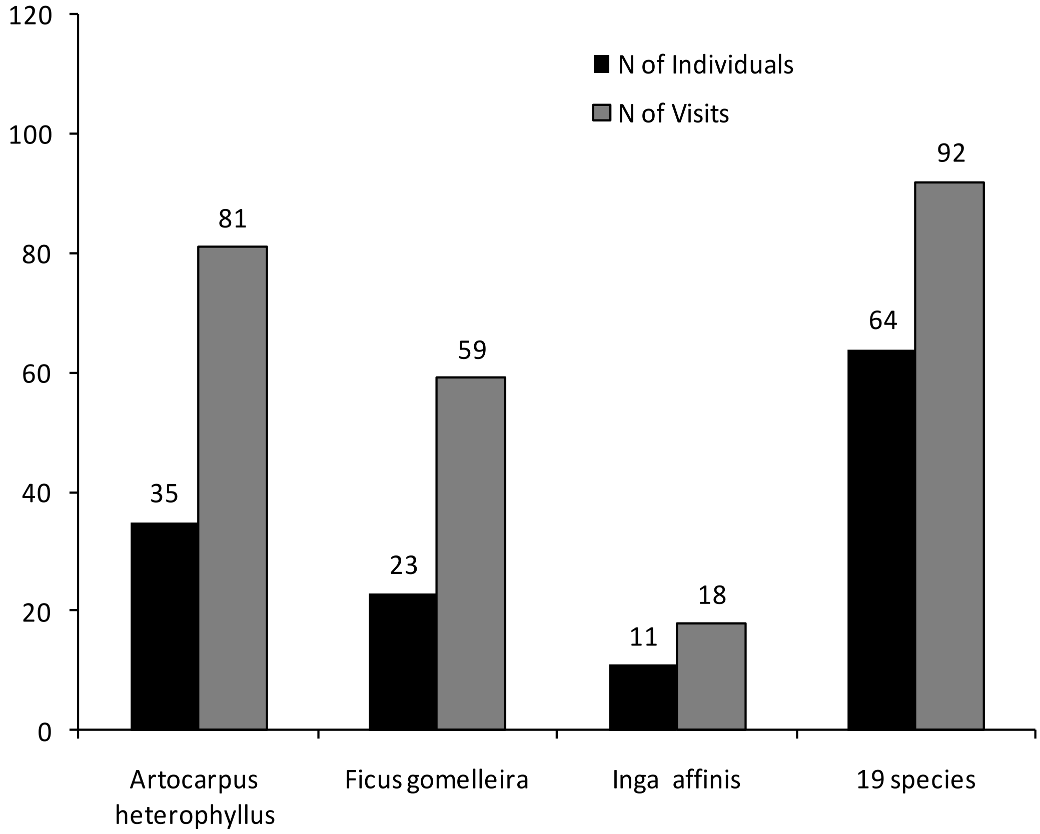

Figure 4a . Number of individuals and number of visits to the five most-used food-tree species compared to 19 infrequently used food-tree species and unidentified food-tree species used by the Santa Rita group in *cabruca*.

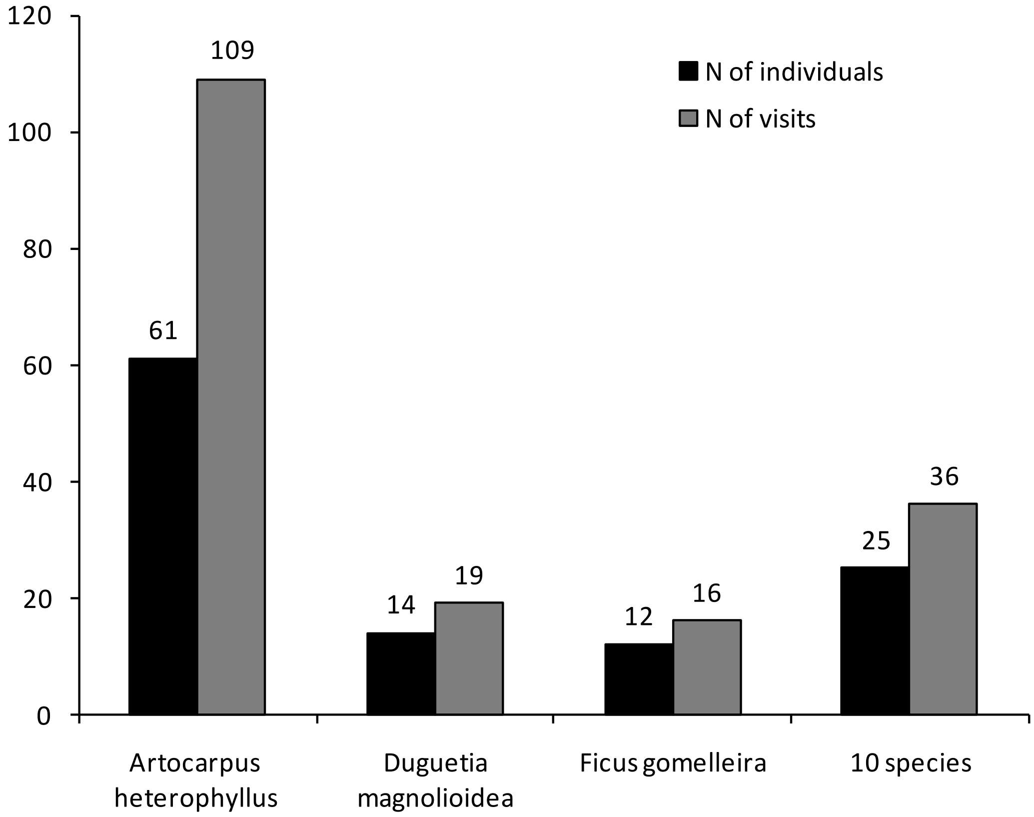

Figure 4b. Number of individuals and number of visits to the five most-used food-tree species compared to 10 infrequently used food-tree species and unidentified food-tree species used by the Almada group in *cabruca*.

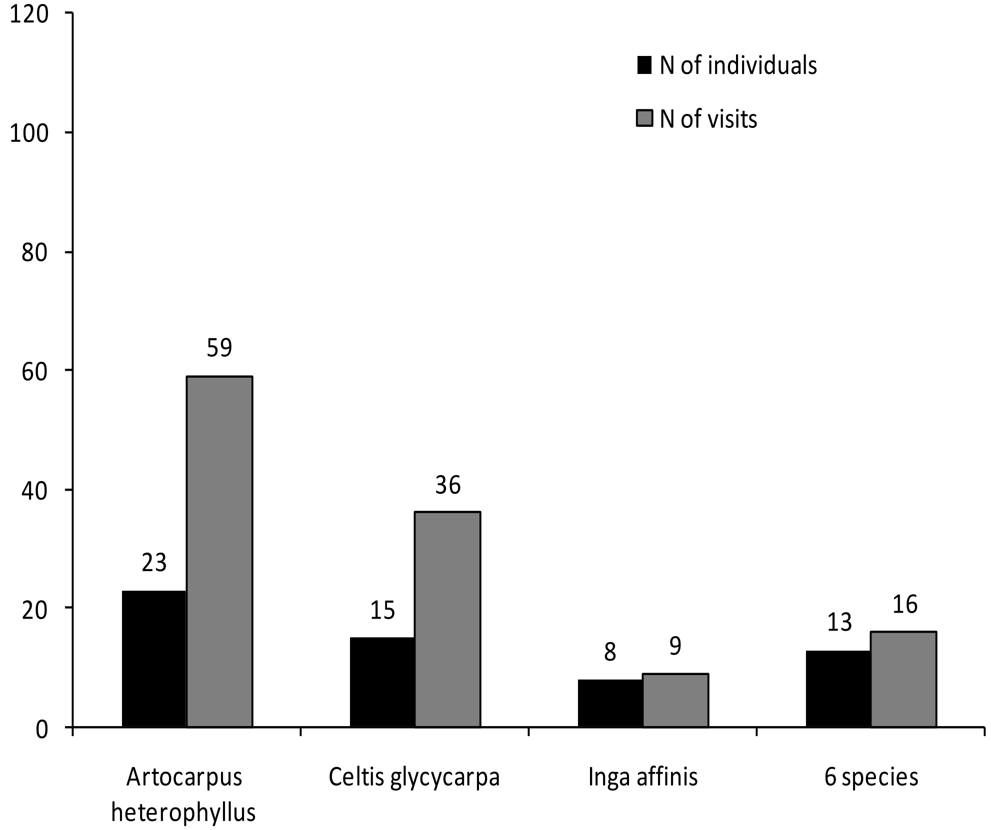

Figure 4c. Number of individuals and number of visits to the five most-used food-tree species compared to 6 infrequently used food-tree species and unidentified food-tree species used by the Bomfim group in *cabruca*.

