RESEARCH ARTICLE

Do Cavity-Nesting Primates Reduce Scent Marking Before Retirement to Avoid Attracting Predators to Sleeping Sites?

SAMUEL P. FRANKLIN[1]*, KIMRAN E. MILLER[2], ANDREW J. BAKER[3], AND JAMES M. DIETZ[1,2]
[1]Program in Behavior, Ecology, Evolution and Systematics, University of Maryland, College Park, Maryland
[2]Department of Biology, University of Maryland, College Park, Maryland
[3]Philadelphia Zoo, Philadelphia, Pennsylvania

The largest population of endangered golden lion tamarins (*Leontopithecus rosalia*, GLTs) decreased from approximately 330 to 220 individuals between 1995 and 2000 due to a dramatic increase in predation at sleeping sites. We used behavioral data from eight social groups in this population to test two hypotheses: First, if GLTs attempt to mitigate the risk of predation at sleeping sites, they should reduce their rates of scent marking just prior to retirement. Second, if the benefits of scent marking prior to entering the sleeping site merit an increase in the rate of marking, then tamarins should increase their rate of pre-retirement scent marking during the breeding season, when such behavior would have its greatest impact on reproductive fitness. We used a generalized linear model (GLM) repeated-measures analysis to compare rates of daytime scent marking with rates of marking just prior to retirement for males and females. In addition, we compared scent marking prior to retiring in the nonbreeding season to marking rates before retirement in the breeding season for males and both sexes considered concurrently. Contrary to our expectations, GLTs significantly increased their rates of scent marking during the 30 min prior to entering their sleeping site–an observation driven by an increase in male (but not female) rates of marking. Rates of marking before entering the sleeping site were greater in the nonbreeding season compared to the breeding season, when both sexes were considered concomitantly and when males were evaluated alone. We conclude that GLTs do not attempt to minimize predation risk by decreasing scent marking in the period before they enter their sleeping site, and that tamarins do not scent mark at this time of day in order to transmit information about reproductive status or to control reproduction of subordinates. We speculate that scent marking in the 30 min prior

*Correspondence to: S.P. Franklin, Department of Microbiology, Immunology, and Pathology, 1619 Campus Delivery, Colorado State University, Fort Collins, CO 80523.
E-mail: sam17franklin@hotmail.com

to entering sleeping sites may serve to reduce predation risk by enabling tamarin groups to return quickly to favored sleeping sites in the evening when crepuscular predators are active. Am. J. Primatol. 69:255–266, 2007. © 2006 Wiley-Liss, Inc.

INTRODUCTION

The endangered golden lion tamarin (*Leontopithecus rosalia*, GLT) is a small cavity-nesting primate that is endemic to the Atlantic coastal rainforest in Brazil. GLTs live in groups that consist of two to 14 individuals, with an average group size of approximately six. They are cooperative breeders, and there is usually one dominant reproductive pair, with subordinate individuals (frequently the offspring of the dominant animals) assisting with care of the neonates. The majority of fertile copulations occur during the dry winter months from May through July [Dietz et al., 1994]. Gestation is approximately 120 days and most parturition occurs in October and November [Dietz et al., 1994]. Tamarins subsist on fruits and also forage for insects [Dietz et al., 1997]. Owing to their small size, they fall prey to a number of predators, including raptors, constrictors, small felids, and possibly *Cebus* spp. monkeys and mustelids [Cheney & Wrangham, 1987; Moynihan, 1970; Sussman & Kinzey, 1984].

The largest population of wild GLTs is in Poço das Antas Biological Reserve, Rio de Janeiro state (22°30–33′S, 42°15–19′W). Due to a dramatic increase in predation, most of which took place at tamarin sleeping sites, this population decreased from approximately 350 to approximately 220 individuals between 1995 and 2000. On at least 16 occasions during this period, a number of GLTs, ranging from several individuals to entire social groups, disappeared from their home ranges. This type and intensity of predation pressure differs from that observed in previous years and the cause is unknown.

After many of these predation events, we found remains such as tamarin bones, blood, hair, and radio collars at or near the tamarin sleeping sites. Frequently these sleeping trees were hollow and the tamarins slept at or near ground level inside the tree. Predators gained access to the tamarins by entering an existing hole or digging a new one. This predation often occurred at sleeping sites used repeatedly by tamarin groups. Various predators are known to take small primates [Alonso & Langguth, 1989; Correa & Coutinho, 1997; Emmons, 1987; Ferrari & Lopes Ferrari, 1990; Heymann, 1987; Terborgh, 1983], but strong circumstantial evidence indicates that tayras (*Eira barbara*) are responsible for most or all of the recent predation on Poço das Antas lion tamarins (unpublished observations).

