

RESEARCH ARTICLE

Predation Risk and the Interspecific Association of Two Brazilian Atlantic Forest Primates in *Cabruca* AgroforestLEONARDO C. OLIVEIRA^{1,2*} AND JAMES M. DIETZ¹¹Department of Biology, University of Maryland, College Park, Maryland²Instituto de Estudos Socioambientais do Sul da Bahia (IESB), Centro, Ilheus, Bahia, Brazil

Forming interspecific associations 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 explaining associations between the endangered golden-headed lion tamarin, *Leontopithecus chrysomelas* and the sympatric Wied's marmoset, *Callithrix kuhlii*. We estimated predation risk by recording the number of encounters between lion tamarins and potential predators in *cabruca* agroforest (shaded cacao 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. To test if the association occurred to improve predator detection and avoidance, we evaluated if associations between the species were more frequent in areas with higher predation risk and during the part of the day when predation risk is higher. We also compared the number of associations 3 months before birth events and 3 months after, when the lion tamarins are more susceptible to predation. Predation risk, mainly by raptors, was significantly higher in *cabruca* than in mosaic forest (0.17 and 0.05 encounters with predators per hour of observation, respectively). Associations were significantly more frequent after birth events and during the part of the day when predation risk was also higher (5–6 am until noon). 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 lion tamarins are more exposed to predation in *cabruca* than in mosaic forest and associations between lion tamarins and Wied's marmosets are related to predation avoidance. *Am. J. Primatol.* 73:852–860, 2011. © 2011 Wiley-Liss, Inc.

Key words: 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 their importance, predation events are rare and unpredictable, which makes them difficult to observe in field studies. The majority of evidence concerning predation on primates consists of anecdotal observations [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; Hart, 2007; Tsukahara, 1993; Ximenez, 1982].

Primates use several strategies to avoid predation. Small primates, for example, may opt to live in large groups as a strategy to increase protection against predators [Chapman & Chapman, 2000a], as large groups provide more ears and eyes to detect predators [Chapman & Chapman, 1996], confound the predator [Morse, 1977] and/or dilute the predation

risk for each individual [Hamilton, 1971]. However, large groups may also face constraints due to reduced foraging efficiency, increased competition for food resources [Terborgh & Janson, 1986] and increased travel distance [Chapman et al., 1995; Chapman and Chapman, 2000b; Janson & Goldsmith, 1995; Wrangham et al., 1993], which can increase exposure to predation [Lucas et al., 1994; McNamara & Houston, 1987].

The social system of some species may also prevent them from increasing their group size [Zuberbuhler,

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2007]. Golden-headed lion tamarins live in groups of from 2 to 15 individuals, with a single breeding female. For the golden-headed lion tamarin, another constraint to the formation of large single-species groups appears to be the availability of suitable sleeping sites. Family groups of lion tamarins sleep together, mainly in tree holes [Raboy & Dietz, 2004; Rylands, 1989]. Large groups may have fewer tree cavities available in their area that are large enough to accommodate all individuals. A possible solution for this constraint on group size is to form an interspecific association during the day. In this way, 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 [Terborgh, 1983], but without competing for shelter 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, 2000a; 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 and guiding to more profitable feeding areas [Chapman & Chapman, 1996; Gautier-Hion et al., 1983; 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, competition for food resources is lower than in large monospecific groups [Zuberbuhler, 2007] and the species involved in the association may have complementary defense skills such as different predator detection abilities [Bshary & Noë, 1997; Noë & Bshary, 1997; Stojan-Dolar & Heymann, 2010a].

In this study, we test two hypotheses explaining the association between the golden-headed lion tamarin, *Leontopithecus chrysomelas* and the Wied's marmoset, *Callithrix kuhlii*. Although both species may benefit from associating, here we evaluate the advantages of this association for lion tamarins only. The first hypothesis is that associations between lion tamarins and marmosets are explained by increased access to food resources. If so, we expect that associations between these two species will occur more frequently in areas where access to food resources is more difficult for monospecific groups than for mixed-species groups [Chapman & Chapman, 1996; Terborgh, 1983], for example, areas where location of specific food resources are known by one species but not the other [Raboy, 2002] or where food is scarce and there is limited dietary overlap between the involved species [Noë & Bshary, 1997]. We also expect to see the two species associate more frequently when lion tamarins are foraging or feeding (either on fruits

or for small animals in bromeliads) than when they are not foraging or feeding. Data on the diet of lion tamarins in *cabruca* (shaded cacao agroforest) and mosaic forest (a mosaic of *cabruca*, primary and secondary forests inside groups home range) show that food resources, mainly jackfruit and bromeliads, two key resources for the lion tamarins [Oliveira et al., 2010] are more abundant and consistently available throughout the year in *cabruca* than in mosaic forest [Oliveira et al., 2011]. Second, we test the hypothesis that association between the two species occurs to reduce risk of predation. We test three predictions associated with this hypothesis. First, if association between the two species serves to decrease predation risk we predict that interspecific associations will be more frequent in areas of high predation risk. Second, because infants are the most vulnerable age class [Caine, 1993; Gould & Sauther, 2007; Izawa, 1978], and the presence of noisy infants may increase the likelihood of detection by predators like raptors [Heymann, 1990] and thus create a need for increased vigilance, we predict that the proportion of time lion tamarins spend in association with marmosets will be higher when groups contain infants. And finally, we predict that the two species will associate more frequently during times of day when predation risk is greatest.

