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ORIGINAL ARTICLE

Preliminary findings on social and ecological correlates of a polyspecific association between a golden-headed lion tamarin (*Leontopithecus chrysomelas*) and Wied's marmosets (*Callithrix kuhlii*)

Leonardo de Carvalho Oliveira[1,3,5] · **Juliana Monteiro de Almeida Rocha**[3] ·
Paula Pedreira dos Reis[3,4] · **James Dietz**[2,6]

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Abstract The advantages of living in a group include feeding benefits and/or predation avoidance, while the disadvantages are typically related to competition. One way to avoid competition while maintaining the benefits of living in a group is to form interspecific associations with species with relatively little dietary overlap. Here we report a stable association between a male golden-headed lion tamarin (GHLT), *Leontopithecus chrysomelas*, and a group of Wied's black-tufted-ear marmosets (WBTMs), *Callithrix kuhlii*. We collected ecological and behavioral data on a duo of GHLTs from May to August 2008, totaling 62 h of observations. On 19 August 2008, the radio-collared GHLT dispersed alone and was located on 28 August in association with WBTMs. To examine possible changes in GHLT ecology and behavior, we monitored the mixed-species group between September and December 2008, totaling 122 h of observations. We found that the GHLT's home range and daily path length decreased by about ten and three times, respectively, after joining the WBTM group, suggesting adaptations to the WBTMs' use of space. All non-agonistic behaviors recorded in the mixed group were directed from GHLT to the WBMTs, whereas all agonistic interactions were directed from the WBMTs to the GHLT, indicating a subordinate position of GHLT in the mixed group. In golden lion tamarins, reproductive success of subordinate adult males that remain in the group is higher than that of those that disperse and "prospect" for a breeding opportunity. If dispersing individuals are unable to find a mate and defend a territory, they will likely die within a year. The dispersing GHLT in this study assumed a subordinate role in a mixed-species group outside a GHLT territory. Apparently, the benefits of waiting for a dispersing female in a relatively safe situation may exceed the costs of prospecting elsewhere or being a subordinate.

Keywords Callithrichidae · Dispersal · Mixed group · Primate hierarchy · Platyrrhini · Sociality

Introduction

Primates form social groups of various sizes and compositions, which provide advantages in predator detection, territory defense and foraging efficiency (van Schaik 1983; van Schaik and van Hooff 1983; Treves and Chapman 1996; Olupot and Waser 2001). Despite the benefits of group living, some disadvantages may arise as group size increases. Larger groups may experience increased competition for food resources (Terborgh and Janson 1986) and travel longer distances to find enough resources for the entire group (Wrangham et al. 1993; Chapman et al. 1995; Janson and Goldsmith 1995; Chapman and Chapman

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✉ Leonardo de Carvalho Oliveira
leonardoco@gmail.com

[1] Departamento de Ciências, Faculdade de Formação de Professores, Universidade do Estado do Rio de Janeiro (UERJ), Rua Dr. Francisco Portela, 1470-Patronato, CEP 24435-005 São Gonçalo, RJ, Brazil

[2] Program in Behavior, Ecology, Evolution and Systematics, University of Maryland, College Park, MD 20742, USA

[3] Programa de pós-graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz (UESC), Salobrinho, CEP 45662-900 Ilhéus, BA, Brazil

[4] Instituto de Estudos Socioambientais do Sul da Bahia (IESB), Rua Araujo Pinho, 72-3° Andar, Centro, CEP 45.653-145 Ilhéus, BA, Brazil

[5] Bicho do Mato Instituto de Pesquisa, Av. Cônsul Antônio Cadar, 600, CEP 30360-082 Belo Horizonte, MG, Brazil

[6] Save the Golden Lion Tamarin, Silver Spring, MD, USA

2000), which ultimately may increase exposure to predators (McNamara and Houston 1987; Lucas et al. 1994). One way of retaining the advantages of being in a larger group without the high costs of intraspecific competition is to form interspecific associations (Heymann and Buchanan-Smith 2000; Ferrari 2009). Competition is expected to be lower among individuals of different species (Terborgh 1990) when associating species have little extensive dietary overlap.

