

Play Behavior of the Golden-Headed Lion Tamarin in Brazilian Cocoa Agroforests

Juliana Monteiro de Almeida Rocha^{a, b} Paula Pedreira dos Reis^{b, c}
Leonardo de Carvalho Oliveira^{a–d}

^aPrograma de Pós-Graduação em Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, ^bInstituto de Estudos Socioambientais do Sul da Bahia, and ^cPrograma de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Ilhéus, and ^dBicho do Mato Instituto de Pesquisa, Belo Horizonte, Brasil

Key Words

Antipredator behavior · *Cabruca* · Golden-headed lion tamarin · *Leontopithecus chrysomelas* · Play · Predation risk

Abstract

During play, primates may become more vulnerable to predation. Our goal was to examine the potential role of predation risk on the play behavior of 3 groups of golden-headed lion tamarin, *Leontopithecus chrysomelas*, in shaded cocoa agroforest (*cabruca*) of Southern Bahia, Brazil. We identified the preferred (and safer) locations on vertical strata during playtime and investigated if frequency and duration of play differed according to group size. All groups preferred to play on the lower levels of vertical strata, which may be perceived as either a safer environment or as a more suitable location for play due to the vegetation structure. The smallest group played less than the others, while the largest group played more and for longer periods. Our data suggest that predation risk can influence where play takes place as well as its frequency and length.

© 2014 S. Karger AG, Basel

Introduction

Play behavior is widely investigated in primate species [Fagen, 1981; Enomoto, 1990; Markus and Croft, 1995; Oliveira et al., 2003; Lewis, 2005; Paukner and Suomi, 2008; Worch, 2012]. Despite some developmental benefits associated with play, both in terms of physiology and behavior [Fagen, 1981; Bekoff and Byers, 1998; Palagi et al., 2004], there are also costs, such as energy expenditure [Martin, 1984], and the risks of both injury [Bekoff and Byers, 1992] and predation [Harcourt, 1991].

KARGER

E-Mail karger@karger.com
www.karger.com/fpr

© 2014 S. Karger AG, Basel
0015–5713/14/0853–0192\$39.50/0

Juliana Monteiro de Almeida Rocha, Universidade Estadual de Santa Cruz, Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Rodovia Jorge Amado Km 16, Pavilhão Maz de Menezes, 1º andar, sala 1DA Salobrinho, Ilhéus, BA 45662-900 (Brazil)
E-Mail almeidarocha.jm@gmail.com

The investment in energy and time during play may differ among habitat types and due to resource availability [Baldwin and Baldwin, 1976; Barrett et al., 1992]. When resources are abundant, individuals need less effort to acquire food and may invest more time and energy in social activities [Baldwin and Baldwin, 1976; Barrett et al., 1992; DeFler, 1995; Sommer and Mendoza-Granados, 1995; Li and Rogers, 2004; Stone, 2008]. For example, the golden-headed lion tamarin (GHLT), *Leontopithecus chrysomelas*, spends more time in social activities in shaded cocoa agroforest than in other habitat types [Reis, 2012]. This is expected as food resources (mostly jackfruit and insects) are abundant both spatially and temporally in this habitat [Oliveira et al., 2011]. Stone [2008] observed a similar pattern for squirrel monkeys, *Saimiri sciureus*, which played less during the dry season, when food is scarce.

Social behaviors represent between 7 and 18% of the activity budgets of GHLTs in primary forest [Raboy and Dietz, 2004], semi-deciduous forest [Guidorizzi, 2008] and shaded cocoa agroforest (locally known as *cabruca*) [Reis, 2012]. Among these behaviors, GHLTs devote approximately 4.7% of their time to play in *cabruca* [Reis, 2012]. *Cabruca* differs from native forest because the understory is replaced by cocoa trees and only some native trees are maintained for shading [Johns, 1999]. Oliveira and Dietz [2011] found an increased predation risk for GHLTs in *cabruca* compared to forest, which is probably due to a discontinuous canopy and a simplified vertical stratum that makes individuals more exposed to predators (mainly raptors). Although there are some potential terrestrial predators in *cabruca*, like tayras (*Eira barbara*) and domestic dogs (*Canis familiaris*), the encounter rate with this type of predator is low compared to raptors [Oliveira and Dietz, 2011].