METHODS

Study Sites

This study was carried out in the cacao growing region of southern Bahia state, Brazil, in the municipalities of Ilhéus, Jussari, Camacan, Arataca and Una. We collected data from seven groups of lion tamarins that were divided into two categories according to the vegetation 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 forest (municipalities of Una, Arataca, Camacan and Jussari: Ararauna, Bem te vi, São José and Teimoso groups, respectively) (Fig. 1) hereafter referred to as mosaic groups. Data from all groups were used to estimate the predation risk, whereas we used data from only six groups to analyze associations between the two species. The group São José was excluded from this analysis because after 3 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 subject to misinterpretation.

Study Species

Both lion tamarins and Wied's marmosets are endemic to southern Bahia state and the northwest corner of Minas Gerais state, Brazil. They are cooperative breeders with group sizes ranging from

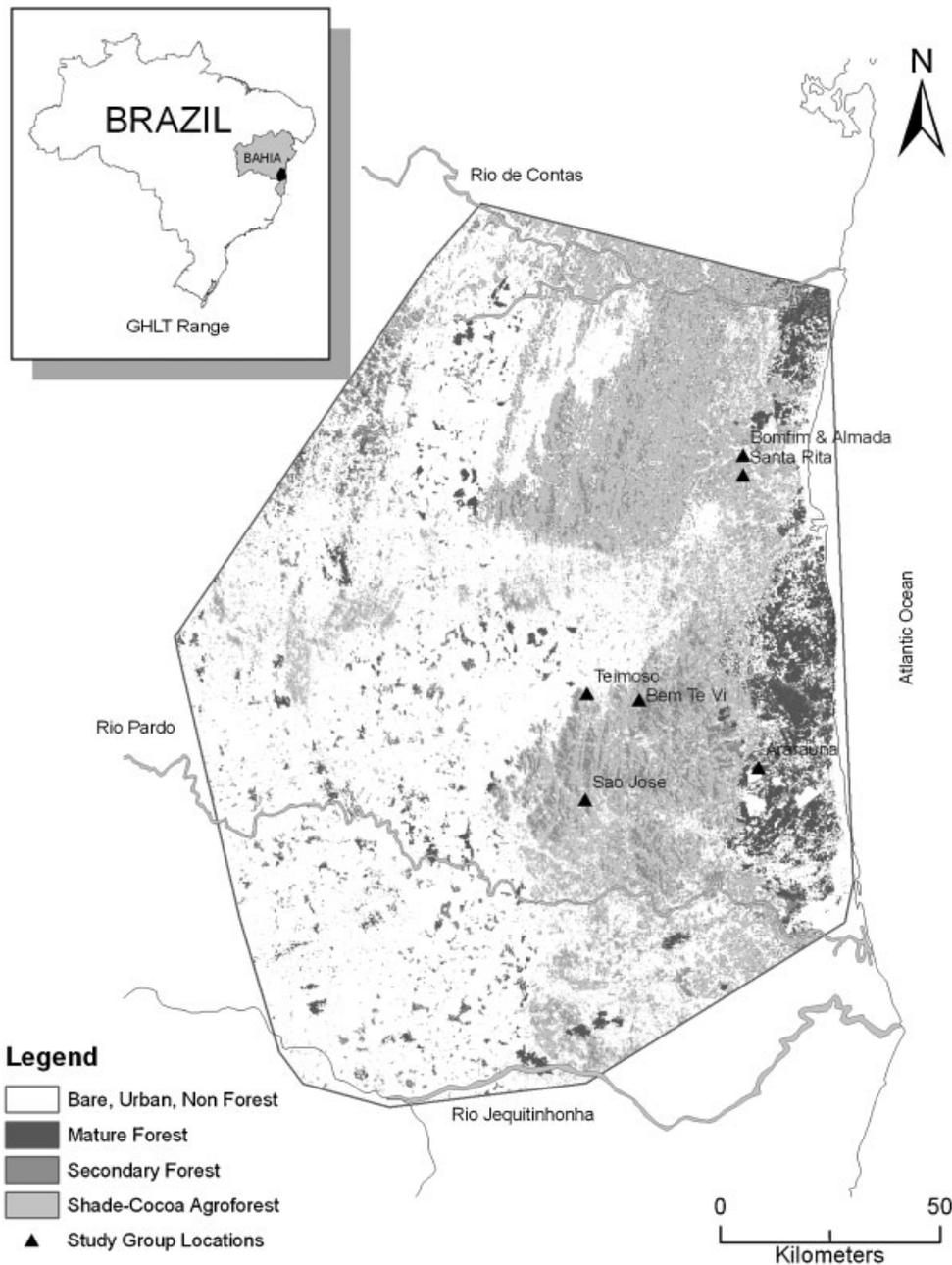


Fig. 1. Geographic distribution of the golden-headed lion tamarin in southern Bahia state, Brazil and the location of the study sites. Map created by Becky Raboy based on a reclassification of land cover at 30 m resolution published in Landau et al. [2003] from 1996 to 1997 Landsat data.

