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Do Habitat Use and Interspecific Association Reflect Predation Risk for the Golden-Headed Lion Tamarin (*Leontopithecus chrysomelas*)?

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Abstract Predation risk may affect the way species use their habitat. Interspecific associations can help to improve predator detection and avoidance. The golden-headed lion tamarin (*Leontopithecus chrysomelas*) is an endangered primate of the Brazilian Atlantic Forest whose geographical range is dominated by shaded cacao agroforest (*cabruca*), where predation risk is high and mainly due to raptors. We investigated whether predation risk affects vertical stratum use and time spent traveling by tamarins, and the role of interspecific association with Wied's marmosets (*Callithrix kuhlii*) in shaping these activities. We compared the behavior of three tamarin groups in *cabruca* (March 2010–June 2011) with that of three groups in mosaic forests (January 2007–December 2008), where predation risk is lower. We predicted that tamarins would use the higher strata level less in

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cabruca than in mosaic forests, and would use it less after encounters with predators than before such encounters. We also predicted increased use of the higher level and increased travel during interspecific associations than when tamarins were alone. We found that tamarins avoided the higher level regardless of habitat, but used it more often in *cabruca* than in mosaic forest, and did not avoid it after encounters with predators. Interspecific associations did not influence tamarins' activities, except for the smallest group of tamarins in mosaic forest, which decreased its use of the lower level when in an interspecific association. Our results suggest that the benefits of interspecies association are not related to the activities investigated here, and that predation risk can influence habitat use but vegetation structure may constrain its optimal use by primates, increasing their vulnerability to predation.

Keywords Agroforest · Antipredator behavior · Callithrichidae · Mixed group · Platyrrhini · Primates

Introduction

Predation is the main cause of mortality in nonhuman primates (Cheney *et al.* 2004) and influences the evolution of primate morphology, behavior, and ecology (Cheney and Wrangham 1987; Gursky and Nekaris 2007). Even if predator attacks are not successful, predation risk—the animal's perception of the possibility of attack by a predator (Hill and Dunbar 1998)—may cause a species to use the different components of its habitat in a substantially different way (Lima and Dill 1990). For example, encounters with predators can alter the behavior of groups for periods ranging from minutes to days (Boinski *et al.* 2000; Dacier e*t al*. 2006; Hankerson and Caine 2004; Lima and Dill 1990).

The main predators of neotropical primates are raptors, carnivores, and snakes (Hart 2007). Domestic dogs are a growing threat, especially in disturbed areas (Galetti and Sazima 2006; Vanak and Gompper 2009). and there are reports of successful predation by dogs on black capuchins (*Sapajus nigritus*: Galetti and Sazima 2006; Oliveira *et al.* 2008) and brown howlers (*Alouatta guariba*: Galetti and Sazima 2006). There is a relationship between body size and range of predators, such that the smaller the body size, the greater the range of potential predators (Ferrari 2009). Callithrichids are the smallest neotropical primates and are thus vulnerable to a wide range of predators (Heymann 1990). with raptors accounting for the largest number of attacks and successful predation events (Hart 2007). As a result, they have developed various antipredator strategies, such as the choice of sleeping sites (Day and Elwood 1999) and high levels of vigilance (Stojan-Dolar and Heymann 2010), and have evolved predator-specific responses (Ferrari 2009; Heymann 1990). One of the most studied antipredator strategies observed in callithrichids is the formation of interspecific associations (Garber and Bicca-Marques 2002; Heymann and Buchanan-Smith 2000; Oliveira and Dietz 2011; Peres 1993; Porter 2001), which occur when individuals of two or more species travel, forage, or sleep in proximity (Chapman and Chapman 2000).

Antipredator benefits linked to interspecific associations are related mainly to increased group size (Terborgh 1986, 1990) through mechanisms such as improved predator detection, due to the presence of more individuals to watch and listen (van Schaik *et al*. 1983); a "dilution effect," meaning a lower individual probability of being captured due to the presence of more alternative prey (Hamilton 1971). and a "confusion effect" on the predator due to a larger number of prey to focus on (Curio 1976). Associating species may also be complementary in their abilities to detect and deter predators (Curio 1978; Peres 1993). improving their success of avoiding predation. Other benefits of associations not related to predation have also been suggested, such as improved foraging efficiency (Gautier-Hion *et al.* 1983) and territory defense (Peres 1992). Interspecific associations also have costs, such as increased risk of attracting predator attention because of the larger group size, and resource competition when species have similar requirements (Stanford 2002). The costs and benefits may be different for each species involved, depending on resource availability, predation pressure, and group size (Garber 1988).