During play, individuals become vulnerable to predators, as those involved in the activity are not alert to possible threats [Fagen, 1981; Biben et al., 1989; Harcourt, 1991; Bekoff and Byers, 1992]. A good strategy to reduce the risk of predation can be choosing safer places to play, as observed for golden lion tamarins, *Leontopithecus rosalia*, in lowland tropical rain forest [Oliveira et al., 2003]. Following such pioneering studies, it is interesting to understand how play behavior of GHLTs is affected by the high predation risk experienced in *cabruca*. To investigate this issue, we studied the play behavior of GHLTs living exclusively in *cabruca*. Following the definition of Martin and Caro [1985], we considered play as all locomotor activity that appears to have no function or immediate benefit, often involving exaggerated and repeated movements.

Our main goal was to examine the potential role of predation risk on play, as this is a risky activity and predators represent an important threat in *cabruca*. We tested the hypothesis that predation risk can influence the frequency of play and also the decision of where and for how long to play, especially under a high-risk situation as observed in *cabruca*. We expected that GHLTs would always play in the safest strata, and thus we assumed that the most frequent strata used during play bouts would be safer for GHLTs to perform this activity. Therefore, we predicted that GHLTs would choose to play at the lower levels of vertical strata in *cabruca*, as they are less exposed to aerial predators and the risk of terrestrial predators is low [Oliveira and Dietz, 2011]. Considering that larger groups may provide more protection against predators [Isbell, 1994; Chapman and Chapman, 2000; Miller, 2002b] providing a safer environment for play behavior, we also predicted that group size would affect the frequency and length of play bouts. Specifically, we expected that larger groups would play more and for longer periods than smaller groups.

Table 1. Group composition during the study period

Group	Almada	Bomfim	Santa Rita
Adults	3.5 (3; 6)	3 (3; 4)	7 (4; 9)
Juveniles	1 (0; 3)	0 (0; 1)	2 (0; 2)
Infants	0.5 (0; 3)	1 (0; 1)	2 (0; 3)
Total	6 (6; 7)	4 (4; 5)	11 (7; 12)

Composition was estimated by summing individuals captured plus those individuals observed during the monitoring. The table shows the median, minimum and maximum values (the last two values in parentheses).

Materials and Methods

Study Site

We carried out this study in the cocoa-growing region in the southeast of the Brazilian State of Bahia, in the municipality of Ilhéus (14°39' S, 39°11' W). We collected data from 3 groups, hereafter called 'Almada', 'Bomfim' and 'Santa Rita', living exclusively in areas of *cabruca* located on 3 private farms.

Study Species

L. chrysomelas is an endangered small primate [IUCN, 2013] endemic to the Brazilian Atlantic Forest. *Cabruca* is the dominant habitat within the species' current geographic distribution, especially in the eastern part of its range [Raboy et al., 2010]. The mean adult body weight is 620 g, and group size varies between 2 and 15 individuals [Oliveira et al., 2011]. The diet is composed mainly of fruits, insects and small vertebrates [Rylands, 1989]. The mean home range of groups is 83 ha (range from 22 to 200 ha), and densities range between 0.04 and 0.21 individuals/ha [Oliveira et al., 2011].

Data Collection

We monitored the groups from January 2010 to March 2011. Group size and composition differed during the study period but Bomfim was always the smallest, Almada was always intermediate and Santa Rita was always the largest group (table 1). We followed each group twice a month either for complete days (from when the group left its sleeping site in the morning until it entered a sleeping site in the evening) or partial days (when we monitored the group only in the morning or afternoon periods). To facilitate location and monitoring, 1 or 2 individuals of each group wore a radio transmitter collar (model RI-2D, Holohil Ltd.). All animal capture and handling procedures used to place the radio collars were approved by the Brazilian Environmental Agency (ICMBio/SISBIO) under permit No. 18444-1 and 12334-1. This research also adhered to the American Society of Primatologists' ethical principles for the treatment of primates.

We used the ad libitum method [Altmann, 1974] for data collection. If we observed the group playing at any time, we recorded the time when play started and the height where the play occurred. To record the height, we divided the vertical strata into 4 levels of equal size, the first level being that closest to the ground and the fourth level the highest. For example, if the canopy has a height of 20 m, then we have 4 levels of 5 m each. We did this to compare areas with different canopy heights, as we assume the first level is the most protected and the fourth level is the most exposed to aerial predators. In the studied *cabruca* areas, the first level is typically composed of cocoa trees.