2 to 15 individuals for the lion tamarins [Oliveira et al., 2011] and 4 to 15 individuals for the marmosets [Raboy et al., 2008]. Both species feed on ripe fruits, insects and small vertebrates [Raboy, 2002; Rylands, 1989], but the marmosets also feed on gum when fruits are less abundant [Raboy et al., 2008; Rylands, 1986]. Wied's marmosets are smaller and lighter (approximately 375 g) [Rylands, 1989] than golden-headed lion tamarins (approximately 620 g) [Oliveira et al., 2011]. Typically, Wied's marmosets have

smaller home ranges (ca. 33 ha) and higher densities (0.5–0.68 individuals/ha) than lion tamarins (83 ha, 0.12 individuals/ha) [Oliveira et al., 2011; Raboy et al., 2008; 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]. Associations between the lion tamarins and marmosets have been reported by other authors [Raboy, 2002; Rylands, 1989] and

based on a random gas model analysis [Waser, 1982] the occurrence of these associations was reported to be nonrandom in space and duration [Raboy, 2002].

Data Collection

We captured seven lion tamarin groups in the study areas using Tomahawk live traps ($48.3 \times 15.2 \times 15.2$ cm) baited with banana and placed on platforms 1.5 m above ground [Dietz et al., 1996]. All handling complied with the protocols approved by the University of Maryland Animal Care and Use Committee (number R-07-75); animal captures were also approved by the Brazilian Environmental Agency (IBAMA/ICMBio) permit numbers 12334-1 and 18444-1. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates (<http://www.asp.org/society/resolutions/EthicalTreatmentOfNonHumanPrimates.html>).

We affixed radio-collars to one or two individuals from each group to facilitate location and monitoring. We followed the lion tamarins during complete days (from the time 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). The groups were observed from April 2008 to September 2009 with a total sample effort of 2,500 hr of observation (106–569 hr of observation per group).

Predation Risk

Predation risk was defined as 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. These were defined as any situation in which an animal posing a potential threat to lion tamarins was seen by the observer 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 time and location of every alarm call made by the lion tamarins (even when 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*), toucans (*Rhamphastos*), and aracarís (*Pteroglossus*).

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 m apart (as used in Raboy [2002] and in certain other studies [Buchanan-Smith, 1990; Buzzard, 2010; Chapman & Chapman, 1996, 2000c; Wachter et al., 1997]).

Data Analysis

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 as the number of hours of observation). We tested the differences between predation risk in *cabruca* groups and mosaic groups using one-way ANOVA. To reduce the effect of observation bias on the estimation of predation risk 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 occur 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 3 months before a birth and the 3 months after a birth (the month of birth plus the 2 consecutive months after the birth). For this analysis we used data from three groups combined: 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 hr) before and after birth. We used a Wilcoxon signed rank test with an α level of 0.05, to compare the predation risk before and after the birth of infants.

In order to evaluate whether predation risk varied 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 complete days of observation. To test whether predation risk differed between the first (half 1) and second (half 2) periods of the day we used a Wilcoxon signed rank test with α level of 0.05.

Association Between the Lion Tamarins and Wied's Marmosets

At 20 min intervals we used presence-absence sampling to determine whether a group of marmosets was less than 50 m 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 or foraging in bromeliads) and when they were not eating. For this analysis we used a Wilcoxon signed rank test with α level of 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 3 months before a birth and the 3 months after a birth (the month of birth plus the 2 consecutive months after the birth). We compared the associations before and after the birth of infants using a Wilcoxon signed rank test with an α 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 predation risk was higher by comparing the number of associations in the first (half 1) and second (half 2) periods of the day as defined above, considering only complete days of observation. To test whether the number of associations between lion tamarins and marmosets differed between the half 1 and half 2 periods of the day, we used a Wilcoxon signed rank test with an α level of 0.05. All statistical analyses were done using SAS version 9.2 (SAS Institute Inc., NC).

RESULTS

We observed 314 encounters between potential predators and lion tamarins in our study groups. In *cabruca* and mosaic forest, raptors were the most commonly observed potential predators (210 records) followed by mammalian carnivores (37 records; Table I). All but one identified species of predator were observed attacking a group of lion tamarins at least once; however, none of the attacks resulted in lion tamarin mortality.

Lion tamarins and marmosets were observed in association in 1,721 of 5,411 records for *cabruca* and mosaic forest combined corresponding to 17–39% of all records respectively (Table II). We observed both species foraging together in the same fruit tree, and foraging for small animals in the same bromeliad on 15 occasions. We also observed individuals of the two species playing together (juveniles mainly) and on a few occasions ($N = 7$), in agonistic behaviors.