Reports of interspecific associations between primate species are relatively common (Terborgh 1990; Buchanan-Smith 1999; Heymann and Buchanan-Smith 2000; Stensland et al. 2003), including cases of single individuals associating with a group of another species (Struhsaker 1988; Fleury and Gautier-Hion 1997). Associations can vary in frequency and duration, ranging from brief encounters to stable mixed groups (Terborgh 1983; Heymann 1990; Peres 1992; Buchanan-Smith 1999; Chapman and Chapman 2000). One possible explanation of why primate species associate is increased foraging efficiency (Whitesides 1989; Peres 1992, 1996; Wachter et al. 1997), such as when species forage at different levels of the vertical strata (Heymann and Buchanan-Smith 2000). Another possible explanation is related to antipredator benefits (Terborgh 1986, 1990), since associations result in larger groups where more individuals can detect potential predators (van Schaik et al. 1983; Peres 1993; Hardie and Buchanan-Smith 1997). Also, larger groups decrease each individual's probability of being captured (Hamilton 1971) and can have a "confusion effect" on the predator (Curio 1976).

Associations between golden-headed lion tamarins (GHLTs), *Leontopithecus chrysomelas*, and Wied's black-tufted-ear marmosets (WBTMs), *Callithrix kuhlii*, are reported in various habitat types, and the occurrence of these encounters is non-random in space and duration (Rylands 1989; Raboy 2002; Oliveira and Dietz 2011). These associations appear to be related to foraging benefits in native forests (Raboy 2002) and to antipredator benefits in shaded cacao plantations, locally known as *cabrucas* (Oliveira and Dietz 2011). The associations reported in these previous studies were not stable and were highly variable in duration (Rylands 1989; Raboy 2002; Oliveira and Dietz 2011). Here, we report what we believe to be a stable association between an adult male GHLT and a breeding group of WBTM. We defined this association as stable since the GHLT spent almost 100 % of its time with the WBTMs. To understand the social dynamics in this mixed-species group, we described the social behaviors observed between the GHLT and the WBTMs, and investigated changes in the GHLT's use of space and feeding behavior after it joined the group.

Methods

Study species

GHLTs (Fig. 1) are endemic to the Atlantic Forest of southern Bahia state and the extreme north-east of Minas Gerais state, Brazil (Kierulff et al. 2008). The species is classified as "endangered" due to population reduction caused by habitat loss, especially in the western part of its distribution (MMA 2014; IUCN 2016). It is a cooperative-breeding species in which groups are usually composed of one reproductive female (parous), one to three adult males, and their offspring (Dietz et al. 1994). The average group size is seven, ranging from two to 15 individuals (Oliveira et al. 2011). Home range size varies from 22 to 200 ha (Oliveira et al. 2011) and daily path lengths average 1753 ± 211 m (± SD) (Raboy and Dietz 2004). GHLT body mass averages 620 g (Oliveira et al. 2011), and the diet consists of ripe fruits, flowers, nectar, insects, small vertebrates, and occasionally gum (Rylands 1989; Raboy and Dietz 2004; Oliveira et al. 2010). GHLTs usually sleep in tree holes and vine tangles, and occasionally palm leaves (Raboy and Dietz 2004; Oliveira et al. 2010).

Fig. 1 Golden-headed lion tamarin (GHLT), *Leontopithecus chrysomelas* (photograph, Renato Grimm)

Fig. 2 Wied's marmoset (*Callithrix kuhlii*) (photograph, Renato Grimm)

WBTMs (Fig. 2) are also endemic to the Atlantic Forest of southern Bahia and the northwest corner of Minas Gerais state (Rylands and Kierulff 2008). It is classified as "near threatened" due to habitat loss (IUCN 2016). It is a cooperative-breeding species with groups averaging four individuals (ranging from four to seven), including one breeding female and one or two adult males (Raboy et al. 2008). Home range size varies from 10 ha (Rylands 1989) to 39 ha (Raboy et al. 2008), with daily path lengths averaging 1498 ± 374.5 m (Raboy et al. 2008). The average adult weight is 375 g (Rylands 1989) and the diet is more frugivorous than that of congeners (Raboy et al. 2008). WBTMs usually sleep in bromeliads and vine tangles (Raboy et al. 2008). GHLTs and WBTMs typically use different strata in primary forests, with GHLTs commonly found in the upper canopy and WBTMs in the lower canopy (Rylands 1989).