We allocated the recorded height of each playing individual to 1 of the 4 levels. In order to obtain a unique stratum level for each play bout of each group, we calculated the median of stratum levels where the individuals from each group were playing. If the play lasted more than 20

Table 2. Sample effort (with number and percentage of days where play behavior was observed), duration of play and number of times when play behavior was recorded in each stratum level for 3 groups of GHLTs (Almada, Bomfim and Santa Rita) in *cabruca* agroforest

Group	Sample effort		Duration, min			Stratum level			
	days with play	total of days	min.	max.	av.	1	2	3	4
Santa Rita	24 (69)	35	5	197	47	14	9	3	2
Almada	20 (63)	32	1	70	20	13	10	4	3
Bomfim	11 (32)	34	3	84	30	5	4	2	1

Days with play give the percentage of the total sample effort for each group in parentheses.

min without interruption, we collected the individuals' height again and calculated a new median value for the group. When there was a change in the level used by the group (median), then the group had changed location during that play bout, so this moment was considered as the beginning of a new play event for the analysis of the use of vertical strata. We also recorded total play duration, considering that the activity finished when all individuals that were playing began other activities. Short breaks (up to 1-min pauses) or changes in the composition of playing individuals, i.e. some stopped but others started playing, were not considered.

Data Analysis

We used χ^2 tests to compare play frequency (the ratio between the number of days where play bouts were observed and the total days of monitoring per group) and Kruskal-Wallis tests to compare length of play (duration of each play bout in minutes) between groups. χ^2 goodness-of-fit tests were performed to test for differences in the use of vertical stratum levels during play (by comparing the observed utilization frequency of each level with a uniform expected frequency of 0.25 for each level), followed by the Bonferroni Z statistic [Neu et al., 1974] to identify which level was more or less used by each group. The analysis was performed in R 3.0.0 [R Core Team, 2013].

Results

The types of play observed consisted of chasing, leaps and wrestling between 2 or more individuals. When GHLTs were playing on the ground, it was common to see a game that consisted of all individuals remaining in trees close to the ground, and occasionally running along the ground to another tree. In this game, when there was an 'encounter' during running, individuals clung together and rolled similar to fight behavior. In some situations, individuals used alarm-like vocalizations during the play.

We recorded 118 play bouts in 54% of monitoring days ($N_{\text{total}} = 101$ days), with a mean of 2 play bouts per day ($SD = 1.23$; range = 1–6). Almada and Santa Rita, the larger groups, had a mean of 57% of individuals participating in each play event ($SD_{\text{Almada}} = 27.7$; range_{Almada} = 28–100%; $SD_{\text{Santa Rita}} = 22.6$; range_{Santa Rita} = 18–100%), while Bomfim had a mean of 73% ($SD_{\text{Bomfim}} = 30$; range_{Bomfim} = 25–100%). There was a significant difference in play frequency between groups ($\chi^2 = 10.34$, d.f. = 2, p value = 0.005), with Bomfim playing on fewer days (table 2). The length of play ranged

Table 3. Frequency of use of vertical stratum levels by each group during play

Stratum level	Bomfim		Almada		Santa Rita	
	freq _{obs}	div.	freq _{obs}	div.	freq _{obs}	div.
1	0.42	no	0.43	+	0.50	+
2	0.33	no	0.33	+	0.32	+
3	0.17	no	0.13	-	0.11	-
4	0.08	no	0.10	-	0.07	-

Results of χ^2 goodness-of-fit tests, considering an equal expected frequency of use for each level (= 0.25); freq_{obs} = observed frequency of vertical stratum use; div. = statistically significant divergence according to confidence intervals generated by Bonferroni Z statistics; + = higher; - = lower; no = none. $\chi^2_{\text{Bomfim}} = 3.33$, d.f. = 3, p = 0.34; $\chi^2_{\text{Almada}} = 9.2$, d.f. = 3, p < 0.026; $\chi^2_{\text{Santa Rita}} = 13.42$, d.f. = 3, p = 0.003.

between 1 and 197 min (overall mean = 32 min) and differed significantly between groups (Kruskal-Wallis $\chi^2 = 12.99$, d.f. = 2, p value = 0.001). On average, Santa Rita played for a longer period compared with the other groups (table 2).