Golden-headed lion tamarins (*Leontopithecus chrysomelas*) and Wied's marmosets (*Callithrix kuhlii*) are primates of the Brazilian Atlantic Forest that form interspecific associations in different habitats (Oliveira and Dietz 2011; Raboy 2002; Rylands 1989). The principal advantage suggested for this association in continuous (mostly mature) forest in Una Biological Reserve, Southern Bahia, Brazil, is improvement in fruit foraging efficiency (Raboy 2002). Both species benefit from the association, but Wied's marmosets seem to benefit more, given that they frequently use tamarins as guides to find resources (Raboy 2002). However, in cacao-growing agroforestry systems, locally known as *cabruca*, also in Southern Bahia, the benefits of this association are apparently related to predator defense (Oliveira and Dietz 2011). In this habitat, the two species associate with each other more frequently and for longer periods than in forested areas, and they tend to do so when predation risk is higher, e.g., at times of the day when more encounters with predators occur and immediately after births (Oliveira and Dietz 2011).

Predation risk for tamarins, measured as the frequency of encounters between prey and potential predators (Hill and Dunbar 1998). is higher in *cabruca* than in primary and secondary forests (Oliveira and Dietz 2011). probably due to differences in habitat structure. In general, areas with high canopy connectivity offer more protection from predators because they offer more routes of escape and concealment (Madden *et al.* 2010). In *cabruca*, the understory is replaced by cacao trees (*Theobroma cacao*) and *ca.* 10% of large native trees are left in place to provide shade for the cacao trees (Johns 1999; Sambuichi 2002). The consequent canopy discontinuity results in tamarins being more exposed to aerial predators in *cabruca* than in natural forests, and encounter rates with predators are higher in *cabruca* compared to natural forest (Oliveira and Dietz 2011). The higher encounter rate with raptors in comparison with terrestrial predators reinforces raptors as the major threat for tamarins in *cabruca* (Oliveira and Dietz 2011). However, because tamarins have fewer options for moving around the canopy, they often need to travel along the forest floor, where they are vulnerable to terrestrial predators such as tayras, *Eira barbara*, and domestic dogs (*Canis lupus familiaris*) (Oliveira and Dietz 2011).

The golden-headed lion tamarin is currently classified as Endangered, mainly because of habitat loss (IUCN 2015). *Cabruca* represents an important habitat for its conservation because it dominates the part of the species' range where the majority of the remaining wild populations are found (Raboy *et al.* 2010; Zeigler *et al.* 2010). Despite the high predation risk, tamarins can survive and reproduce entirely in *cabruca* (Oliveira *et al.* 2011). We here aimed to investigate how the tamarins cope with the increased predation risk in *cabruca* and particularly if interspecific associations with Wied's marmosets affect tamarin antipredator behavior. A study of the same tamarin groups found that food resources are very abundant in *cabruca*, mainly because of the abundance of jackfruits (*Artocarpus heterophyllus*: Oliveira *et al.* 2011). This, combined with the lack of marked climatic seasonality in the region (Gouvêa *et al.* 1976; Mori *et al.* 1983). leads us to assume that tamarins do not experience periods of food scarcity, and thus to discount the possibilities of foraging benefits and competition between the two species. Further, although the diet of the two species is very similar, comprising fruits, insects, and small vertebrates, their prey size and use of vertical strata differ (Rylands 1989). which decreases the likelihood of interspecific competition. In addition, Wied's marmosets' dentition allows them to extract gum from trees, whereas the lion tamarins consume this resource only when it is freely available (Rylands 1993).

We investigated the use of vertical strata and the proportion of time spent traveling by tamarin groups in two habitat types to evaluate whether these activities differ under different levels of predation risk and in the presence of Wied's marmosets. To this end, we compared groups living in *cabruca* with groups living in mosaic forests (a mix of primary and/or secondary forest), where predation risk is lower. We tested two hypotheses:

> Hypothesis 1: Predation risk may affect the way species use their habitat (Boinski *et al.* 2000; Bshary and Noë 1997a; Dacier e*t al.* 2006; Hankerson and Caine 2004; Lima and Dill 1990). Prediction 1a: Tamarins will use the higher forest levels in *cabruca* less than in mosaic forests because of increased predation risk from aerial predators in *cabruca* (Oliveira and Dietz 2011). Prediction 1b: After encounters with raptors, tamarins will use lower forest levels more than before such encounters, as lower strata offer more protection from this type of predator (Heymann 1990; Izawa 1978).
> Hypothesis 2: Interspecific associations allow the associated species to explore risky portions of their habitat (Bshary and Noë 1997b; McGraw and Bshary 2002; Peres 1993; Porter 2001). Prediction 2a: Tamarins will explore the higher—and consequently more exposed—levels more frequently while associating with Wied's marmoset, and use lower levels when they are alone. Prediction 2b: Tamarins will spend more time traveling while associating with Wied's marmoset than when they are alone, as groups are more exposed to predators when traveling (Boinski *et al.* 2000; Lucas *et al.* 1994; McNamara and Houston 1987).