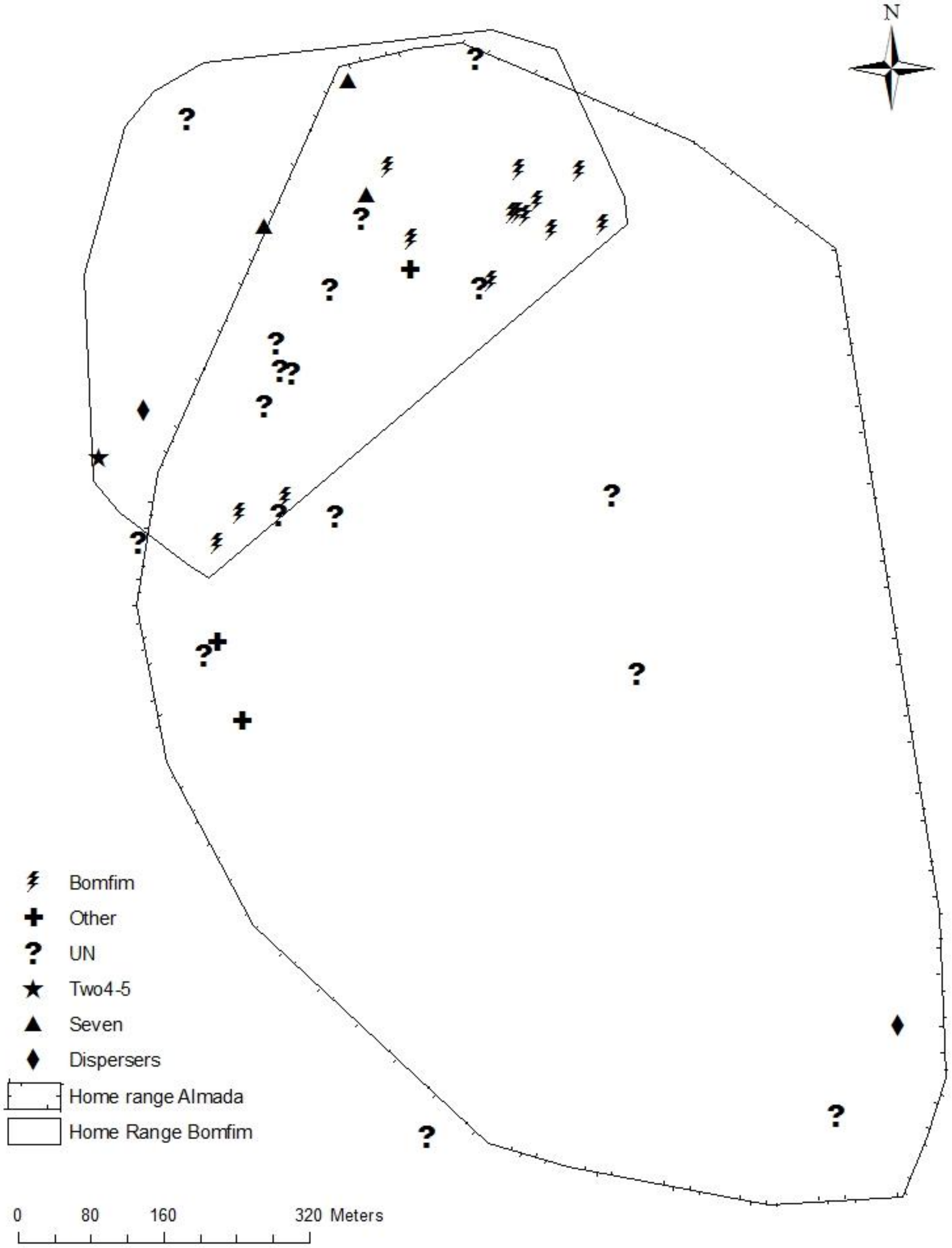

Figure 5a. Conspecific encounters in the ranges of the Almada and Bomfim *cabruca* groups. Results suggest that at least five reproductive groups are located in the area of overlap of these two home ranges.

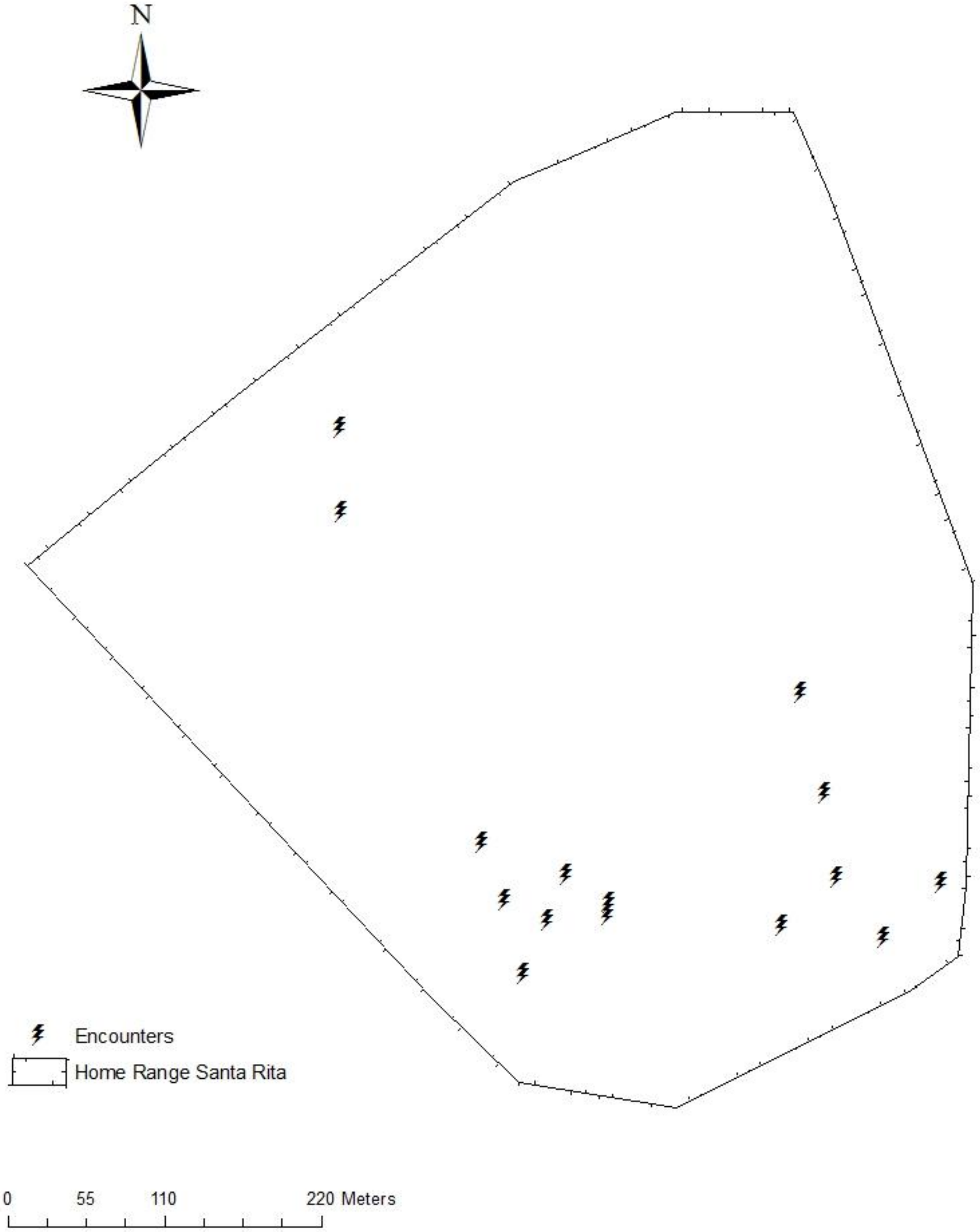

Figure 5b. Conspecific encounters between the Santa Rita group and three other groups inside its home range.