We recorded the vertical strata position during 65 play bouts. The groups moved between vertical levels during only 5 play bouts. For these cases, we considered the moment of change as the beginning of a new event, increasing the sample size to 70 play bouts for these analyses. All groups showed the same pattern, playing more frequently in the first and second levels of vertical strata, but this difference was not statistically significant for the Bomfim group (table 3).

Discussion

Although play behavior is widely investigated in primates, research efforts are concentrated on studies of great apes [Lewis, 2005] and studies in captivity [Worch, 2012]. Here, we conducted a study of play in the wild, focusing on a threatened Neotropical primate in a human-altered habitat.

The play patterns observed for GHLTs in *cabruca* supported our hypothesis, suggesting that predation risk can influence this behavior. All studied groups showed a similar pattern, playing more frequently on the ground and in cocoa trees (approx. 3–4 m tall), which supports our prediction that GHLTs may be perceiving the lower levels of *cabruca* as safer, as these levels are more protected from aerial predators. Oliveira et al. [2003] observed a similar pattern for groups of golden lion tamarins, which avoided play both on the ground and close to the canopy, where they are more exposed to predators. Despite the presence of some terrestrial predators in *cabruca*, the benefits of play may outweigh the risks of play on the ground. Although this pattern was not statistically significant for the Bomfim group, it was probably an effect of the fewer days with play bouts, as the pattern was the same as observed in the other groups.

Another explanation for GHLTs choosing to play on the lower levels should be considered. The discontinuity of the *cabruca* canopy can make it difficult to play at the highest levels and increases the risk of falling and injury [Bekoff and Byers, 1992]. Oliveira et al. [2003] investigated if golden lion tamarins chose to play on the ground due to a reduced risk of injury, but they did not find such a pattern. As the groups avoided play on the ground, and considering the high predation risk in their study area (especially by tayras), the authors concluded that the places chosen by their study groups for play were not influenced by the risk of injury but by the risk of predation. In our case, based on the findings of Oliveira and Dietz [2011], we assume that predation risk by terrestrial predators is low. We consider that the choice of places to play in *cabruca* may also be related to habitat structure, and groups may perceive cocoa trees as safer and more suitable locations to play, as they are low and offer dense cover. Unfortunately, we are not able to distinguish between these two possibilities with our data, but one possibility does not exclude the other.

As we predicted, the larger group played more frequently and for longer periods, while the smallest group played less. Small groups are more vulnerable to predation because there are fewer individuals to search for approaching predators [Pulliam, 1973; Miller, 2002a], so play can be very risky [Harcourt, 1991; Blumstein, 1998]. In fact, Bomfim is probably the group that suffers the greatest predation pressure, as it never had more than 1 immature offspring at the same time during the study period, while the other groups contained up to 3 immature individuals at the same time [unpubl. data]. Another possibility to explain why larger groups play more than small groups would be the larger number of individuals available for play, but our data suggest that this is not the case for GHLTs in *cabruca*. We observed that the smallest group usually had almost all individuals involved in play bouts, while the larger groups usually had half of the group involved. Thus, the absolute number of individuals in each group during play bouts was very similar, which would not justify an increase in playtime in the larger groups. Oliveira et al. [2003] found no significant positive correlation between the total duration of play and total group size (they found a significant correlation only when they considered the number of potential play partners in the group, based on the age of individuals). These findings support the idea that larger group size may not be directly related to an increase in the number of playing individuals. In this way, we believe that increased playtime for larger groups in our study can be related to predation risk.

We observed that all members of the Bomfim group participated in many of the play bouts, with no vigilant individuals during play. This situation rarely occurred in the other groups because normally there were some individuals (2–3) not involved in play that could detect a threat and warn the playing group members. Oliveira et al. [2003] observed that adults of golden lion tamarin were vigilant while the immature group members played, and also that adults were more vigilant during this activity in comparison with other activities. The authors relate the increasing vigilance of adults as a way of reducing the risks associated with play. We believe the lack of potentially vigilant individuals can make play activity more risky for Bomfim than for the other groups, and that the relatively low frequency of play observed for this group may be a strategy adopted to minimize risks. It may reflect a species' plasticity to adopt different strategies in different contexts: keeping individuals vigilant during play bouts (larger groups) versus playing less (smaller groups). However, this assertion needs to be tested with a larger sample size.