Foraging Benefits Hypothesis

Contrary to what we predicted, the number of interspecific associations between the two species was significantly higher in *cabruca* than in mosaic forest ($\chi^2 = 123.47$; $df = 1$; $P < 0.0001$). There was no significant difference (Wilcoxon signed-ranks test: $Z = 3.5$, $P = 0.562$, $N = 7$) in the percentage of associations between lion tamarins and marmosets when the lion tamarins were eating fruits or foraging in bromeliads ($33.8 \pm 7.4\%$) and when they were not eating ($32.2 \pm 8.7\%$) in both *cabruca* and mosaic forest.

Predation Avoidance Hypothesis

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 III). The rate of tamarin alarm calls also was significantly higher in *cabruca*

TABLE I. Number of Encounters With Potential Predators and Alarm Calls by Lion Tamarins in the Study Areas

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

TABLE II. 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	<i>Cabruca</i>	1,211	39
Bomfim	<i>Cabruca</i>	591	34
Santa Rita	<i>Cabruca</i>	1,315	39
Ararauna	Mosaic	816	27
Bem te Vi	Mosaic	244	17
Teimoso	Mosaic	1,234	23

TABLE III. 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	No. of encounters	Rate
Almada	<i>Cabruca</i>	567.5	87	0.153
Bomfim	<i>Cabruca</i>	216.9	28	0.128
Santa Rita	<i>Cabruca</i>	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

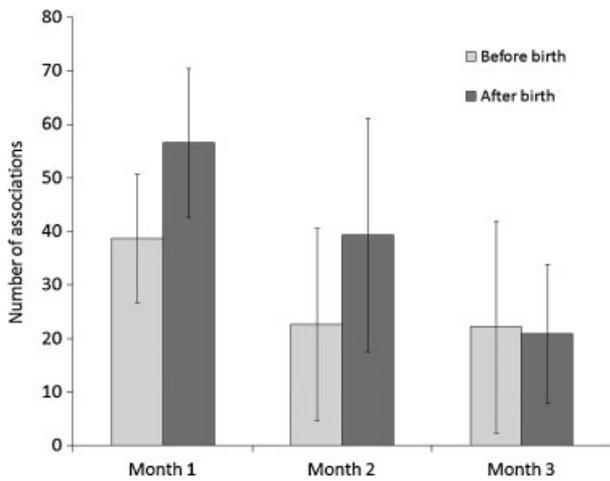


Fig. 2. Number of associations between lion tamarins and marmosets during the 3 months before a birth and the 3 months after a birth (154 ± 6 hr before and after birth) for *cabruca* and mosaic groups combined. Error bars represent standard deviations.

than in mosaic forest, both when no predators were observed ($F = 15.76$; $df = 6$; $P = 0.0106$) and when predators were observed by the field team ($F = 17.61$; $df = 6$; $P = 0.0085$). The rate of attack on lion tamarins by predators 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 3 months before the reproductive female giving birth and the first 3 months after infants were born into a group when combining all three groups (Wilcoxon signed-rank test: $Z = 18$, $P = 0.274$, $N = 5$). However, the rate of association between lion tamarins and marmosets was significantly higher during the 3 months after the birth of infants than the 3 months before birth events when combining all three groups (Wilcoxon signed-ranks test: $Z = -50$, $P = 0.003$, $N = 5$). Association was highest during the first month after birth and showed a decrease in subsequent months (Fig. 2).

Predation risk was significantly higher in the first half of the day than in the second half of the day (Wilcoxon signed-ranks test: $Z = 10.5$, $P = 0.03$, $N = 7$) in both *cabruca* and mosaic forests (Fig 3). Association was also significantly higher (Wilcoxon signed-ranks test: $Z = 10.5$, $P = 0.03$, $N = 7$) during the first half of the day (half 1) in both *cabruca* and mosaic forest (Fig. 4).

DISCUSSION

Although *cabruca* has been described as a suitable habitat for golden-headed lion tamarins [Alves, 1990; Oliveira et al., 2011; Raboy et al., 2004], its structure with lower density and diversity of trees (approximately 10 % compared with native forest), [Alves, 1990; Sambuichi, 2002] and its management (weeding of understory and not replacing dead shade trees) [Sambuichi & Haridasan,

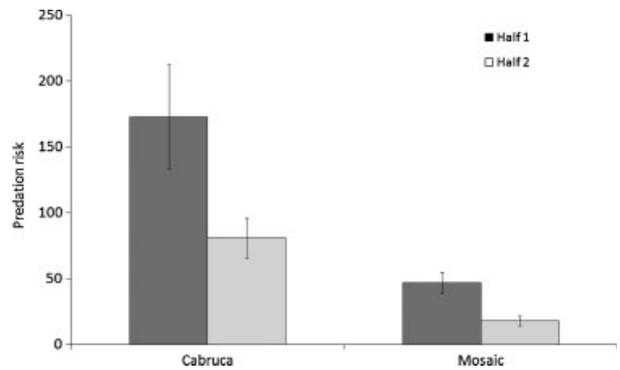


Fig. 3. Predation risk in both portions of the day (half 1 and half 2) in *cabruca* and mosaic forests. Error bars represent standard deviations.