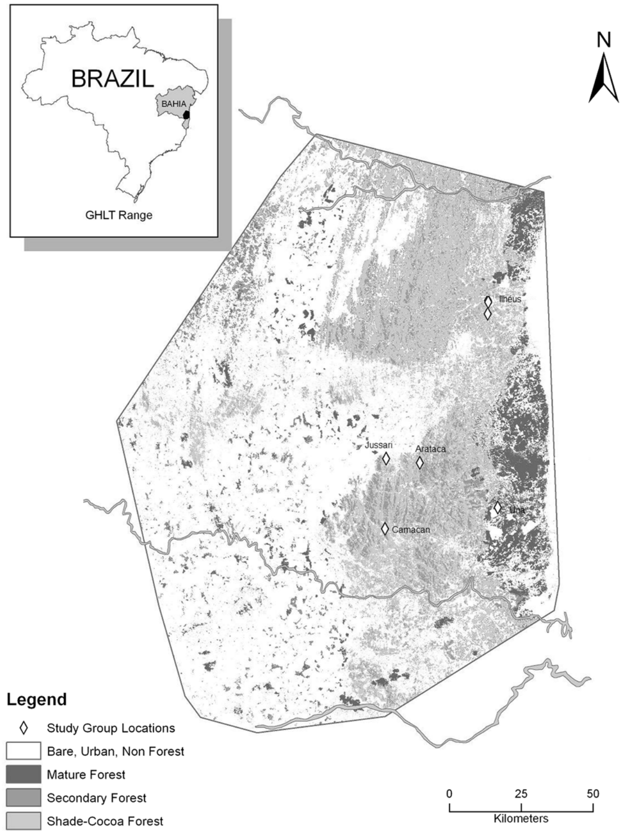

Fig. 3 Geographic distribution of GHLT and the location of the study sites in southern Bahia state, Brazil. Map based on a reclassification of land cover at 30-m resolution, published in Landau et al. (2003), from 1996–1997 Landsat data

Study area

This study is part of a larger project on GHLT population monitoring, carried out in the cacao-growing region of southern Bahia state, Brazil, in the municipalities of Ilhéus, Jussari, Camacan, Arataca and Una (Fig. 3). Our study site is located in the area of two privately owned cocoa farms—São José (15°21′31″S and 39°33′19″W) and Sempre Viva (15°23′11″S and 39°31′17″W) in the municipality of Camacan. The vegetation of the São José farm is a mix of primary forest, secondary forest (predominant habitat) and *cabruca*, while the Sempre Viva farm is dominated by *cabruca*. We defined primary forest as forest with little or no sign of past human disturbance, a closed canopy, trees with an average height of 20 m and a large diameter (>30 cm), bromeliads in a wide range of sizes and an extensive layer of vines. Secondary forest was defined as forest with visible signs of previous human disturbance, either clear-cutting or selective logging. Finally, *cabruca* is an agroforest system where the understory has been replaced by cocoa trees and a few tall, native trees (around 10 % of trees prior to thinning) are kept to provide shade to cocoa trees (Johns 1999).

Data collection

Study animals were monitored using radiotelemetry. We captured GHLT groups in the study areas using Tomahawk live traps (trap measures, 48.3 × 15.2 × 15.2 cm) baited with banana and placed on platforms 1.5 m above the

Table 1 Social behaviors observed between a male golden-headed lion tamarin (*GHLT*), *Leontopithecus chrysomelas*, and Wied's marmosets (*WBTMs*), *Callithrix kuhlii*, in a mixed group studied in the municipality of Camacan, state of Bahia, Brazil