We investigated the role of predation risk on GHLT play behavior. Many factors may affect play, such as habitat characteristics (e.g. availability and quality of food resources [Stone, 2008], vegetation structure [Barrett et al., 1992], type of terrain [Berger, 1980]), social context (e.g. group composition, group size and dominance relationships [Enomoto, 1990]) and predation risk [Oliveira et al., 2003]. Understanding how play behavior affects the fitness of GHLTs in areas with different predation risks as well as evaluating the effect of group size and composition are interesting aspects of the species' ecology and behavior that remain to be addressed. Despite our small sample size (3 groups), our data suggest that predation risk influences not only the decision of where to play but also the frequency and the length of such a behavior.

Acknowledgments

We are grateful to the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, Instituto Chico Mendes de Biodiversidade and the Brazilian Research Council for permission to conduct this study. We thank the owners and employees of the farms Almada, Santa Rita, Bomfim and Riachuelo, for permission to work on their properties and for their support. We also thank our field assistant Jiomário dos Santos Souza for help in data collection, and the Instituto de Estudos Socioambientais do Sul da Bahia for administrative support. Finally, we thank the anonymous reviewers for their suggestions that improved the earlier versions of this paper. Financial support was provided by the Lion Tamarins of Brazil Fund, Rufford Small Grants Foundation, Zoological Garden of Antwerp, Coordenação de Aperfeiçoamento de Pessoal de Nível Superior and Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro.

Disclosure Statement

None of the authors has any conflict of interest to declare.

References

- Altmann J (1974). Observational study of behaviour: sampling methods. *Behaviour* 49: 227–267.
- Baldwin JD, Baldwin JI (1976). Effects of food ecology on social play: a laboratory simulation. *Zeitschrift für Tierpsychologie* 40: 1–14.
- Barrett L, Dunbar RIM, Dunbar P (1992). Environmental influences on play behaviour in immature gelada baboons. *Animal Behaviour* 44: 111–115.
- Bekoff M, Byers JA (1992). Time, energy and play. *Animal Behaviour* 44: 981–982.
- Bekoff M, Byers JA (1998). *Animal Play – Evolutionary, Comparative and Ecological Perspective*. Cambridge, Cambridge University Press.
- Berger J (1980). The ecology, structure and functions of social play in Bighorn sheep (*Ovis canadensis*). *Journal of Zoology* 192: 531–542.
- Biben M, Symmes D, Bernhards D (1989). Vigilance during play in squirrel monkeys. *American Journal of Primatology* 17: 41–49.
- Blumstein DT (1998). Quantifying predation risk for refuging animals: a case study with golden marmots. *Ethology* 104: 501–516.
- Chapman AP, Chapman LJ (2000). Constraints on group size in primates: the importance of travel costs. In *On the Move: How and why Animals Travel in Groups* (Boinski S, Garber P, eds.), pp 24–42. Chicago, University of Chicago Press.
- Defler TR (1995). The time budget of a group of wild woolly monkeys (*Lagothrix lagotricha*). *International Journal of Primatology* 16: 107–120.
- Enomoto T (1990). Social play and sexual behavior of the bonobo (*Pan paniscus*) with special reference to flexibility. *Primates* 31: 469–480.