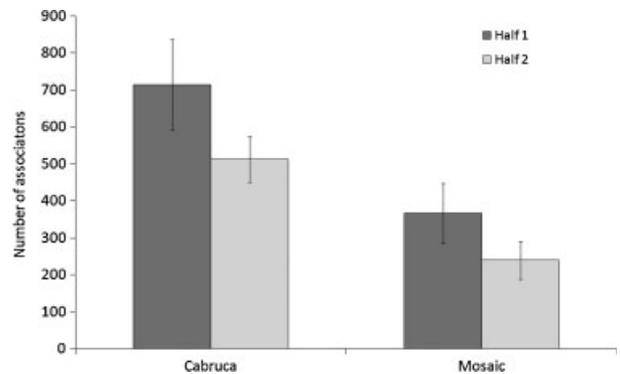


Fig. 4. Association between lion tamarins and marmosets in both portions of the day (half 1 and half 2) in *cabruca* and mosaic forests. Error bars represent standard deviations.

2007] result in lion tamarins being exposed to a higher predation risk from all predators, but mainly from raptors compared with mosaic forest. In *cabruca*, the canopy has lower connectivity and the understory has reduced complexity [see Johns, 1999 for details]. These two habitat characteristics are important in protecting arboreal primates against predators [Ferrari, 2009]. Our results corroborate previous studies suggesting that relatively small-bodied arboreal primates are more vulnerable to raptors [Gilbert, 2000; Hart, 2007; Sherman, 1991; Vasquez & Heymann, 2001] than to terrestrial predators. However, lion tamarins living in *cabruca* are also vulnerable to terrestrial predators. The lack of canopy connectivity and the low complexity of the understory frequently force lion tamarins to travel on the ground in *cabruca*, (we observed lion tamarins on the ground in 84 instances in *cabruca* agroforest and only once in mosaic forest), where they are likely more vulnerable to terrestrial predators [Boinski & Garber, 2000]. The three mammalian carnivores that we observed attacking lion tamarins, *Eira barbara*; *Leopardus wiedii* and *Canis lupus familiaris* in *cabruca* and mosaic forest also have been reported to prey on other primates [Ferrari, 2009].

Foraging Benefits Hypothesis

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 potentially result in competition for food, as both species have similar diets [Raboy et al., 2008; Rylands, 1989]. However, difference in the size of animal prey exploited by the two species, use of different strata while foraging, and differences in range size [Rylands, 1989] suggests low dietary niche overlap between the two species. This, combined with the high abundance of jackfruit (spatial and mainly temporal) and bromeliads in the home ranges of the groups in *cabruca* [Oliveira et al., 2011], suggest that the cost of the association due to food competition is low in *cabruca* or that the cost of not being associated possibly due to higher predation risk outweigh the cost of food competition. We also note that interspecific agonistic interactions at feeding sites involving lion tamarins and marmosets were extremely rare.

Our data did not support our prediction that associations would take place preferentially in areas with low resource availability or in areas with limited access to food resources such as jackfruit and bromeliads. Raboy [2002] studying lion tamarins and Wied's marmosets suggested that association between both species was a win-win relationship where one species, leads the other to ephemeral food resources. Our data do not reveal any direct foraging-related advantages, at least for lion tamarins. However, interspecific associations do not always benefit both species equally [Porter, 2001; Smith et al., 2004] and only one species may benefit from such associations [King & Cowlishaw, 2009].

Predation Avoidance Hypothesis

As predicted, 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 (*cabruca*). Second, associations were more frequent after the birth of infants, when presumably groups are at greater risk of predation and finally, associations between the two species happened more frequently during the first part of the day, when predation risk was also high. Our results corroborate other studies that identified predation avoidance as an explanation for interspecific associations in Old World primates [Bshary & Noë, 1997; Buzzard, 2010; Enstam, 2007; Gould & Sauther, 2007; Noë & Bshary, 1997; Wachter et al., 1997] and other Neotropical primates [Peres, 1993; Smith et al., 2004; Stojan-Dolar & Heymann, 2010a,b]. In contrast, Garber and Bicca-Marques [2002]

report no evidence of predation benefits in the interspecific association between tamarins of the genus *Saguinus*. The tamarins in single-species groups, when foraging at experimental feeding platforms, did not forage in a more predator sensitive way than when they were in association with other tamarin species, nor was there evidence of cooperative vigilance between associated species [Garber & Bicca-Marques, 2002]. However, costs and benefits of association may vary with season [Gautier-Hion et al., 1997], and also may vary in different habitat types [Haugaasen & Peres, 2009], over small spatial scales [Chapman & Chapman, 2000c] and between species involved, which limit generalizations about why species form interspecific associations.