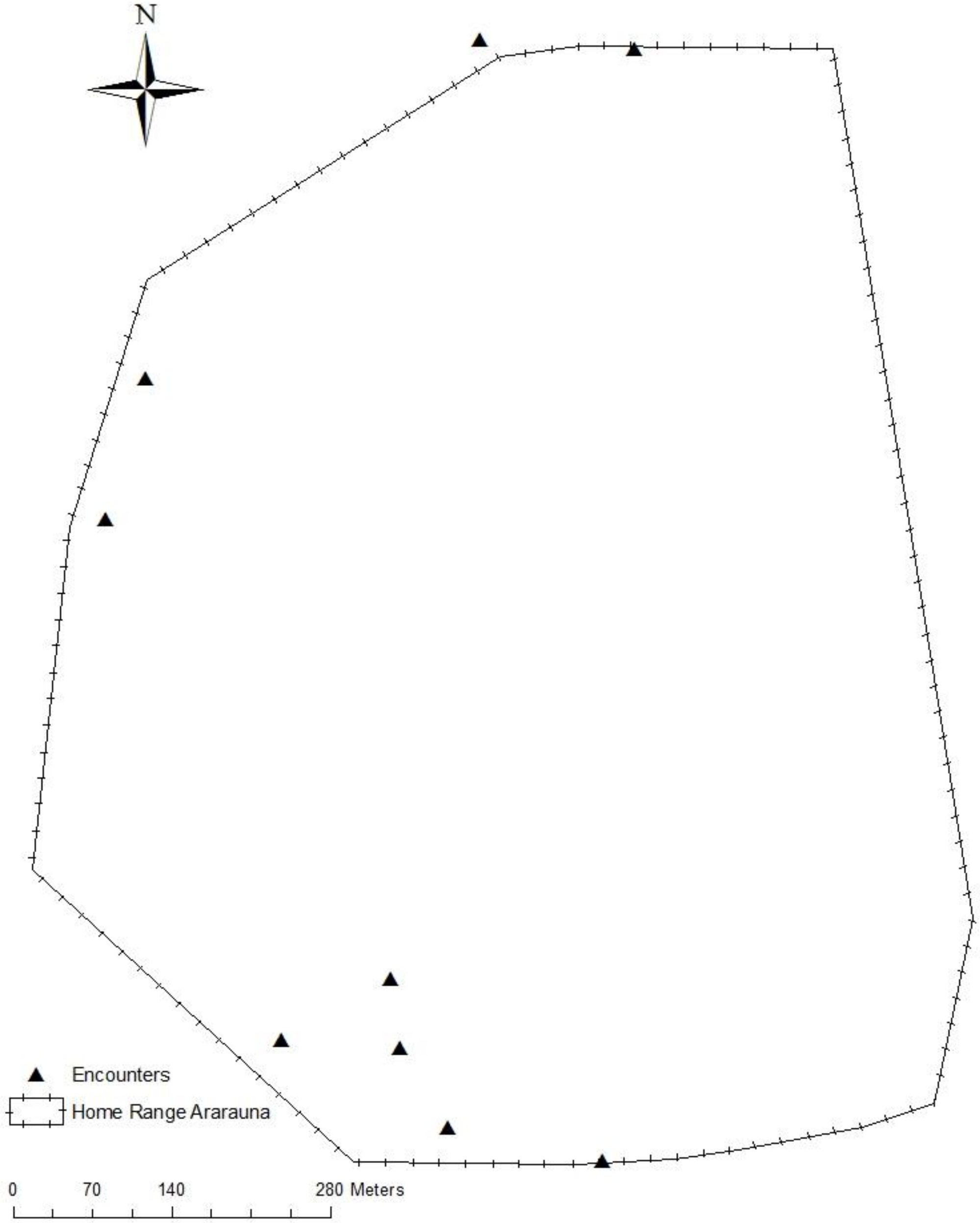

Figure 5c. Conspecific encounters between the Ararauna group and three other groups inside its home range.

Chapter 3: Predation risk and the interspecific association of two Brazilian Atlantic Forest primates in *cabruca* agroforest

Abstract

Primates are susceptible to a large number of terrestrial and aerial predators. Environmental characteristics of the habitat such as canopy and understory complexity may affect the degree of protection of primates against predators. Interspecific association is one of many strategies adopted by primates in order to avoid predation. In addition to improved predator detection and avoidance, benefits of interspecific associations relate to improved foraging efficiency. In this study we tested these two hypotheses in two primate species endemic to the Atlantic Forest of Bahia state in Brazil; the endangered golden-headed-lion tamarin, *Leontopithecus chrysomelas* and the sympatric Wied's marmoset, *Callithrix kuhlii*. We estimated predation risk to lion tamarins by recording the number of encounters between lion tamarins and potential predators, in both *cabruca* agroforest (shaded cocoa plantation) and in mosaic forest, a mix of *cabruca*, primary and secondary forest. To evaluate if the association between the two species was related to foraging benefits we recorded the number of associations between the two species when the lion tamarins were eating and when they were not eating in both *cabruca* and mosaic forest. To test if the association occurred to improve predator detection and avoidance, we evaluated if the associations between the species were more frequent in areas with higher predation risk. We also compared the number of associations three months before birth events and three months after, when the tamarins are more succeptible to predation. We also evaluated whether interspecific associations occurred more frequently during the part of the day when predation risk is higher. We observed that lion tamarins in *cabruca* encounter predators, mainly raptors, significantly more often than in mosaic forest (0.17 and 0.05 encounters per hour of observation, respectively). Associations were significantly more frequent after birth events and during the part of the day (5-6 am until noon) when predation risk was also higher. We did not observe any direct evidence of foraging-related advantages of interspecific associations for the lion tamarins. The tamarins did not associate more when they were foraging. Our findings suggest that predation risk to lion tamarins is higher in cabruca agroforest than in other forest types and that associations between lion tamarins and Wied's marmosets are related to predation avoidance.

Keywords: Predation risk; Interspecific association; *Leontopithecus chrysomelas*; Cabruca, Agroforest

Introduction

Predation is an important evolutionary force that shapes animal behavior and ecology (Cheney & Wrangham 1987; Stanford 2002). Despite its importance, predation events are rare and unpredictable, which make them difficult to observe in the field. The majority of evidence of predation on primates consists of anecdotal observations by field researchers (Bartecki & Heymann 1987; Chapman 1986; Condit & Smith 1994; Passamani et al. 1997) or studies in which primate remains were found in stomach contents or fecal samples of predators (Bianchi & Mendes 2007; Fay et al. 1995; Tsukahara 1993; Ximenez 1982).