Behavior	*n*	Description of the behavior
Eating together (jackfruit)	9	Both species eat the same fruit or are in the same fruit tree
Grooming	2	GHLT initiates grooming WBTM female with two infants
Sharing food	2	GHLT gives jackfruit to a young WBTM
Sleeping together[a]	8	Both species sleep in the same tree, vine tangles or bromeliad
Playing	2	GHLT plays with WBTM
Agonistic behavior	2	Two individual WBTMs bite GHLT while they eat jackfruit. Two individual WBTMs bite GHLT when it tries to take a baby from the female

n Number of sightings for each behavior

[a] We observed the GHLT and the WBTMs in the same tree and twice saw them sleeping together, once in a vine tangle and once in a bromeliad. At other times we observed them entering the same tree and leaving the tree together in the morning

ground (Dietz et al. 1996). We affixed a radio collar to one individual of each group to facilitate location and monitoring. In May 2008, we captured a duo of adult GHLTs. We assume that these individuals were dispersing from their natal group, a behavior that is common in lion tamarins (Baker et al. 1993). We followed these GHLTs during complete days (from when they left the 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). Information about behavior, habitat use, location of feeding trees and sleeping sites was collected ad libitum (Altmann 1974). This observational method was chosen because some behaviors are rare and probably would not be detected with other methods such as scan sampling. At 20-min intervals we recorded subjects' geographic location and whether or not GHLTs were in association with WBTMs. We defined an association as when GHLTs and WBTMs were <50 m apart, following Raboy (2002) and Oliveira and Dietz (2011).

We collected data on the dispersing duo for 3 consecutive months in a mosaic forest area (a mix of secondary forest in different stages of regeneration and *cabruca* managed in various ways). On 19 August 2008, one GHLT disappeared and the other, with the radio collar, moved away from the area. On 28 August 2008, we found the radio-collared individual associating with a group of nine WBTMs in a *cabruca* area ca. 4 km from where it was captured. We continued monitoring this individual until December 2008, when the radio failed and we lost contact.

We used the geographic locations to estimate the GHLT's home range and to calculate its daily path length. We compared data collected on the GHLT duo and the mixed-species group to investigate possible changes in the GHLT's use of space and feeding behavior. Additionally, we collected data on social interactions in the mixed group to understand the GHLT's position in the social hierarchy. When possible, we also collected information on food items consumed by the GHLT.

Statistical analysis

All comparisons related to rates of association, home range size and daily path length before and after the dispersal event were done using χ^2-tests (α-level of 0.05) using the software R 3.3.1 (R Core Team 2016). We calculated rates of interspecific association as the proportion of 20-min scans where the GHLT associated with WBTMs. We estimated home range sizes through the minimum convex polygon method (Mohr 1947) using the extension Hawth's tools (Beyer 2004) in the software ArcGIS 9.3.1 (ESRI 2009). To calculate daily path lengths, we summed the straight-line distances traveled between 20-min scans on complete days of monitoring using the software ArcGIS 9.3.1. We also compared the daily and the average travel speed (meters per minute) before and after the GHLTs dispersal using a Mann–Whitney–Wilcoxon test in R 3.3.1.

Results

Rates of association

We monitored the GHLT duo for seven complete and partial days totaling 62 h of observations. The two GHLTs spent ca. 16 h in association with WBTMs (around 26 % of the observation time). After the radio-collared GHLT joined the WBTM group, we monitored the mixed group for 16 complete and partial days, totaling 122 h of observations. The GHLT associated with the WBTMs for about 114 h (or 94 % of the observation time), which indicates a stable association and differs significantly from the association rate observed for the duo (χ^2-test, $\chi^2_1 = 87.47$, $P < 0.0001$).

Social behaviors

We noted interspecific social behaviors including grooming, sharing food, playing, using the same sleeping site, and agonistic interactions. The non-agonistic interactions reported here were always directed from GHLT to WBTMs, whereas all agonistic interactions were from WBTMs to GHLT (Table 1).

Home range size, daily path length, and speed

We observed a decrease in home range size after GHLT joined the WBTM group (Fig. 4). The estimated home range size for the GHLT duo was 144 ha, decreasing to 14 ha in the mixed group (χ^2-test, $\chi^2_1 = 34.68$; $P < 0.0001$). Daily path length was also significantly reduced in the mixed group: 2649 ± SD 533.3 m for the GHLT duo and 865 ± SD 288.9 m for the mixed group (χ^2-test, $\chi^2_1 = 905$; $P < 0.0001$). Similarly, there was a decrease in GHLT travel speed in the mixed group: 4.43 ± SD 1.27 m/min in the GHLT duo vs. 1.50 ± SD 1.05 m/min in the mixed group (Wilcoxon rank sum test, $W = 4$; $P = 0.0003$).