Methods

Study Sites

We studied three tamarin groups in *cabruca* on three privately owned farms: Almada, Bomfim, and Santa Rita (Fig. 1), in the cacao-growing region of

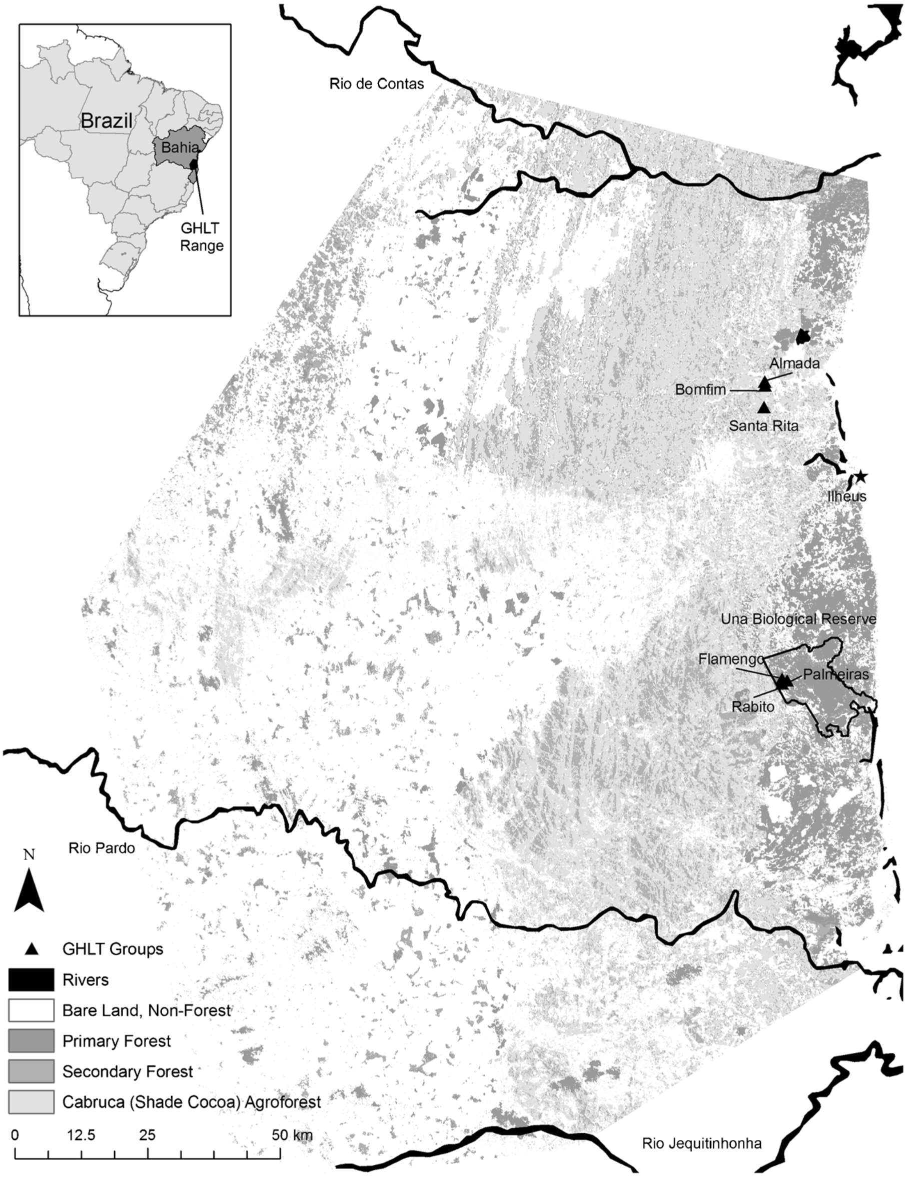

Fig. 1 Geographical range of the golden-headed lion tamarin (*Leontopithecus chrysomelas*) with the territories of Almada, Bomfim, and Santa Rita groups in Southern Bahia State, and Una Biological Reserve, where we studied Flamengo, Rabito, and Palmeiras groups. (Map: Dr. Sara Zeigler).

Southern Bahia State, Brazil, in the municipality of Ilhéus (14°39′S, 39°11′ W). We compared these groups with three groups living in mosaic forest in the western part of the Una Biological Reserve (18,500 ha), in the municipality of Una (15°10′S, 39°03′W). This reserve is composed of a mosaic of secondary forest in different stages of regeneration, interspersed with regenerating pasture and small abandoned agricultural areas (*cabruca* or rubber tree plantations).

Study Groups

We studied three tamarin groups—Almada (6–7 individuals), Bomfim (3–5 individuals), and Santa Rita (9–12 individuals; Fig. 2)—in *cabruca* areas between March 2010 and June 2011. These groups had been habituated to human observers in earlier studies (Oliveira and Dietz 2011; Oliveira *et al.* 2011). We compared these groups with three mosaic forest groups—Flamengo (8–14 individuals), Rabito (3–7 individuals), and Palmeiras (5–10 individuals; Fig. 2)—monitored between January 2007 and December 2008. Both studies used the same methods of capture, monitoring and data collection (those used in Dietz *et al.* 1996).