Mammalian carnivores, raptors and snakes are the major predators of primates (Bianchi & Mendes 2007), and nearly all recorded predation events on primates involved species in one of these groups. Predation by snakes appears to be relatively rare in comparison with raptors and mammals and usually involves relatively small-bodied primates and large-bodied constrictor snakes (Ferrari 2009).

Primates use several strategies to avoid predation. When threatened by an aerial predator, arboreal primates may adopt anti-predator behaviors such as moving quickly to the understory (Miranda et al. 2006) or freezing and searching for a safe microhabitat (Searcy & Caine 2003). Body size may also be a deterrent against predation. In general, smaller prey species have more potential predators, thus small-bodied primates such as callitrichids are vulnerable to many raptor species (Ferrari 2009). Small primates may live in large groups for protection against predators (Chapman & Chapman 2000a; Chapman & Chapman 1996) providing more ears and eyes to detect predators (Chapman & Chapman 1996), confound the predator (Morse

1977), and/or to dilute the risk to any individual (Hamilton 1971). However, large groups also face constraints related to reduced foraging efficiency, increased competition for food resources (Terborgh & Janson 1986) and increased travel distance (Chapman et al. 1995; Chapman & Chapman 2000b; Janson & Goldsmith 1995; Wrangham et al. 1993), which ultimately will increase exposure to predation (Lucas et al. 1994; McNamara & Houston 1987).

Another constraint for some small species such as the golden-headed lion tamarin is the availability of suitable sleeping sites. Family groups of lion tamarins sleep together, mainly in tree holes (Raboy & Dietz 2004; Rylands 1989) and thus, large groups may have fewer tree cavities large enough to accommodate all individuals. A possible solution for this constraint on group size is to form an interspecific association in which the associated species may increase the effectiveness of predator avoidance in the same way that more individuals of the same species may improve predator detection (Chapman & Chapman 1996; Terborgh 1983) but without competing for shelther space.

Interspecific associations occur when individuals of two or more species travel or forage in close proximity. Benefits of these associations have been widely debated in the literature (Chapman & Chapman 2000b; Cords 2000; Heymann & Buchanan-Smith 2000) and are generally grouped into explanations based on improved foraging efficiency and improved predator detection and avoidance. Interspecific associations may increase foraging benefits by increasing access to plant food or feeding sites (Chapman & Chapman 1996; Gautier-Hion et al. 1983; Terborgh 1983); guiding to more profitable feeding areas (Chapman & Chapman

1996; Terborgh 1983), increasing access to invertebrate prey (Peres 1992), or increasing resource exploitation in different forest strata (McGraw & Bshary 2002; Porter 2001; Wolters & Zuberbuhler 2003). In contrast with same-species groups, individuals in interspecific groups do not compete for mates, do not compete for food if there is not a niche overlap, and the species involved in the association may have complementary defense skills (Bshary & Noë 1997; Noë & Bshary 1997; Stojan-Dolar & Heymann 2010a).

The goals of this study were to test two hypotheses concerning the association between the golden-headed-lion tamarins, *Leontopithecus chrysomelas* and the Wied’s marmoset, *Callithrix kuhlii*. Although both species may benefit from association, here we evaluated the advantages of this association only for lion tamarins. The first hypothesis is that associations between lion tamarins and marmosets are explained by increased access to food resources. If so, we expected that associations between these two species would be more frequent in areas where access to food resources is more difficult in monospecific groups than in mixed-groups [so they would take advantage of being in association; (Chapman & Chapman 1996; Terborgh 1983)] or where food availability is lower and there is no or little diet overlap (Noë & Bshary 1997). We also expected to see the two species associate more frequently when lion tamarins were foraging (either on fruits or for small animals in bromeliads) than when they were not eating. Our study of the diet of lion tamarins in *cabruca* and mosaic forest (Chapter 2 of this dissertation) showed that food resources in *cabruca* (mainly jackfruit and bromeliads) are abundant and easily accessed by lion tamarins. Thus we assumed that *cabruca* has higher availability of trophic resources than mosaic forests.

Second, we tested the hypothesis that the association between the two species occurs to reduce risk of predation. We used three methods to examine this hypothesis. First, if association between the two species serves to decrease predation risk we predicted that interspecific associations would be more frequent in areas of high predation risk. Second, because infants are the most vulnerable age class (Caine 1993; Chapman & Chapman 2000c; Izawa 1978), and the presence of noisy infants may increase the risk of predation (Heymann 1990) and thus the need for increased vigilance, we predicted that the proportion of time lion tamarins spend in association with marmosets would be higher when the groups have infants than without infants. And finally, we predicted that association between the two species would be more frequent during times of day when predation is most frequent.

Methods

Study sites

This study was carried out in the cocoa growing region of southern Bahia state, Brazil, in the municipalities of Ilhéus, Jussari, Camacan, Arataca and Una. Study sites (Fig. 1) included four privately owned areas (Almada, Santa Rita, Riachuelo and São José farms), two private reserves (Teimoso and Ararauna) and one rural settlement (Bem te Vi). Groups were divided into two categories according to the habitat types in which they were found: groups that lived exclusively in *cabruca* (municipality of Ilhéus: Almada, Bomfim and Santa Rita groups), and groups that used a mosaic of *cabruca*, primary and secondary forests (municipalities of Una, Arataca, Camaca and Jussari: Ararauna, Bem te vi, São José and Teimoso groups, respectively) hereafter referred to as mosaic groups. Definitions of vegetation types may be found in chapter 2 of this dissertation. For this chapter we did not consider tamarin groups that lived in primary forest because there was no information about predation risk in that vegetation type.

Study species

Both primate species are endemic to southern Bahia state and the northwest corner of Minas Gerais state, Brazil. They are cooperative breeders with group sizes ranging from 2 to15 individuals for the lion tamarins (chapter 2 of this dissertation) and 4 to15 individuals for the marmosets (Raboy et al. 2008). Both species feed on ripe fruits, insects and small vertebrates (Raboy 2002; Rylands 1989), but marmosets also feed heavily on gum when fruits are less abundant (Raboy et al. 2008; Rylands 1986). Wied's marmosets are smaller and lighter (±350g) than lion tamarins (550 - 590 g). Typically, Wied's marmosets have smaller home ranges and higher densities than lion tamarins (Raboy et al. 2008; Raboy & Dietz 2004; Rylands 1989). The lion tamarins and marmosets typically use different strata in primary forest; lion tamarins are commonly found in the upper canopy and marmosets in the lower canopy (Rylands 1989). Interaction between the lion tamarins and marmosets was reported by other authors (Raboy 2002; Rylands 1989) and the occurrence of these associations was non-random in space and duration of the encounters (Raboy 2002).

Data collection

We monitored seven groups of lion tamarins using radio-telemetry (see details in chapter 2, this dissertation). The groups were observed from April 2008 to September 2009 with a total sample effort of 2,500 hours of observation (106 to 569 hours of observation per group, Table 1). We followed the lion tamarins during full days (from when the group left its sleeping site in the morning until they entered a sleeping site in the evening) or partial days (either from the time they left the sleeping site until noon, or from noon until they entered a sleeping site).

Predation risk

Predation risk has several definitions (Janson 1998); in our study we used that of Hill and Dunbar (1998) in which predation risk is the animal's own perception of the likelihood of being subject to an attack by a predator, irrespective of whether or not the attack is successful (Hill & Dunbar 1998). We documented all encounters between lion tamarins and potential predators that included any situation in which an animal that poses a potential threat to lion tamarins was seen near the group [(as in (Franklin et al. 2007)]. We also documented when a predator mounted an attack on the lion tamarins. We recorded the time and geographic coordinates of the encounter and when possible the identity of the predator. We recorded every alarm call made by the lion tamarins (even when the potential predators were not seen by us). We discarded all alarm calls made by lion tamarins to birds that we did not regard as potential predators, such as vultures (*Cathartes, Coragypis*), the squirrel cuckoo (*Piaya cayana*) and toucans and aracaris (*Rhamphastos and Pteroglossus*). Although the São José group was not a reproductive group (two dispersing males) we were able to follow the individuals and evaluate the number of encounters with potential predators and thus included it in this analysis.