Diet

We had very few observations on feeding behavior of GHLTs before and after dispersal (Table 2). We recorded six species being consumed nine times by GHLT before dispersal and only two species being consumed 20 times after it joined the WBTM group (Table 2).

Discussion

We report a stable association between an adult GHLT and a breeding group of WBTMs. Although interactions between these species have been reported elsewhere (Rylands 1989; Raboy 2002; Oliveira and Dietz 2011), to our knowledge this is the first report of a GHLT behaving as if it were a member of a WBTM group. Even though GHLTs are more than twice the weight of WBTMs (Rylands 1989; Oliveira et al. 2011) and WBTMs often follow GHLTs in mixed-species groups (Raboy 2002), this dispersing GHLT assumed a subordinate position in the WBTM group. It is plausible that the individual assumed a subordinate role to ensure its permanence in the group (Garber 1997) and thereby gain benefits such as access to food, sleeping sites and protection against predators.

Social behaviors

Unidirectional agonistic interactions between males are indicative of a dominance relationship (Abbott 1984; Baker et al. 1993). During associations, aggressive behaviors are typically displayed by GHLTs toward WBTMs (personal observations), but in this specific mixed group all agonistic interactions were directed from WBTMs to the GHLT. Also, only non-agonistic behaviors were directed from the GHLT to WBTMs. Although behavioral interactions such as eating together, scent marking in the same tree and playing together are not indicative of social rank, observations of the GHLT grooming WBTMs (and never being groomed in return) may indicate subordinate status

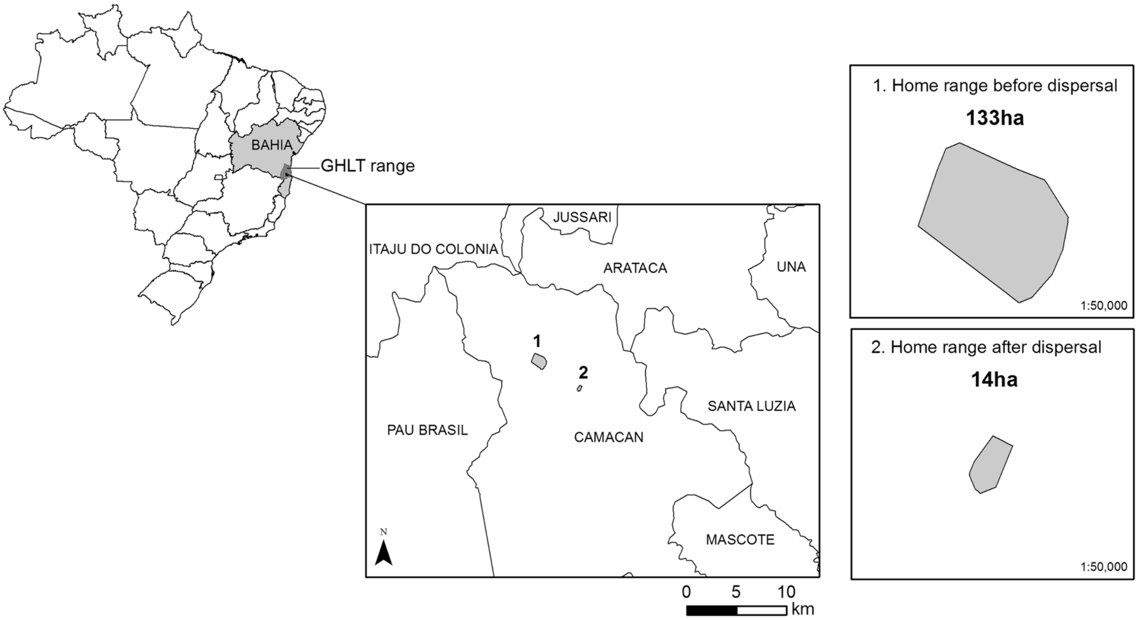

Fig. 4 Home range estimated by minimum convex polygon of the GHLT duo (before dispersal), and after one of the GHLT individuals joined the Wied's marmoset group