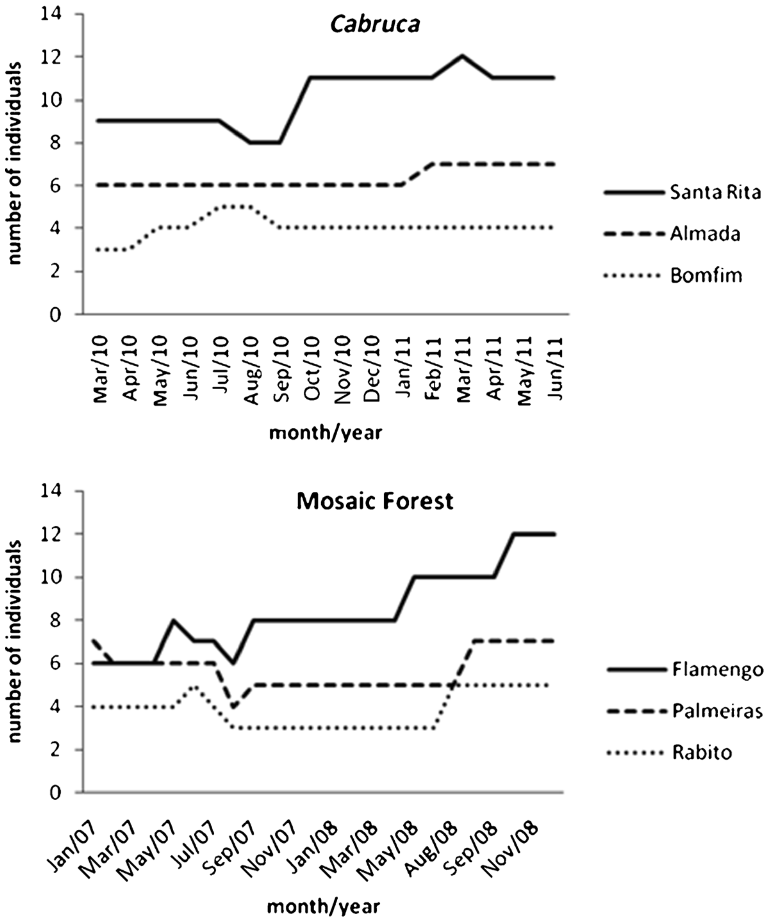

Fig. 2 Variation in group size in six groups of golden-headed lion tamarins (*Leontopithecus chrysomelas*) during data collection in *cabruca* (March 2010–June 2011) and mosaic forest (January 2007–December 2008).

Data Collection

We followed each group at least once a week, for complete days (from the time they left their sleeping site until they retired to sleep) or partial days (when we could not find or leave the group in the sleeping site). To facilitate location and monitoring of the tamarins, we affixed radio-collars (Model RI-2D, Holohil Ltd.) to one or two individuals from each group. To do this, we captured the groups using Tomahawk live traps (48.3 × 15.2 × 15.2 cm) baited with banana and placed on platforms 1.5 m above ground (following Dietz *et al.* 1996).

We collected data using scan sampling (Altmann 1974). Every 20 min we conducted a scan of the group for a maximum duration of 5 min, when we identified as many individuals as possible and collected the following data: state of association with Wied's marmoset (yes or no); vertical stratum use and whether groups were travelling or not. We considered groups to be in association when the distance between groups of lion tamarins and Wied's marmosets was ≤ 50 m, following Raboy (2002) and Oliveira and Dietz (2011). We considered scans in which all visible group members were in locomotion as traveling.

We scored vertical stratum use based on the subject's height above ground. We used the crowns of all trees at the location where each individual was observed during the scan to determine the maximum canopy height at that location, and divided this value into four strata of equal depth (Fig. 3). When subjects were located in trees that had no connectivity with neighboring trees, we considered only the height of that tree (Fig. 3). Subsequently, we allocated each subject to one of the four strata based on its height above ground. The use of these strata instead of absolute height allowed comparisons of the relative degree of security experienced by individuals regardless of total canopy height. The lowest (first) stratum always offered the greatest protection from aerial predators, and the highest (fourth) was always the most exposed, in both *cabruca* and mosaic forest.

In addition to these scans, we recorded all encounters with predators, regardless of whether the predator attempted an attack or not, to assess whether these led to changes in vertical stratum use. Because we were interested in measuring the antipredator reactions of tamarins, rather than actual predation attempts, we also included cases when we did not see the predator but the tamarins gave a typical antipredator reaction (quick alarms and/or fleeing).

Fig. 3 Division of vertical stratum into four levels, using the crowns of all trees to determine the maximum canopy height. The lower scale represents cacao trees without a connection to higher trees.

Data Analysis

Criteria for Data Exclusion We excluded all data on individuals younger than 6 mo old (following Raboy and Dietz 2004) from our analyses, because individuals of this age class are not completely independent and are frequently carried by adults. We also excluded all occasions where the group was not visible, except when we knew the entire group to be in the same location and were able to reliably determine their height, such as when they were gathered in a single bromeliad. We also excluded all occasions when the groups were next to capture stations, where their behavior may be influenced by the presence of bait, and during encounters with other groups, where we remained distant to avoid influencing the encounter.