Association between lion tamarins and Wied's marmosets

At 20 min intervals we recorded the geographic location of the lion tamarin group under observation and noted whether they were in association with marmosets. We defined two groups as being in association when the lion tamarins and marmosets were less than 50 meters apart. Although other studies used smaller distance criteria [15 m (Porter 2001); 20 m (Cords 1990) and 25 m (Noë & Bshary 1997)], 50 meters was the distance used by Raboy (2002), to determine if the golden-headed lion tamarin and the marmosets were in association, as well as in studies on other species (Buchanan-Smith 1990; Chapman & Chapman 1996, 2000c; Wachter et al. 1997). Because vegetation structure varied significantly between areas in our study, we did not use vocalizations as criteria for defining associations. We excluded analysis of associations for the São José group because after three months of observation, one individual disappeared and the other joined a group of marmosets in a *cabruca* area. Thus, the amount of time the lion tamarins spent with marmosets would be overestimated and misinterpreted.

<u>Data analysis</u>

Predation risk

We estimated predation risk by dividing the number of encounters with predators (including alarm calls) for each group of lion tamarins by the sample effort for that group (measured in number of hours). We tested the differences between predation risk in *cabruca* groups and in mosaic groups using one-way ANOVA. To reduce the effect of observation bias on the estimation of predation risk (one might say that the predation risk was higher in *cabruca* because the open canopy and lack of understory made it easier for observers to see predators) we also recorded the number of alarm calls made by the lion tamarins when we did and did not observe the predator. We assumed that the lion tamarins could detect predators equally well in *cabruca* and in mosaic forests. We tested the difference between the numbers of alarm calls in the two vegetation types using one-way ANOVA. We also evaluated the number of predator attacks on lion tamarins in both *cabruca* and mosaic forest. We defined an attack to be when a predator was flying toward the lion tamarins (for raptors) or running toward the lion tamarins (carnivores). We tested the differences between the number of observed predator attacks on lion tamarins in *cabruca* groups and in mosaic groups using one-way ANOVA.

We evaluated whether the predation risk was higher with infants in the group by comparing predation risk during the three months prior to a birth with the three months following a birth (the month of birth plus the two consecutive months after the birth). For this analysis we used data from three groups: two from *cabruca* (Almada and Santa Rita) and one from mosaic forest (Teimoso). The sample effort (number of hours of observation) was standardized per month of observation across all three groups (154±6 hours) before and after birth. We used a Wilcoxon signed rank test with an alpha level at 0.05, to compare the predation risk before and after the birth of infants.

We also evaluated whether predation risk differed over the day. We divided the day into two periods, from the time the lion tamarins left the sleeping site until noon (half 1) and from noon until they entered a sleeping site (half 2). For this analysis we considered only full days of observation. To test whether the predation risk differed between the first (half 1) and second (half 2) periods of the day we used a Wilcoxon signed rank test with alpha level at 0.05.

Association between the lion tamarins and Wied's marmosets

At 20min intervals we used presence-absence sampling to determine whether a group of marmosets was less than 50m from, and thus in association with our focal group of lion tamarins. To test whether the association between the lion tamarins and the marmoset differed between *cabruca* and mosaic groups we used a chi-square test. To test whether the association between the two species was related to increased foraging benefits, we compared the percentage of records in which the lion tamarins were in association with marmosets when the lion tamarins were eating (fruits and foraging in bromeliads) and when they were not eating. For this analysis we used a Wilcoxon signed rank test with alpha level at 0.05.

We evaluated whether the association between the lion tamarins and marmosets was higher when infants were in the group by comparing the number of associations during the three months prior to a birth with the three months following a birth (the month of birth plus the two consecutive months after the birth). We compared the associations before and after the birth of infants using a Wilcoxon signed rank test with an alpha level of 0.05. We used the same groups as for the analysis of predation risk. We evaluated whether the association between the two species occurred more frequently when the predation risk was higher. To address this question, we estimated the numbers of associations in the two periods, half 1 and half 2 as defined above. For this analysis we considered only full days of observation. To test whether the number of associations between lion tamarins and marmosets differed between the first (half 1) and second (half 2) periods of the day, we used a Wilcoxon signed rank test with an alpha level at 0.05. All statistical analyses were done using the program SAS version 9.2 (SAS Institute Inc).

Results

Predation risk

We observed a total of 314 encounters between potential predators and lion tamarins in our study groups. We identified 13 species of potential predators (10 raptors and three mammals in the order Carnivora (Table 1). In *cabruca* and mosaic forest, raptors were the most commonly observed potential predators on lion tamarins (210 records) followed by mammalian carnivores (37 records; Table 2). Overall, the domestic dog was the most abundant predator species recorded in our study. We were unable to identify the potential predators, all raptors, on 115 occasions. All but one identified species of predator were observed attacking a group of lion tamarins at least once (Table 1). Based on the number of observed attacks on lion tamarins, the mantled hawk *Leucopternis polionotus* was the most threatening raptor species (six attacks) while the tayra, *Eira barbara* was the most threatening mammal species (six attacks). However, none of these attacks resulted in lion tamarin mortality.

Predation risk was significantly higher in *cabruca* than in mosaic forest (F= 18.32; df= 6; P=0.008) with an average of 0.17 vs. 0.05 encounters per hour of observation in *cabruca* and in mosaic forest, respectively (Table 3). The rate of alarm calls was also significantly higher in *cabruca* than in mosaic forest (Table 4), both when no predators were observed by the field team (F= 15.76; df= 6; P= 0.0106) and when predators were recorded by the field team (F= 17.61; df= 6; P= 0.0085). The rate of attacks on lion tamarins by predators (Table 5) was significantly higher in *cabruca* than in mosaic forest (F= 10.28; df= 7; P= 0.0238). Predation risk did not differ significantly in the three months prior to the reproductive female giving birth and the first three months after infants were born into a group when combining all three groups (T=18, P= 0.274). Predation risk was significantly higher in the first half of the day than in the second half of the day (T=10.5 P= 0.03) in both *cabruca* and mosaic forests (Fig 2).

Association between the lion tamarins and Wied's marmosets

Lion tamarins and marmosets were observed in association in 1721 of 5411 records for *cabruca* and mosaic forest combined. We observed both species traveling, and resting together. In a few cases, we saw them foraging together on the same individual fruit, and foraging for small animals in the same individual bromeliad. We also observed individuals of the two species playing together (juveniles mainly) and on a few occasions, in agonistic behaviors.

Lion tamarins and the marmosets were in association in 17 to 39% of all records (Table 6) and the number of interspecific associations was significantly higher in *cabruca* than in mosaic forest (X^2= 123.47; df= 1; P<0.0001). There was no significant difference in the percentage of associations between lion tamarins and marmosets when the lion tamarins were eating (fruits and foraging in bromeliads) and when they were not eating (T=3.5, P= 0.562) in both *cabruca* and mosaic forest (Table 7). The rate of association between lion tamarins and marmosets was significantly higher during the three months after the birth of infants than the three months prior to birth events when combining all three groups (T=-50, P= 0.003). Association was highest during the first month after birth and showed a decrease in subsequent months (Fig. 3). Association was also significantly higher (T=10.5, P= 0.03) during the first half of the day (half 1) in both *cabruca* and mosaic forest (Fig. 4) when predation risk was also higher.