Table 2 Number of individuals and frequency of tree species in the diet of the GHLT duo before and after one of them joined a group of WBTM

Species	*n* (individuals)	Frequency of use
Before dispersal		
Miconia mirabilis (Aubl.) L. Wms.	1	1
Lacmellea aculeate (Ducke) Monach	2	2
Theobroma cacao L.	1	1
Artocarpus heterophyllus Lam.	1	1
Myrcia cauliflora (C.Mart.) O.Berg.	1	1
Musa paradisiaca L.	2	3
After dispersal		
Artocarpus heterophyllus Lam.	10	17
Ficus sp.	2	3

For abbreviations, see Table 1

(Seyfarth 1976, 1977; Schino 2001). We also observed the GHLT offering food to juvenile WBTMs and trying to take an infant from the mother, which are behaviors indicative of cooperation between callithrichids (Garber 1997). The fact that the GHLT always followed the WBTMs and never led the group, as observed in Raboy (2002), also suggests that this individual was trying to join the group as a subordinate rather than a dominant leader.

Home range, daily travel distances and speed

Typically, WBTMs have a smaller home range than GHLTs (Rylands 1989; Raboy et al. 2008; Oliveira et al. 2011) and travel less per day than GHLTs (Raboy et al. 2008). Thus the observed decreases in home range size and path length may reflect an adaptation by the GHLT to the WBTM group's behavior. Forest types used by the GHLT differed before and after it joined the WBTM group, and this may have affected the use of space. *Cabruca* is relatively rich in food resources, especially jackfruit, *Artocarpus heterophyllus*, which reduces the need to forage for food. In fact, the smallest home range reported for GHLTs (22 ha) was in a *cabruca* in the municipality of Ilhéus (Oliveira et al. 2011). However, considering that the GHLT duo also frequently used *cabruca* and the similarity between the home range size of the mixed group and those reported for WBTM's [10 ha (Rylands 1989); 34–39 ha (Raboy et al. 2008)], it is unlikely that the reduced range size observed here is explainable only by differences in habitat type.

The travel speed decrease in the mixed group was expected, as the GHLT was dispersing before entering the mixed group. However, Raboy (2002) observed a lower travel speed in WBTMs compared to GHLTs (2.30 ± 0.92 and 2.78 ± 1.32 m/min, respectively) so we conclude that both dispersing and adaptation to the WBTMs' habits possibly determined the decrease in GHLT's travel speed.

Diet

Despite having few observations on GHLT's feeding, we observed a decrease in diversity of fruit consumed by GHLT after joining the WBTM group. This decrease may be explained by the fact that the GHLT duo's home range included primary and secondary forest in addition to *cabruca*. Furthermore, *cabruca*, the only habitat used by the GHLT after dispersal, is typically dominated by species of the Moraceae family, including the genera *Ficus* and *Artocarpus* (Sambuichi and Haridasan 2007). These were the only food items seen to be consumed by GHLTs after dispersal.

In a long-term study of golden lion tamarins, *Leontopithecus rosalia*, Baker et al. (1993) reported that reproductive success of subordinate adult males that remained in the natal group as non-reproducers was greater than that of subordinate males that dispersed and "prospected" for breeding opportunities elsewhere. Dispersing lion tamarins are chased aggressively by adults on established territories and have a low probability of surviving for more than a year. In this study, the dispersing GHLT apparently became a subordinate member of a WBTM group, thereby having access to food and shelter and possibly a reduced likelihood of predation. Moreover, the WBTM territory was not occupied by other GHLTs; conceivably the dispersing GHLT's short-term loss in reproductive success was outweighed by the benefits of waiting for a dispersing mate in a relatively safe and resource-rich environment.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All animal captures were approved by the Brazilian Environmental Agency (ICMBio/SISBIO) under permit nos. 18444-1 and 12334-1. In addition, this research adhered to the American Society of Primatologists' ethical principles for the treatment of primates.