Rates of Interspecific Association We compared the proportion of time spent in association (the number of scans in association divided by the total number of scans) between *cabruca* and mosaic forest groups. For this analysis, we used a Kruskal–Wallis test.

Vertical Stratum Use For each scan, we calculated the modal level where individuals were recorded to represent the location of the group. Then we determined the total number of scans for which each group was observed on each of the four vertical strata. We considered only the scans for which we observed at least half of the group members, to ensure that we had a representative sample of the entire group. Finally, we calculated the proportion of scans where the group was observed in each level (number of scans in each level divided by the total number of scans) by day. We used both complete and partial days in analysis. We used linear mixed-effect models (LMEMs) to compare the proportion of use of each vertical stratum in each habitat. In the model, we used habitat type (*cabruca* or mosaic forest) as a fixed effect and identity of groups as a random effect on the response variable (proportion of use). We also used LMEMs to assess whether use of vertical strata changed when tamarins were in association with Wied's marmosets. In this case, we used association state ("yes" or "no") as a fixed effect and group identity as a random effect.

We analyzed the group's reaction only to aerial predators, as they represent the main threat to tamarins, especially in *cabruca* (Oliveira and Dietz 2011). We compared vertical stratum use during the hour before each encounter with that during the hour after each encounter, a period that we consider sufficient to detect immediate changes in behavior resulting from the predator's presence. When there was more than one encounter on the same day, we analyzed only the first one, because the group's behavior during subsequent encounters may have been affected by the first one. When the group was not visible in one of the periods (1 h before or after the encounter) we did not analyze this encounter. We categorized the group's reaction, noting whether the group remained in the same stratum, descended or climbed. We used a Wilcoxon paired test to test whether there was a difference in the strata used before and after encounters.

Movement To compare the proportion of time spent traveling when in and not in association with Wied's marmosets we calculated the daily proportion of scans where the group was traveling (number of scans when groups were traveling divided by the total number of scans) for each state of association and used LMEMs to test whether association influenced travel by tamarins. In the model, we used state of association ("yes" or "no") as a fixed effect and group identity as a random effect. We performed analyses for each habitat type separately.

We conducted all statistical tests in R 3.0.2 (R Core Team 2013). For Kruskal–Wallis tests, we used the function kruskal.test in the stats package (R Core Team and contributors worldwide). For LMEMs we used the function lme in the nlme package (Pinheiro *et al.* 2013). For Wilcoxon paired tests, we used the function wilcox.test in the stats package (R Core Team and contributors worldwide).

Ethical Note

All animal capture and handling procedures used to place the radio-collars were approved by the Brazilian Environmental Agency (ICMBio/SISBIO) under permit numbers 18444-1 and 12334-1. In addition, this research adhered to the American Society of Primatologists' ethical principles for the treatment of primates and to the guidelines for the treatment of animals in behavioral research and teaching (Animal Behavior Society 2012). We anesthetized individuals with 10 mg/kg of ketamine and 0.3 mg/kg of midazolam (Dormire®) to fit the radio-collar. We kept individuals in captivity until the next morning, when they were released in the same location where they were captured. We recaptured groups every 6 mo to change the radio-collars, evaluate their health state, and take biometric measures. The radio-collars were not removed at the end of this study because these groups are still being monitored as part of another research project.

Results

The total sampling effort was 750 h (83 days) in *cabruca* and 1028 h (119 days) in mosaic forest (Table I). This comprised 1489 and 2300 scans in *cabruca* and mosaic

Table I Sampling effort and total number of scans collected for six golden-headed lion tamarin groups when in and not in association with Wied's marmosets in two habitats in Southern Bahia, Brazil: *cabruca* (March 2010–June 2011) and mosaic forest (January 2007–December 2008)

Group	Total hours	Total days	Total scans	Scans in association	Scans not in association
Almada	241	29	567	187	380
Bomfim	279	31	583	70	513
Santa Rita	230	23	339	103	236
Cabruca	750	83	1489	360	1129
Flamengo	387	44	798	130	668
Rabito	288	36	681	55	626
Palmeiras	353	39	821	72	749
Mosaic forest	1028	119	2300	257	2043

forest, respectively. The proportion of time spent in association with Wied's marmoset was significantly higher in *cabruca* (mean$_{\text{all groups}}$: 0.25, SD: 0.21) than in mosaic forest (mean$_{\text{all groups}}$: 0.14, SD: 0.16) (Kruskal–Wallis test:χ^2=4.2341, df = 1, P = 0.040).

Vertical Stratum Use

Cabruca vs. Mosaic Forest In *cabruca*, all tamarin groups used the lower three strata to a similar extent, and stratum 4 less frequently (Table II). In mosaic forest, however, the proportion of use of the strata decreased with increasing height. There was a significant difference between habitats in the use of all strata except stratum 2 (Table II). Although stratum 4 was used less than other strata in both habitats, it was used more frequently in *cabruca* than in mosaic forest (Table II).