- Fagen R (1981). *Animal Play Behavior*. New York, Oxford University Press.
- Guidorizzi CE (2008). *Ecologia e Comportamento do Mico-Leão-da-Cara-Dourada, Leontopithecus chrysomelas (Kuhl, 1820) (Primates, Callithrichidae), em um fragmento de floresta semidecidual em Ito-roró, Bahia, Brasil*. Dissertation, Universidade Estadual de Santa Cruz, Bahia.
- Harcourt R (1991). Survivorship costs of play in the South American fur seal. *Animal Behaviour* 42: 509–511.
- Isbell LA (1994). Predation on primates: ecological patterns and evolutionary consequences. *Evolutionary Anthropology* 3: 61–71.
- IUCN (2013). IUCN red list of threatened species. Version 2013.1. <http://www.iucnredlist.org/> (accessed July 23, 2013).
- Johns ND (1999). Conservation in Brazil's chocolate forest: the unlikely persistence of the traditional cocoa agroecosystem. *Environmental Management* 23: 31–47.
- Lewis KP (2005). Social play in the great apes. In *The Nature of Play – Great Apes and Humans* (Pellegrini AD, Smith PK, eds.), pp 27–53. New York, Guilford Press.
- Li Z, Rogers E (2004). Habitat quality and activity budgets of white-headed langurs in Fusui, China. *International Journal of Primatology* 25: 41–54.
- Markus N, Croft DB (1995). Play behaviour and its effects on social development of common chimpanzees (*Pan troglodytes*). *Primates* 36: 213–225.
- Martin P (1984). The time and energy costs of play behaviour in the cat. *Zeitschrift für Tierpsychologie* 64: 298–312.
- Martin P, Caro TM (1985). On the functions of play and its role in behavioral development. *Advances in the Study of Behavior* 15: 59–103.
- Miller LE (2002a). An introduction to predator sensitive foraging. In *Eat or Be Eaten – Predator Sensitive Foraging among Primates* (Miller LE, ed.), pp 1–17. Cambridge, Cambridge University Press.
- Miller LE (2002b). The role of group size in predator sensitive foraging decisions for wedge-capped capuchin monkeys (*Cebus olivaceus*). In *Eat or Be Eaten – Predator Sensitive Foraging among Primates* (Miller LE, ed.), pp 95–106. Cambridge, Cambridge University Press.
- Neu CW, Byers CR, Peek JM (1974). A technique for analysis of utilization-availability data. *The Journal of Wildlife Management* 38: 541–545.
- Oliveira CR, Ruiz-Miranda CR, Kleiman DG, Beck BB (2003). Play behavior in juvenile golden lion tamarins (Callitrichidae: Primates): organization in relation to costs. *Ethology* 109: 1–20.
- Oliveira LC, Dietz JM (2011). Predation risk and the interspecific association of two Brazilian Atlantic forest primates in cabruca agroforest. *American Journal of Primatology* 73: 852–860.
- 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. *Environmental Management* 48:248–262.
- Palagi E, Cordoni G, Borgognini Tarli SM (2004). Immediate and delayed benefits of play behaviour: new evidence from chimpanzees (*Pan troglodytes*). *Ethology* 110: 949–962.
- Paukner A, Suomi SJ (2008). Sex differences in play behavior in juvenile tufted capuchin monkeys (*Cebus apella*). *Primates* 49: 288–291.
- Pulliam HR (1973). On the advantages of flocking. *Journal of Theoretical Biology* 38: 419–422.
- Raboy BE, Dietz JM (2004). Diet, foraging, and use of space in wild golden-headed lion tamarins. *American Journal of Primatology* 63: 1–15.
- Raboy BE, Neves LG, Zeigler S, Saraiva N, Cardoso N, Santos G, Ballou J, Leimgruber P (2010). Strength of habitat and landscape metrics in predicting golden-headed lion tamarin presence or absence in forest patches. *Biotropica* 42: 388–397.
- R Core Team (2013). R: a language and environment for statistical computing. Vienna, R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Reis PP (2012). *Comportamento do mico-leão-da-cara-dourada, Leontopithecus chrysomelas, em áreas de cabruca do sudeste da Bahia*. Dissertation, Universidade Estadual de Santa Cruz, Bahia.
- Rylands AB (1989). Sympatric Brazilian callithrichids: the black tufted-ear marmoset, *Callithrix kuhli*, and the golden-headed lion tamarin, *Leontopithecus chrysomelas*. *Journal of Human Evolution* 18: 679–695.
- Sommer V, Mendoza-Granados D (1995). Play as an indicator of habitat quality: a field study of langur monkeys (*Presbytis entellus*). *Ethology* 99: 177–192.
- Stone AI (2008). Seasonal effects on play behavior in immature *Saimiri sciureus* in Eastern Amazonia. *International Journal of Primatology* 29: 195–205.
- Worch EA (2012). Play initiating behaviors and responses in red colobus monkeys. *American Journal of Play* 5: 104–119.