References

Abbott DH (1984) Behavioral and physiological suppression of fertility in subordinate marmoset monkeys. Am J Primatol 6:169–186

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–267

Baker AJ, Dietz JM, Kleiman DG (1993) Behavioral evidence for monopolization of paternity in multi-male groups of golden lion tamarins. Anim Behav 46:1091–1103

Beyer HL (2004) Hawth's analysis tools for ArcGIS. http://www.spatialecology.com/htools. Accessed 4 Sept 2016

Buchanan-Smith HM (1999) Tamarin polyspecific associations: forest utilization and stability of mixed-species groups. Primates 40:233–247

Chapman CA, Chapman LJ (2000) Interdemic variation in mixed-species association patterns: common diurnal primates of Kibale National Park, Uganda. Behav Ecol Sociobiol 47:129–139

Chapman CA, Chapman LJ, Wrangham RW (1995) Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behav Ecol Sociobiol 36:59–70

Curio E (1976) The ethology of predation. Springer, Berlin

Dietz JM, de Sousa SN, da Silva JRO (1994) Population structure and territory size in golden-headed lion tamarins, *Leontopithecus chrysomelas*. Neotrop Primates 2(Suppl):21–23

Dietz JM, de Sousa SN, Billerbeck R (1996) Population dynamics of golden-headed lion tamarins in Una Reserve, Brazil. Dodo J Wildl Preserv Trusts 32:115–122

ESRI (2009) ArcGIS desktop: release 9.3.1. Environmental Systems Research Institute, Redlands

Ferrari FS (2009) Predation risk and antipredator strategies. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB (eds) South American primates—comparative perspectives in the study of behavior, ecology and conservation. Springer, Chicago, pp 251–277

Fleury M, Gautier-Hion A (1997) Better to live with allogenerics than to live alone? The case of single male *Cercopithecus pogonias* in troops of *Colobus satanas*. Int J Primatol 18:967–974

Garber PA (1997) One for all and breeding for one: cooperation and competition as a tamarin reproductive strategy. Evol Anthropol 5:187–198

Hamilton WD (1971) Geometry for the selfish herd. J Theor Biol 31:295–311

Hardie SM, Buchanan-Smith HM (1997) Vigilance in single- and mixed-species groups of tamarins (*Saguinus labiatus* and *Saguinus fuscicollis*). Int J Primatol 18:217–234

Heymann EW (1990) Interspecific relations in a mixed-species troop of moustached tamarins, *Saguinus mystax*, and saddleback tamarins, *Saguinus fuscicollis* (Primates: Callitrichidae), at the Rio Blanco, Peruvian Amazonia. Am J Primatol 21:115–127

Heymann EW, Buchanan-Smith HM (2000) The behavioural ecology of mixed-species troops of callitrichine primates. Biol Rev 75:169–190

IUCN (2016) The IUCN red list of threatened species. Version 2016.1. http://www.iucnredlist.org. Accessed 20 Aug 2016

Janson CH, Goldsmith ML (1995) Predicting group size in primates: foraging costs and predation risks. Behav Ecol 6:326–336

Johns ND (1999) Conservation in Brazil's chocolate forest: the unlikely persistence of the traditional cocoa agroecosystem. Environ Manage 23:31–47

Kierulff MCM, Rylands AB, Mendes SL, de Oliveira MM (2008) *Leontopithecus chrysomelas*. The IUCN red list of threatened species 2008: http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T40643A10347712.en. Accessed 28 Aug 2015

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 (eds) Corredor de Biodiversidade da Mata Atlãntica do Sul da Bahia. IESB/DI/CABS/UFMF/UNICAMP, Publicação em CD-ROM, Ilhéus, Brazil

Lucas JR, Waser MP, Creel SR (1994) Death and disappearance: estimating mortality risks associated with philopatry and dispersal. Behav Ecol 5:135–141

McNamara JM, Houston AI (1987) Starvation and predation as factors limiting population size. Ecology 68:1515–1519

MMA (2014) Lista nacional oficial de espécies da fauna ameaçadas de extinção. Portaria no. 444, 17 dezembro 2014

Mohr C (1947) Table of equivalent populations of North American small mammals. Am Midl Nat 37:223–449

Oliveira LC, Dietz MJ (2011) Predation risk and the interspecific association of two Brazilian Atlantic Forest primates in *cabruca* agroforest. Am J Primatol 73:852–860