Effect of Interspecific Associations Only one group showed any change in their use of vertical strata when they were in association with Wied's marmosets (Table III). Rabito group (mosaic forest) decreased their use of stratum 1 when with Wied's marmosets.

Effect of Predator Encounters We observed a total of 154 encounters with predators (127 in *cabruca* and 27 in mosaic forest) including raptors, snakes, and carnivores

Table II Summary of the linear mixed-effect models comparing the proportion of vertical strata levels use (response variable) by six golden-headed lion tamarin's groups (random effects) in Southern Bahia, Brazil, on two habitats (fixed effects): *cabruca* (March 2010–June 2011) and mosaic forest (January 2007–December 2008)

Strata level	Proportion of use				Linear mixed effect models' results					
	Cabruca		Mosaic forest		Effects					
	Mean	SD	Mean	SD						
1	0.27	0.20	0.50	0.20	Random effects:	SD (intercept: 0.000; residual: 0.199)				
					Fixed effects:	value	SE	Df	*t*-value	*P*-value
					Intercept (*cabruca*)	0.27	0.02	196	12.360	<0.001
					Mosaic forest	0.23	0.03	4	8.012	0.001
2	0.31	0.15	0.34	0.16	Random effects:	SD (intercept: 0.031; residual: 0.157)				
					Fixed effects:	value	SE	Df	*t*-value	*P*-value
					Intercept (*cabruca*)	0.31	0.02	196	12.277	<0.001
					Mosaic forest	0.03	0.03	4	0.960	0.391
3	0.30	0.15	0.15	0.12	Random effects:	SD (intercept: 0.002; residual: 0.134)				
					Fixed effects:	value	SE	df	*t*-value	*P*-value
					Intercept (*cabruca*)	0.30	0.02	196	15.860	<0.001
					Mosaic forest	–1.52	0.03	4	–5.955	0.004
4	0.12	0.11	0.01	0.04	Random effects:	SD (intercept: 0.001; residual: 0.077)				
					Fixed effects:	value	SE	df	*t*-value	*P*-value
					Intercept (*cabruca*)	0.12	0.01	196	14.513	<0.001
					Mosaic forest	–0.11	0.01	4	–9.840	0.001

Table III Results of linear mixed-effect models comparing the proportion of use of four levels of vertical strata by golden-headed lion tamarins in two habitats in Southern Bahia, Brazil—*cabruca* (March 2010–June 2011) and mosaic forest (January 2007–December 2008)—with respect to interspecific association with Wied's marmosets: in association (Yes) and not in association (No)

	Level 1					Level 2					Level 3					Level 4				
Group	No	Yes	df	*t*-value	*P*-value	No	Yes	df	*t*-value	*P*-value	No	Yes	df	*t*-value	*P*-value	No	Yes	df	*t*-value	*P*-value
Almada	0.26	0.21	32	–0.697	0.491	0.32	0.26	32	–0.721	0.476	0.28	0.39	32	1.599	0.120	0.14	0.14	32	0.050	0.960
Bomfim	0.25	0.11	38	–2.016	0.051	0.26	0.28	38	0.453	0.653	0.35	0.39	38	0.582	0.564	0.14	0.22	38	1.371	0.178
Santa Rita	0.29	0.27	28	–0.328	0.746	0.31	0.36	28	0.700	0.489	0.23	0.28	28	0.876	0.389	0.16	0.09	28	–1.217	0.234
Flamengo	0.50	0.44	61	–0.794	0.431	0.34	0.37	61	0.470	0.640	0.15	0.19	61	0.840	0.404	0.00	0.01	61	–1.565	0.123
Palmeiras	0.54	0.40	45	–1.679	0.100	0.29	0.33	45	0.638	0.527	0.15	0.23	45	1.743	0.088	0.02	0.04	45	0.900	0.373
Rabito	0.48	0.32	46	–2.357	0.023*	0.37	0.43	46	1.032	0.307	0.14	0.23	46	1.806	0.078	0.02	0.02	46	0.209	0.835

*Significant value.

(Table IV). In 42 of these encounters (27% of events) tamarins were associated with Wied's marmosets. We only analyzed encounters with raptors, which correspond to 120 events (78% of all events), 105 of which were in *cabruca* and 15 in mosaic forest.

We discarded 51 encounters, which were not the first encounter of the day (only two of these were in mosaic forest). Of the remaining encounters, 37 had sufficient scans (at least one scan) in the hour before and after the encounter to compare (Table V). Of these, 29 were in *cabruca* and eight in mosaic forest. The tamarins used either the first or second stratum in the hour prior to the majority of these encounters (first: 12; second: 15; third: 5; fourth: 6). In six situations when groups remained in the same stratum, they were in stratum 1 before the encounter, so they could only remain there or climb higher. After encounters, tamarins used strata 1 and 3 most frequently (first: 14; second: 9; third: 11; fourth: 4), maintaining the general pattern of vertical strata use observed in *cabruca*. There was no significant difference in the use of strata before and after encounters (Wilcoxon paired test: $V=169$, $P = 0.874$, $N = 38$).