Discussion

Predation risk

Although *cabruca* proved to be a suitable habitat for the lion tamarins (Chapter 2 of this dissertation), its structure (lower density and diversity of trees) and its management (weeding of understory and not replacing dead shade trees) exposes lion tamarins in *cabruca* to higher predation risk than in mosaic forest. In *cabruca,* the canopy has lower connectivity and the understory has little complexity. These two habitat components are important in protecting arboreal primate species against predators. In comparison with open ground, forest canopy provides better cover and concealment from aerial predators, and facilitates detection of the approach of other animals (Ferrari 2009). Arboreal primates are more vulnerable to predation when they are near forest edges, in open-canopy forest where the sparseness of vegetation makes them more visible and more accessible than when they are in dense forest (Isbell 1994). Small-bodied primates such as callitrichids typically occupy relatively dense vegetation and are well protected from attack by raptors in the lower strata, where they are also able to detect and avoid the approach of carnivores (Ferrari 2009). Moving to the understory is a common anti-predator behavior among small arboreal primates possibly because raptors are unable to follow them through the vegetation fast enough to capture individuals (Boinski & Chapman 1995). Cunha et al. (2006) observed a high frequency of use of the understory by the common marmoset (*C. jacchus*) when hawks, *Leucopternis lacernulata* and *Rupornis magnirostris* were close to them.

Our results corroborate previous studies suggesting that arboreal primates are more vulnerable to raptors (Gilbert 2000; Sherman 1991; Vasquez & Heymann 2001) than to terrestrial predators. Although we can’t confirm that all raptor species we categorized as potential predators are effective predators on lion tamarins, the relatively frequent attacks confirm Coimbra-Filho’s assertion that raptors are important predators of lion tamarins (Coimbra-Filho 1975) and the assertion by Isbell (1994) that raptors are more of a threat in open canopy.

Lion tamarins living in *cabruca* are also vulnerable to terrestrial predators. The lack of canopy connectivity and the low complexity of understory force lion tamarins to travel on the ground in *cabruca*, where they are more vulnerable to terrestrial predators. The three mammals in the order Carnivora that we observed attacking lion tamarins in *cabruca* and mosaic forest were also reported as predators on primates in others studies [*Callithrix geoffroyi* by Margay *Leopardus wiedii* in (Passamani et al. 1997); *Saguinus geoffroyi* in (Moynihan 1970) and *Callithrix jacchus* in (Bezerra et al. 2009) by tayras, *Eira barbara*; and *Cebus nigritus* by domestic dogs, *Canis lupus familiaris* (Oliveira et al. 2008)]. Tayras are considered a potential predator of several callitrichid species [Santarem marmoset, *Callithrix humeralifer intermedius* (Rylands 1981); the buffy-headed marmoset, *Callithrix flavicepes* (Ferrari & Lopes 1990)] and they may prey upon some of the larger species of Cebidae (Camargo & Ferrari 2007; Phillips 1995). Tayras have been recorded taking a wide variety of prey items both in trees and on the ground, including small rodents, iguanas, marsupials, birds, rabbits and small deer (Konecny 1989; Presley 2000; Sunquist et al. 1989), and primate species [Geoffroy's Tamarin *Saguinus geoffroyi* (Moynihan 1970) and the common marmosets, *Callithrix jacchus* (Bezerra et al. 2009)]. Tayras may have been responsible for the decimation of entire social groups of golden lion tamarins (*Leontopithecus rosalia*) in Rio de Janeiro state (Franklin et al. 2007). In the present study, the number of observed tayra attacks suggests that this mustelid is a threat to lion tamarins in *cabruca* areas.

Domestic dogs are very common in *cabruca* areas because farm workers use dogs for opportunistic hunting (unpublished observations). Domestic dogs are a significant threat as predators on lion tamarins and other groups of vertebrates in Brazil (Campos et al. 2007; Galetti & Sazima 2006; Oliveira et al. 2008). In addition, they also may carry and spread diseases to wild animals (Butler et al. 2004; Curi et al. 2006).

Association between lion tamarins and Wied's marmosets

Foraging benefits

Interspecific associations are likely to represent a compromise between competition and compatibility, but the benefits to participants should outweigh any potential costs incurred through increased feeding competition (Noë & Bshary 1997; Porter 2001). The costs of association between lion tamarins and marmosets may be related to competition for food, as both species have similar diets (Raboy 2002; Raboy et al. 2008; Rylands 1989). However, difference in size of prey exploited by the two species, in use of strata while foraging and in range sizes (Rylands 1989) would suggest low niche overlap of the two species. This, combined with the high abundance of jackfruit (spatial and temporal) and bromeliads in the home ranges of the groups in *cabruca* (Chapter 2 of this dissertation), suggest that the cost of the association due to food competition is low in *cabruca*.

Our data did not support our prediction that associations would take place in areas with low resource availability, or areas with difficult access for food resources. Raboy (2002) suggested that associations between lion tamarins and marmosets may be explained by one species leading the other to ephemeral food resources and resulted in a win-win relationship. Our data do not reveal any direct foraging-related advantages, at least for the lion tamarins. However, interspecific associations do not always benefit both species equally (Porter 2001; Smith et al. 2004). In some cases, only one species benefits from associations, a commensal relationship (King & Cowlishaw 2009). Lion tamarins associated more frequently with marmosets in our study than in the study of Raboy (2002) in Una Biological Reserve (range from 17 to 39%, and from 8 to34%, respectively). The costs and benefits of association may vary with season, especially during the period of fruit shortage (Gautier-Hion et al. 1997).

Frequency and seasonality of associations between two species may vary in different habitat types (Haugaasen & Peres 2009) and over small spatial scales (Chapman & Chapman 2000c). Both studies (Raboy 2002) were conducted in different vegetation types with different habitat structure, and possibly, with different cost and benefits for each species involved in the association.

Predation avoidance

In our study, three findings suggest that lion tamarins and marmosets form mixed-species associations to decrease the risk of predation. First, associations between the two species were more frequent in areas with higher predation risk. Second, associations were more frequent after the birth of infants, when presumably they are at the greatest risk of predation (Chapman & Chapman 2000c) and finally, associations between the two species happened more frequently during the first part of the day, when predation risk was also high. These results support the explanation that association between these species is related to reducing predation risk. This conclusion corroborates other studies that also identified predation avoidance as an explanation for interspecific associations in old world primates (Bshary & Noë 1997; Castro 1990; Noë & Bshary 1997; Wachter et al. 1997) and other Neotropical primates (Peres 1993; Smith et al. 2004; Stojan-Dolar & Heymann 2010a; Stojan-Dolar & Heymann 2010b).

The importance of raptors as predators on lion tamarins and marmosets may be a key factor explaining their association. Predation by raptors is prevented primarily by vigilance and avoidance and the only effective way to avoid predation by a raptor is to detect the bird in time to take appropriate evasive action (Castro 1990). More individuals in a group would seem to be beneficial in areas of higher predation risk by raptors and low structural complexity, such as *cabruca* areas. In areas with the characteristics mentioned above conspecific as well as interspecific cooperation became important components of anti-raptor strategies (Chapman & Chapman 1996; Ferrari 2009).

Predation avoidance vs food benefits

The complexity of poly-multi-hetero or interspecific associations makes it difficult to separate hypotheses explaining these associations. Although predation pressure and food availability are the most common determinants of primate mixed species associations (Chapman & Chapman 2000b; Cords 2000; Heymann & Buchanan-Smith 2000) these explanations are not mutually exclusive. Social and reproductive advantages may also contribute to the formation and stability of mixed species groups (Stensland et al. 2003). Increased in safety by forming mixed group of primate species allowed individuals to exploit their ecological niche more broadly, to forage more efficiently, and to engage in more social behavior, suggesting that the benefits of mixed species groups are more diverse than previously thought (Wolters & Zuberbuhler 2003). Interspecific associations may, for example, allow a niche extension for involved species, thus indirectly providing foraging advantages (McGraw & Bshary 2002). These authors observed that the western red colobus (*Piliocolobus badius*) and Diana monkeys (*Cercopithecus diana*) descend to low forest levels and to the forest floor significantly more often when associated with mangabeys (*Cercocebus atys*), a species more efficient in detecting terrestrial predators. Likewise, association between lion tamarins and marmosets may decrease time spent in vigilance and allow lion tamarins to spend more time foraging.