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 primate vigilance and avoidance. 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 be particularly beneficial in areas of high predation risk and low structural complexity, such as *cabruca* agroforest, where detection risk is high and escape route options limited. In areas with the characteristics mentioned above, conspecific as well as interspecific cooperation become important components of antiraptor strategies.

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REFERENCES

- Alves MC. 1990. The role of cacao plantations in the conservation of the Atlantic forest of Southern Bahia, Brazil. Master Thesis. University of Florida, Gainesville, FL. 120p.
- Bartecki U, Heymann EW. 1987. Field observation of snake-mobbing in a group of saddle-back tamarins, *Saguinus fuscicollis nigrifrons*. *Folia Primatologica* 48:199–202.
- Bianchi RC, Mendes SL. 2007. Ocelot (*Leopardus pardalis*) predation on primates in Caratinga Biological Station, southeast Brazil. *American Journal of Primatology* 69: 1173–1178.
- Boinski S, Garber P. 2000. On the move: how and why animals travel in groups. Chicago: University of Chicago Press. 811p
- Bshary R, Noë R. 1997. Red colobus and diana monkeys provide protection against predators. *Animal Behaviour* 54:1461–1474.
- Buchanan-Smith HM. 1990. Polyspecific associations of two tamarin species, *Saguinus labiatus* and *Saguinus fuscicollis* in Bolivia. *American Journal of Primatology* 22:205–214.
- Buzzard PJ. 2010. Polyspecific associations of *Cercopithecus campbelli* and *C. petaurista* with *C. diana*: what are the costs and benefits? *Primates* 51:307–314.
- Caine NG. 1993. Flexibility and co-operation as unifying themes in *Saguinus* social organization and behavior: the role of predator pressure. In: Rylands AB, editor. *Marmosets and tamarins: systematics, behaviour and ecology*. Oxford: Oxford University Press. p 200–219.
- Castro IP. 1990. A comparative study of anti-predator behavior in the three species of lion tamarins *Leontopithecus* in captivity. Master Thesis, University of Maryland, College Park (MD). 143p.
- Chapman CA. 1986. *Boa constrictor* predation and group response in white-faced cebus monkeys. *Biotropica* 18:171–172.
- Chapman CA, Chapman LJ. 1996. Mixed-species primate groups in the Kibale Forest: ecological constraints on association. *International Journal of Primatology* 17:31–50.
- Chapman AP, Chapman LJ. 2000a. Constraints on group size in primates: the importance of travel costs. In: Boinski S, Garber P, editors. *On the move: how and why animals travel in groups*. Chicago: University of Chicago Press. p 24–42.
- Chapman CA, Chapman LJ. 2000b. Constraints on group size in red colobus and red-tailed guenons: examining the generality of the ecological constraints model. *International Journal of Primatology* 21:565–584.
- Chapman CA, Chapman LJ. 2000c. Interdemic variation in mixed-species association patterns: common diurnal primates of Kibale National Park, Uganda. *Behavioural Ecology and Sociobiology* 47:129–139.
- Chapman AC, Wrangham RW, Chapman LJ. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioural Ecology and Sociobiology* 36:59–70.
- Cheney DL, Wrangham RW. 1987. Predation. In: Smuts B, Cheney D, Seyfarth R, Wrangham R, Struhsaker T, editors. *Primate societies*. Chicago: University of Chicago Press. p 227–239.
- Condit VK, Smith EO. 1994. Predation on a yellow baboon (*Papio cynocephalus cynocephalus*) by a lioness in the Tana River National Primate Reserve, Kenya. *American Journal of Primatology* 33:57–64.
- Cords M. 2000. Mixed-species association and group movement. In: Boinski S, Garber P, editors. *On the move: how and why animals travel in groups*. Chicago: The University of Chicago Press. p 73–99.