Movement

We recorded groups traveling on 156 scans in 335 days of monitoring (274 in *cabruca* and 61 in mosaic forest). There was no significant difference in the proportion of time spent traveling when in and not in association with Wied's marmosets in either habitat type (Fig. 4). In *cabruca*, the mean frequency of travelling was 0.22 ± SE 0.02 when in association and 0.20 ± SE 0.02 when not in association ($t = 0.75$; $P = 0.45$; df = 97). In mosaic forest, the mean frequency of traveling was 0.06 ± SE 0.03 in association and 0.08±SE 0.01 out of association ($t = -1.11$; $P = 0.27$; df = 47).

Discussion

In this study, we found that golden-headed lion tamarins use lower levels of vertical strata more frequently than higher levels regardless of habitat type, in accordance with the common pattern for small-bodied primate species (Fleagle 1988; Sussman and Kinzey 1984). Contrary to our predictions, the tamarins used higher levels more often

Table IV Potential predators of the golden-headed lion tamarin encountered in two habitats on Southern Bahia, Brazil: *cabruca* (March 2010–June 2011) and mosaic forest (January 2007–December 2008)

Predator type	*Cabruca*	Mosaic forest
Raptors	82	15
Unidentified aerial	23	0
Domestic dogs	7	3
Wild cats	0	2
Tayras	2	1
Snakes	1	5
Unidentified terrestrial	12	1
Total	127	27

Unidentified indicates predators that we did not see but whose presence we inferred from an antipredator reaction by the tamarins.

Table V Reactions of golden-headed lion tamarins to encounters with potential predators in *cabruca* (March 2010–June 2011) and mosaic forest (January 2007–December 2008) in Southern Bahia, Brazil

Habitat	Group	Descend	Remain	Climb	Total
Cabruca	Almada	5	2	3	10
Cabruca	Bomfim	3	6	3	12
Cabruca	Santa Rita	1	2	4	7
Mosaic forest	Flamengo	2	0	3	5
Mosaic forest	Palmeiras	1	1	0	2
Mosaic forest	Rabito	1	0	0	1
Total		13	11	13	37

in *cabruca*, where canopy connectivity is lower, than in mosaic forest. This presumably results in groups being more exposed to aerial predators in *cabruca* than in mosaic forest. We also found that tamarins did not increase the use of lower levels after encounters with predators in *cabruca*, suggesting this strategy may not be efficient in this habitat. Finally, there was no change in the overall way tamarins use their habitat (vertical stratum and travel) as a result of associations with Wied's marmoset in both habitats. It suggests that benefits of this interspecific association are not related with the aspects investigated here.

Vertical Strata Use

Cabruca vs. Mosaic Forest The risk of predation in *cabruca* is considerably greater than in forested areas, and most predator encounters involve raptors (Oliveira and Dietz 2011). In the forested areas surveyed in this study the overall predation risk is lower, but raptors were nevertheless the main predator group seen during encounters (Oliveira *et al. unpub. data*). We predicted that tamarins would avoid the highest strata more in *cabruca* than in the mosaic forest. However, tamarins avoided stratum 4 in both

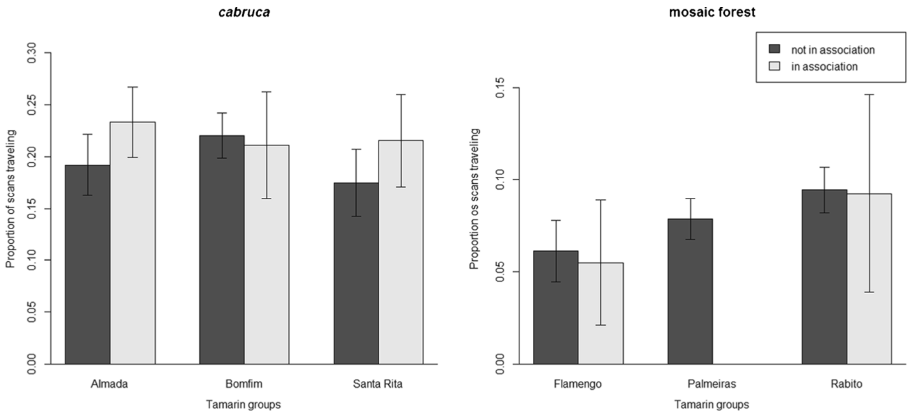

Fig. 4 Mean ± standard error proportion of scans spent traveling when in association and not in association with Wied's marmosets for golden-headed lion tamarin groups in *cabrucas* (March 2010–June 2011) and mosaic forests (January 2007–December 2008) in Southern Bahia, Brazil.

habitats, and in the mosaic forest they also avoided stratum 3, suggesting that it is the predominant predator type, i.e., raptors in both habitats, rather than the level of perceived predation risk that determines tamarins' vertical stratum use in these habitat types.