Tables

Table 1. Species identified as potential predators on lion tamarins with the total number of observations of each species, and number of observed attacks (in parentheses) by each species in each vegetation type.

Species	**Popular name**	**Number of observations**	
		Cabruca	**Mosaic**
Carnivorous			
Canis lupus familiaris	Domestic dog	19 (4)	1
Eira barbara	Tayra	9 (4)	6 (2)
Leopardus wiedii	Margay	0	2 (1)
Raptors			
Caracara plancus	Southern crested caracara	13 (2)	6
Buteo albonotatus	Zone-tailed hawk	16 (1)	2
Leptodon cayenensis	Gray-headed kite	13 (2)	4 (1)
Milvago chimachima	Yellow-headed caracara	16 (1)	0
Leucopternis polionotus	Mantled hawk	12 (5)	2 (1)
Buteo magnirostris	Roadside hawk	3 (2)	2
Tyto alba	Barn owl	1 (1)	2
Geranospiza caerulescens	Crane hawk	1 (1)	0
Pulsatrix perspicillata	Spectacled owl	1 (1)	0
Herpethotheres cachinans	Laughing falcon	1	0

Table 2. Number of encounters with potential predators and alarm calls by lion tamarins in the study areas.

Vegetation	Raptor	Carnivores	Alarms calls	Total
Cabruca	169	28	52	249
Mosaic forest	41	9	15	65
Total	210	37	67	314

Table 3. Predation risk measured as the number of lion tamarin alarm calls and encounters between the study groups and potential predators per hour of observation.

Group	Vegetation type	Sample effort	N of Encounters	Rate
Almada	*Cabruca*	567.5	87	0.153
Bomfim	*Cabruca*	216.9	28	0.128
Santa Rita	*Cabruca*	569.6	134	0.235
Ararauna	Mosaic	304.0	19	0.062
Bem te Vi	Mosaic	106.0	6	0.056
São José	Mosaic	183.6	9	0.049
Teimoso	Mosaic	553.9	31	0.055

Table 4. Tamarin alarm calls per hour of observation (rate) when study groups were in encounters with potential predators and when predators were seen by the field team.

Group	Vegetation type	Sample effort	N of alarm calls	Rate
Almada	*Cabruca*	567.5	41	0.07
Bomfim	*Cabruca*	216.9	16	0.07
Santa Rita	*Cabruca*	569.6	47	0.08
Ararauna	Mosaic	304.0	13	0.04
Bem te Vi	Mosaic	106.0	5	0.05
São José	Mosaic	183.6	2	0.01
Teimoso	Mosaic	553.9	9	0.02

Table 5. Number of attacks by potential predators on study groups per hour of observation (rate) in *cabruca* and mosaic forest.

Group	Vegetation type	Sample effort	N of attacks	Rate
Almada	*Cabruca*	567.5	7	0.0123
Bomfim	*Cabruca*	216.9	5	0.0231
Santa Rita	*Cabruca*	569.6	23	0.0404
Ararauna	Mosaic	304.0	1	0.0033
Bem te Vi	Mosaic	106.0	2	0.0189
São José	Mosaic	183.6	1	0.0054
Teimoso	Mosaic	553.9	1	0.0018

Table 6. Percentage of observations in which lion tamarins and marmosets were observed in association in *cabruca* and mosaic forest.

Group	Vegetation type	Total of observations	% of association
Almada	*Cabruca*	1211	39
Bomfim	*Cabruca*	591	34
Santa Rita	*Cabruca*	1315	39
Ararauna	Mosaic	816	27
Bem te Vi	Mosaic	244	17
Teimoso	Mosaic	1234	23

Table 7. Percentage of observations in which lion tamarins and marmosets were observed in association when the lion tamarins were eating (fruits or foraging in bromeliads) and when they were not eating, in *cabruca* and mosaic habitat.

Group	Vegetation type	Eating in association %	Not eating in association %
Almada	*Cabruca*	43	45
Bomfim	*Cabruca*	39	36
Santa Rita	*Cabruca*	35	36
Ararauna	Mosaic	25	29
Bem te Vi	Mosaic	25	20
Teimoso	Mosaic	36	27

Figures

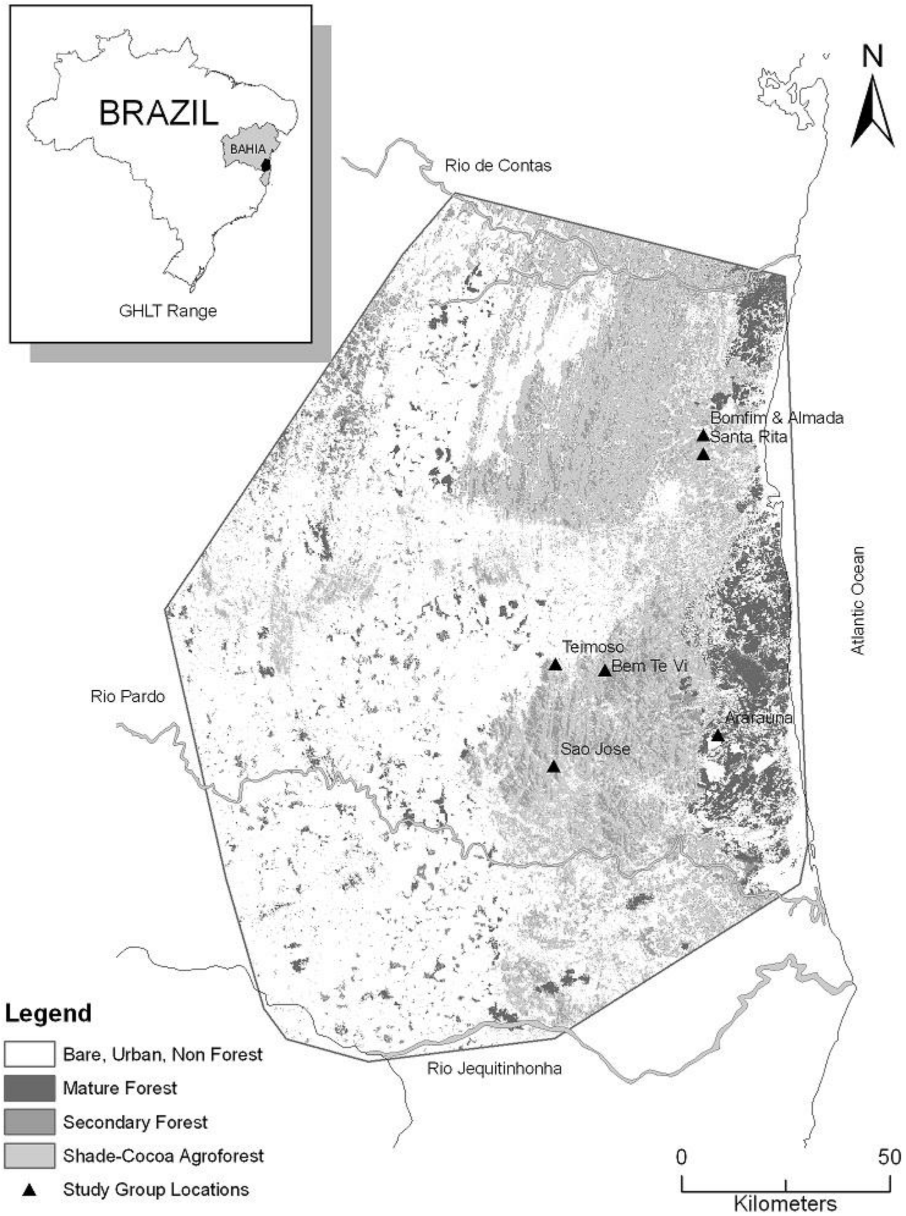

Figure 1. Geographic distribution of the golden-headed lion tamarin in southern Bahia state, Brazil and the location of the study sites. Map created by Becky Raboy based on a reclassification of land cover at 30m resolution published in (Landau et al. 2003) from 1996-1997 Landsat data."