- Dietz J, de Sousa S, Billerbeck R. 1996. Population dynamics of golden-headed lion tamarins in Una Reserve, Brazil. *Dodo Journal of Wildlife Preservation Trusts* 32:115–122.
- Enstam KL. 2007. Effects of habitat structure on perceived risk of predation and anti-predator behavior of vervet (*Cercopithecus aethiops*) and patas (*Erythrocebus patas*) monkeys. In: Gursky S, Nekaris KAI, editors. *Primate anti-predator strategies (developments in primatology: progress and prospects)*. New York: Springer Publishing. p 308–338.
- Fay JM, Carroll R, Kerbis Peterhans JC, Harris D. 1995. Leopard attack and consumption of gorillas in the Central African Republic. *Journal of Human Evolution* 29:93–99.
- Ferrari S. 2009. Predation risk and antipredator strategies. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB, editors. *South American primates: comparative perspectives in the study of behavior, ecology, and conservation*. Chicago: Springer. p 251–277.
- Franklin SP, Hankerson SJ, Baker AJ, Dietz JM. 2007. Golden lion tamarin sleeping-site use and pre-retirement behavior during intense predation. *American Journal of Primatology* 69:325–335.
- Garber PA, Bicca-Marques JC. 2002. Evidence of Predator Sensitive Foraging and traveling in single and mixed-species tamarin troops. In: Miller L, editor. *Eat or be eaten: predator sensitive foraging in primates*. Cambridge: Cambridge University Press. p 138–153.
- Gautier-Hion A, Quris R, Gautier J. 1983. Monospecific versus polyspecific life: a comparative study of foraging and antipredatory tactics in a community of *Cercopithecus* monkeys. *Behavioural Ecology and Sociobiology* 12:325–335.
- Gautier-Hion A, Gautier J-P, Moungazi A. 1997. Do black colobus in mixed-species groups benefit from increased foraging efficiency? *Comptes Rendus de l'Academie des Sciences* 320:67–71.
- Gilbert KA. 2000. Attempted predation on a white-faced saki in the Central Amazon. *Neotropical Primates* 8:103–104.
- Gould L, Sauther ML. 2007. Anti-predator strategies in a diurnal prosimian, the ring-tailed lemur (*Lemur catta*), at the Beza Mahafaly Special Reserve, Madagascar. In: Gursky S, Nekaris KAI, editor. *Primate anti-predator strategies (developments in primatology: progress and prospects)*. New York: Springer Publishing. p 275–288.
- Hamilton WD. 1971. Geometry for a selfish herd. *Journal of Theoretical Biology* 31:295–311.
- Hart D. 2007. Predation on primates: a biogeographical analysis. In: Gursky S, Nekaris KAI, editors. *Primate anti-predator strategies (developments in primatology: progress and prospects)*. New York: Springer Publishing. p 27–59.
- Haugaasen T, Peres CA. 2009. Interspecific primate associations in Amazonian flooded and unflooded forests. *Primates* 50:239–251.
- Heymann EW. 1990. Reactions of wild tamarins, *Saguinus mystax* and *Saguinus fuscicollis* to avian predators. *International Journal of Primatology* 11:327–337.
- Heymann EW, Buchanan-Smith HM. 2000. The behavioral ecology of mixed-species troops of callitrichine primates. *Biological Reviews* 75:169–190.
- Hill RA, Dunbar RIM. 1998. An evaluation of the roles of predation risk as selective pressure on primate grouping behaviour. *Behaviour* 135:411–430.
- Izawa K. 1978. A field study of the ecology and behavior of the black-mantle tamarin (*Saguinus nigricollis*). *Primates* 19:241–274.
- Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. *Behavioural Ecology* 6:326–336.
- Johns ND. 1999. Conservation in Brazil's Chocolate Forest: the unlikely persistence of the traditional cocoa agroecosystem. *Environmental Management* 23:31–47.
- King AJ, Cowlshaw G. 2009. Foraging opportunities drive interspecific associations between rock kestrels and desert baboons. *Journal of Zoology* 227:111–118.