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. Anim Conserv 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* agroforest. Environ Manage 48(2):248–262

Olupot W, Waser PM (2001) Activity patterns, habitat use and mortality risks of mangabey males living outside social groups. Anim Behav 61:1227–1235

Peres CA (1992) Prey-capture benefits in a mixed-species group of Amazonian tamarins, *Saguinus fuscicollis* and *S. mystax*. Behav Ecol Sociobiol 31:339–347

Peres CA (1993) Anti-predator benefits in a mixed-species group of Amazonian tamarins. Folia Primatol 61:61–76

Peres CA (1996) Food patch structure and plant resource partitioning in inter-specific associations of Amazonian tamarins. Int J Primatol 17:695–723

Raboy BE (2002) The ecology and behavior of wild golden-headed lion tamarins (*Leontopithecus chrysomelas*). Department of Biology, University of Maryland, College Park, MD

Raboy BE, Dietz JM (2004) Diet, foraging, and the use of space in wild golden-headed lion tamarins. Am J Primatol 63:1–15

Raboy BE, Canale G, Dietz JM (2008) Ecology of *Callithrix kuhlii* and a review of eastern Brazilian marmosets. Int J Primatol 29:449–467

R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/. Accessed 4 Sept 2016

Rylands AB (1989) Sympatric Brazilian callitrichids: the black tufted-ear marmoset, *Callithrix kuhli*, and the golden-headed lion tamarin, *Leontopithecus chrysomelas*. J Hum Evol 18:679–695

Rylands AB, Kierullf MCM (2008) *Callithrix kuhlii*. IUCN red list of threatened species 2008: http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T3575A9955873.en. Accessed 28 Aug 2015

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. Biodivers Conserv 16:3681–3701

Schino G (2001) Grooming, competition and social rank among female primates: a meta-analysis. Anim Behav 62:265–271

Seyfarth RM (1976) Social relationships among adult female baboons. Anim Behav 24:917–938

Seyfarth RM (1977) A model of social grooming among adult female monkeys. J Theor Biol 65:671–698

Stensland E, Angerbjorn A, Berggren P (2003) Mixed species groups in mammals. Mamm Rev 33:205–223

Struhsaker TT (1988) Male tenure, multi-male influxes, and reproductive success in redtail monkeys (*Cercopithecus ascanius*). In: Gautier-Hion A, Bourliere F, Gautier JP, Kingdon J (eds) A primate radiation; evolutionary biology of the African guenons. Cambridge University Press, London, pp 340–363

Terborgh J (1983) Five new world primates. Princeton University Press, Princeton

Terborgh J (1986) The social systems of new world primates: an adaptationist view. In: Else JG, Lee PC (eds) Primate ecology and conservation. Cambridge University Press, Cambridge, pp 199–211

Terborgh J (1990) Mixed flocks and polyspecific associations: costs and benefits of mixed groups to birds and monkeys. Am J Primatol 21:87–100

Terborgh J, Janson CH (1986) The socioecology of primate groups. Annu Rev Ecol Syst 17:111–136

Treves A, Chapman CA (1996) Conspecific threat, predation avoidance, and resource defense: implications for grouping in langurs. Behav Ecol Sociobiol 39:43–53

van Schaik CP (1983) Why are diurnal primates living in groups? Behaviour 87(1/2):120–144

van Schaik CP, van Hooff JA (1983) On the ultimate causes of primate social systems. Behaviour 85:91–117

van Schaik CP, van Noordwijk MA, Warsono B, Sutriono E (1983) Party size and early detection of predators in Sumatran forest primates. Primates 24:211–221

Wachter B, Schabel M, Noe R (1997) Diet overlap and polyspecific associations of red colobus and Diana monkeys in the Tai National Park, Ivory Coast. Ethology 103:514–526

Whitesides GH (1989) Interspecific associations of Diana monkeys, *Cercopithecus diana*, in Sierra Leone, West Africa: biological significance or chance? Anim Behav 37:760–776

Wrangham RW, Gittleman JL, Chapman CA (1993) Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. Behav Ecol Sociobiol 32:199–210