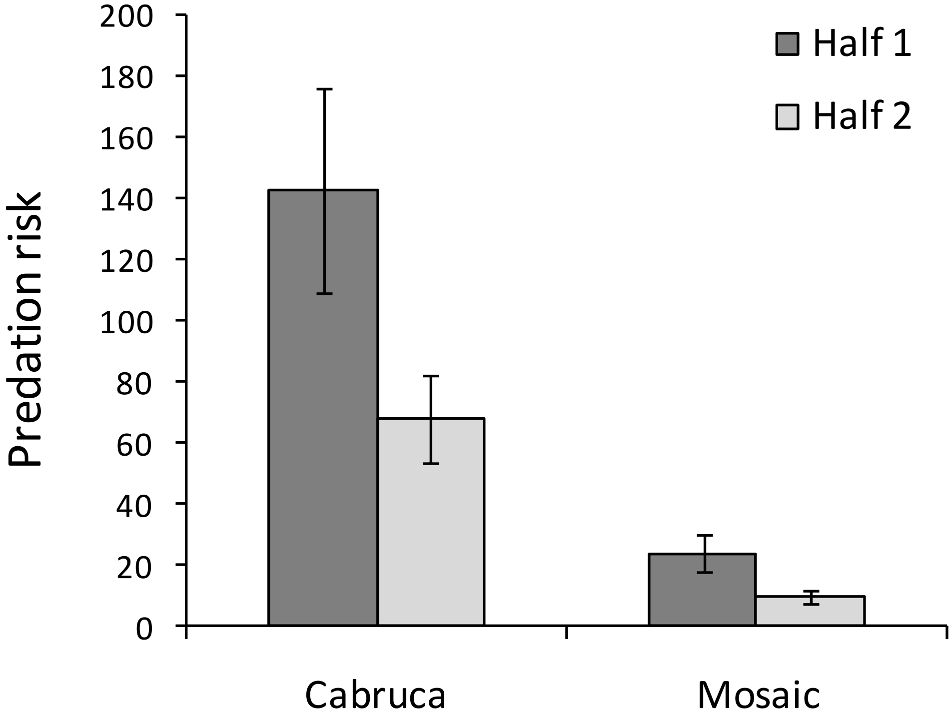

Figure 2. Predation risk in both portions of the day (half 1 and half 2) in *cabruca* and mosaic forests. Erro bars represent standard deviation.

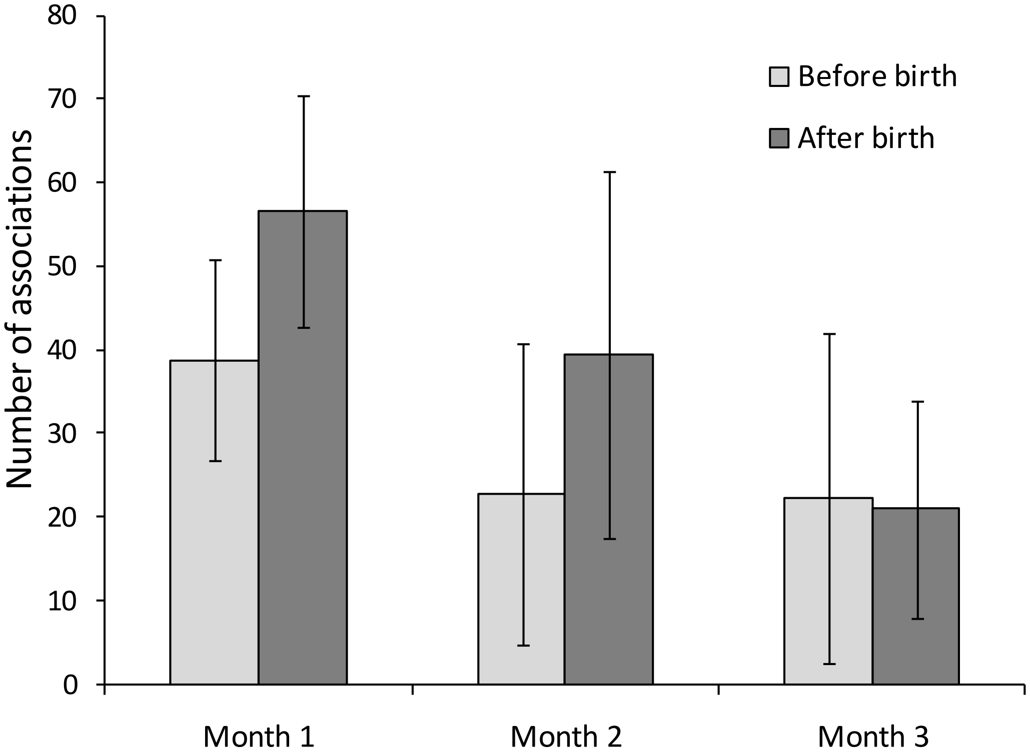

Figure 3. Number of associations between lion tamarins and marmosets during the three months prior to a birth and the three months following a birth (154±6 hours before and after birth) for *cabruca* and mosaic groups combined. Erro bars represent standard deviation.

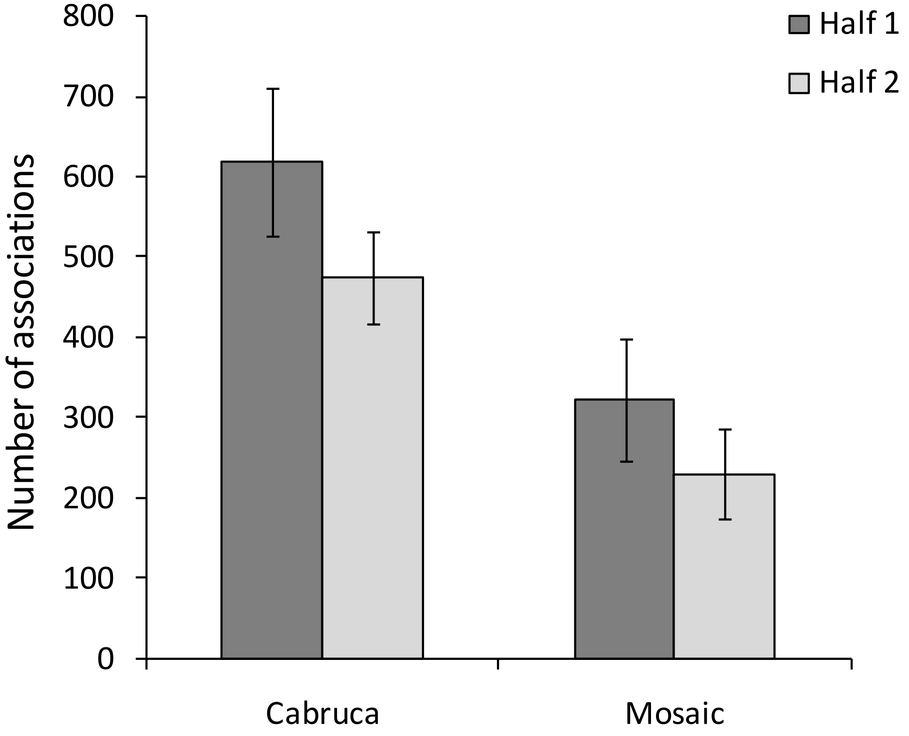

Figure 4. Association between lion tamarins and marmosets in both portions of the day (half 1 and half 2) in *cabruca* and mosaic forests. Erro bars represent standard deviation.

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