Predation pressure on callithrichids is thought to have led to the evolution of a preference for using dense vegetation at lower levels in secondary forest habitats (Sussman and Kinzey 1984). Owing to the replacement of understory trees by cacao trees, *cabrucas* are less dense than forests (Sambuichi 2006). Consequently, the first two strata in the mosaic forest of our study have denser vegetation and are used more often by the tamarins, particularly stratum 1 (the understory). Given that the tamarins' preferred strata are available in mosaic forest, there is no need for them to use the more exposed strata, which may explain why they use strata 3 and 4 less frequently in mosaic forest habitat. In *cabruca*, the vegetation structure is greatly simplified and discontinuous, so that strata 1 and 2, and to a lesser degree 3 and 4 as well, offer far fewer resources and potential travel routes than the corresponding strata in a secondary forest. In *cabruca*, stratum three would be suboptimal for tamarins, as it is in mosaic forest, but it may offer more travel routes and opportunities for performing more activities, given the discontinuity of the canopy.

Effect of Interspecific Association Given that interspecific associations allow groups to move and forage more safely because they increase a group's efficiency in detecting predators (Buchanan-Smith and Hardie 1997; Heymann and Buchanan-Smith 2000; Peres 1993), we predicted that groups of tamarins would use the highest stratum more during associations with Wied's marmosets than when they were alone. However, the tamarins pattern of vertical strata use was independent of association in *cabruca*, contrary to our prediction. Although tamarins used the higher level of vertical strata less than the other levels in both habitats, they used this level more in *cabruca*. Thus, increasing the use of this level even more during associations may not be a good strategy.

In the mosaic forest groups, differences in the use of vertical strata during associations were significant only for smallest of the forest groups (Rabito), which decreased its use of stratum 1. The fact that it did not increase its use of stratum 4, as predicted, may be explained by the greater abundance of resources provided by all strata in forest, compared with *cabruca*. Forest groups may therefore be able to continue avoiding the most exposed stratum while still fulfilling their needs by using mostly strata 2 and 3, even during associations. The fact that we found this pattern only for the smallest group suggests that further studies of groups of different sizes are needed to test the effect of group size.

Effect of a Predator Encounter Although the most common immediate response to aerial predators is alarm and descending to a lower stratum of the forest (Hankerson and Caine 2004; Miranda *et al*. 2006). we found no difference between stratum use before and after encounters. The small number of suitable predator encounters in mosaic forest prevented us from drawing any broad conclusions for this habitat. For *cabruca*, the majority of encounters occurred in the first and second strata. The lack of connectivity in this habitat (Johns 1999) may mean that tamarins in the lower strata are also exposed to aerial predators, which can attack both from above and along the horizontal axis (Smith *et al.* 2004). On one occasion we observed a predation attempt by a hawk (unidentified species) on the Bomfim group in stratum 1 of a cacao tree, which should offer the highest protection from this type of predator. It seems likely that spending more time in the lower strata is not effective for avoiding predation by aerial predators in *cabruca*, and that other antipredator mechanisms, such as vigilance, may be more efficient.

Movement

We predicted that tamarins would spend more time moving while in association with Wied's marmosets, thus presumably increasing their foraging success. Our results did not support this prediction: groups did not travel more when in association with Wied's marmosets in either *cabruca* or mosaic forest. These patterns contrast with those for Goeldi's monkey (*Callimico goeldii*), which spent a considerable amount of time resting quietly in the understory when they were alone, but traveled longer distances and enjoyed a broader diet when associated with saddleback tamarins (*Saguinus fuscicollis*) and red-bellied tamarins (*S. labiatus*) (Porter and Garber 2007) and emperor tamarins (*S. imperator*), which also traveled greater distances when associated with saddleback tamarins (Terborgh 1983). A possible explanation for the lack of a difference in travel when in association and when not in association in *cabruca* might be the high availability of resources (Oliveira *et al.* 2011). which may decrease the need for groups to travel long distances to forage. For the mosaic forest, previous studies have shown that tamarins did not alter their behavior while in association with Wied's marmosets in forests, but both species benefitted by gaining access to ephemeral resources (Raboy 2002). which does not necessarily require increased movement.

Our study shows that golden-headed lion tamarins avoid using the higher vertical strata regardless of habitat type. However, they used the higher strata more often in *cabruca* than in forested areas, even though exposure to raptors is greater there. This is probably due to limitations imposed by habitat structure, which increase the risk of predation further. The reasons for associating with other species are likely to differ between habitats and species, and may be related to predation in some areas but to other factors in other areas. It would be interesting to test whether interspecific associations enhance protection against predators in other ways that we have not investigated here, such as cooperative vigilance. However, with the caveat of a small sample size, our study suggests that associations between golden-headed lion tamarins and Wied's marmosets may be a particularly important antipredator strategy for small groups.

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