- Landau EC, Hirsch A, Musinsky J. 2003. Cobertura Vegetal e Uso do Solo do Sul da Bahia-Brasil. In: Prado PI, Landau EC, Moura RT, Pinto LPS, Fonesca GAB, Alger K, editors. Corredor de Biodiversidade da Mata Atlântica do Sul da Bahia. Publicação em CD-ROM, Ilhéus, Brazil: IESB/DI/CABS/UFMF/UNICAMP.
- Lucas JR, Waser MP, Creel SR. 1994. Death and disappearance: estimating mortality risks associated with philopatry and dispersal. *Behavioural Ecology* 5:135–141.
- McGraw WS, Bshary R. 2002. Association of terrestrial mangabeys (*Cercocebus atys*) with arboreal monkeys: experimental evidence for the effects of reduced ground predator pressure on habitat use. *International Journal of Primatology* 23:311–325.
- McNamara JM, Houston AI. 1987. Starvation and predation as factors limiting population size. *Ecology* 68:1515–1519.
- Morse DH. 1977. Feeding behavior and predator avoidance in heterospecific groups. *Bioscience* 27:332–339.
- Noë R, Bshary R. 1997. The formation of red colobus-diana monkey associations under predation pressure from chimpanzees. *Proceedings of the Royal Society of London* 264:253–259.
- Oliveira LC, Hankerson S, Dietz JM, Raboy BE. 2010. Key tree species for the golden-headed lion tamarin and implications for shade-cocoa management in Southern Bahia, Brazil. *Animal Conservation* 13:60–70.
- Oliveira LC, Neves LG, Raboy BE, Dietz JM. 2011. Abundance of jackfruit (*Artocarpus heterophyllus*) affects group characteristics and use of space by golden-headed lion tamarins (*Leontopithecus chrysomelas*) in cabruca agro-forest. *Environmental Management*; in press. DOI: 10.1007/s00267-010-9582-3.
- Passamani M, Mendes SL, Chiarello AG, Passamani JA, Laps RR. 1997. Reintrodução do sagui-da-cara-branca (*Callithrix geoffroyi*) em fragmentos de Mata Atlântica no Sudeste do Brasil. In: Ferrari SF, Schneider H, editors. *A primatologia no Brasil*. Belém: Sociedade Brasileira de Primatologia. p 119–128.
- Peres CA. 1992. Prey-capture benefits in a mixed-species group of Amazonian tamarins, *Saguinus fuscicollis* and *S. mystax*. *Behavioural Ecology and Sociobiology* 31:339–347.
- Peres CA. 1993. Anti-predation benefits in a mixed-species group of Amazonian tamarins. *Folia Primatologica* 61:61–76.
- Porter LM. 2001. Benefits of polyspecific associations for the Goeldi's monkey (*Callimico goeldii*). *American Journal of Primatology* 54:143–158.
- Raboy B. 2002. The ecology and behavior of wild golden-headed lion tamarins (*Leontopithecus chrysomelas*). Ph.D. Dissertation, College Park (MD), University of Maryland. 161p.
- Raboy B, Dietz J. 2004. Diet, foraging, and the use of space in wild golden-headed lion tamarins. *American Journal of Primatology* 63:1–15.
- Raboy BE, Christman MC, Dietz JM. 2004. The use of degraded and shade cocoa forests by endangered golden-headed lion tamarins *Leontopithecus chrysomelas*. *Oryx* 38:75–83.
- Raboy B, Canale G, Dietz JM. 2008. Ecology of *Callithrix kuhlii* and a review of eastern Brazilian marmosets. *International Journal of Primatology* 29:449–467.
- Rylands AB. 1986. Ranging behavior and habitat preference of a wild marmoset group, *Callithrix humeralifer* (Callitrichidae, Primates). *Journal of Zoology* 210:489–514.
- Rylands AB. 1989. Sympatric Brazilian callitrichids: the black tuffed-ear marmoset, *Callithrix kuhlii*, and the golden headed lion tamarin, *Leontopithecus chrysomelas*. *Journal of Human Evolution* 18:679–695.
- Sambuichi RHR. 2002. Fitossociologia e diversidade de espécies arbóreas em cabruca (Mata Atlântica raleada sobre plantação de cacau) na região sul da Bahia, Brasil. *Acta Botanica Brasílica* 16:89–101.
- Sambuichi RHR, Haridasan M. 2007. Recovery of species richness and conservation of native Atlantic forest trees in the cacao plantations of southern Bahia in Brazil. *Biodiversity and Conservation* 16:3681–3701.
- Sherman PT. 1991. Harpy eagle predation on a red howler monkey. *Folia Primatologica* 56:53–56.
- Smith AC, Kelez S, Buchanan-Smith HM. 2004. Factors affecting vigilance within wild mixed-species troops of saddleback (*Saguinus fuscicollis*) and moustached tamarins (*S. mystax*). *Behavioural Ecology and Sociobiology* 56:18–25.
- Stanford CB. 2002. Avoiding predators: expectations and evidence in primate antipredator behavior. *International Journal of Primatology* 23:741–757.
- Stojan-Dolar M, Heymann EW. 2010a. Vigilance in a cooperatively breeding primate. *International Journal of Primatology* 31:95–116.
- Stojan-Dolar M, Heymann EW. 2010b. Vigilance of mustached tamarins in single-species and mixed-species groups—the influence of group composition. *Behavioural Ecology and Sociobiology* 64:325–335.
- Terborgh J. 1983. *Five New World Primates*. Princeton, NJ: Princeton University Press.
- Terborgh J, Janson CH. 1986. The socioecology of primate groups. *Annual Review of Ecology and Systematics* 17: 111–135.
- Tsukahara T. 1993. Lions eat chimpanzees: the first evidence of predation by lions on wild chimpanzees. *American Journal of Primatology* 29:1–11.
- Vasquez MRO, Heymann EW. 2001. Crested eagle (*Morphnus guianensis*) predation on infant Tamarins (*Saguinus mystax* and *Saguinus fuscicollis*, Callitrichinae). *Folia Primatologica* 72:301–303.
- Wachter B, Schabel M, Noë R. 1997. Diet overlap and polyspecific associations of red colobus and Diana monkeys in the Taï National Park, Ivory Coast. *Ethology* 103: 514–526.
- Waser PM. 1982. Primate polyspecific associations: do they occur by chance? *Animal Behaviour* 30:1–8.
- Wolters S, Zuberbuhler K. 2003. Mixed-species associations of Diana and Campbell's monkeys: the costs and benefits of a forest phenomenon. *Behaviour* 140:371–385.
- Wrangham RW, Gittleman JL, Chapman CA. 1993. Constraints on group size in primates and carnivores: population density and day range as essays of exploitation competition. *Behavioural Ecology and Sociobiology* 32: 199–209.
- Ximenez A. 1982. Notas sobre picales VIII: observaciones sobre el contenido estomacal y el comportamiento alimentar de diversas especies de felinos. *Revista Nordestina de Biología* 5:89–91.
- Zuberbuhler K. 2007. Predation and primate cognitive evolution. In: Gursky S, Nekaris KAI, editors. *Primate anti-predator strategies (developments in primatology: progress and prospects)*. New York: Springer publishing. p 3–26.