Although predation is thought to pose a serious threat to small primates, observations or evidence of predation events are relatively rare [Cheney & Wrangham, 1987], likely due to the secretive nature of predators and their shyness of human observers [Stanford, 1988]. Despite the paucity of data on predator pressure, predators have long been presumed to exert a strong influence on primate behavior over evolutionary and ecological time scales [Caine, 1993], leading to selection of prey behaviors that minimize predator success and maximize the inclusive fitness of individuals in prey species [Edmunds, 1974; Endler, 1986]. Increased vigilance and decreased social behavior before retiring

have been considered behaviors that contribute to a primate's ability to detect predators in the vicinity of a sleeping site. Similarly, decreased vocalizations and increased rates of locomotion near the sleeping site are believed to assist in the evasion of predators and concealment of the sleeping location [Alonso & Langguth, 1989; Anderson, 1984, 1998; Caine, 1984, 1987; Dawson, 1979; Day & Elwood, 1999; Heymann, 1995; Neyman, 1977; Reichard, 1998]. Following numerous predation events at tamarin sleeping sites, we began to question whether GLTs behave "appropriately" in the vicinity of their sleeping sites so as to minimize predation risk.

The objective of this study was to quantify GLT rates of scent marking at different times of day and in both the wet and dry seasons. With these data we tested two hypotheses: First, If GLTs attempt to avoid predation at sleeping sites, they should reduce their rates of scent marking during the period just before they enter their sleeping sites. Although relatively little is known about the costs of olfactory signals [Penn & Potts, 1998], it seems theoretically feasible that scent marks could incur a cost by attracting predators [Gosling, 2000], and a growing body of empirical evidence strongly suggests that olfactory cues are exploited by mammalian predators to locate prey [Cushing, 1984]. Furthermore, individuals of prey species have been shown to decrease their scent-marking behavior based on a perceived risk of predation, presumably to mitigate that risk [Roberts et al., 2001].

Our second hypothesis is that if the benefits of scent marking prior to entering the sleeping site merit an increase in the rate of marking, then tamarins should increase their rate of pre-retirement scent marking during the breeding season, when such behavior would have its greatest impact on reproductive fitness. If scent marking serves reproductive functions via intragender competition or intergender signaling, then scent marking should increase during the mating season [Pochron et al., 2005], as has been observed in male ring-tailed lemurs (*Lemur catta*) [Gould, 2002].

MATERIALS AND METHODS

Study Site and Data Collection

We conducted this study on GLTs in the 6,300-ha Poço das Antas Biological Reserve from May 1998 through April 1999. Poço das Antas and surrounding areas were heavily logged prior to creation of the reserve and are now covered by forests in various phases of secondary succession, swamp forest, and exotic grasses [Dietz et al., 1997]. The topographic relief ranges from 20 to 200 m above sea level, and precipitation is seasonal [Dietz et al., 1994]. The dry season months during this study included May–August 1998 and April 1999, while the wet season extended from September 1998 through March 1999.

We collected data on 49 individuals in eight social groups of GLTs. The study groups varied in size from two to eight individuals, with a mean of 4.6. The majority of groups consisted of one reproductive female, one or two non-natal adult males, and one to two litters of offspring. We collected behavioral data on all animals in these groups, except for infants (0–3 months of age) and two adults that were not habituated to the presence of human observers. The groups were located using radiotelemetry, and all individuals were identifiable by dye marks applied after live capture [Dietz et al., 1997]. We followed groups for 125 days (58 full-day follows (dawn to dusk) and 67 half-day follows during which individuals were observed only in the morning).

We quantified all instances of sternal or circumgenital scent marking during 15-min observation periods on randomly selected focal individuals. We did not differentiate between sternal scent marking or circumgenital marking because GLTs can do either by dragging their bodies horizontally along a branch [Kleiman et al., 1988], and it is difficult to distinguish between the two. During the 15-min observation period only one focal animal was observed, and any time that individual was not visible during the observation period was noted and quantified. Finally, we collected data on the time of group entry/egress from the sleeping site.

Data Analysis

We classified observations as occurring during the wet or dry season and during one of two time periods relative to a group's entry into their sleeping site. If the 15-min observation period commenced less than 30 min before a GLT group entered its sleeping site, any scent marking observed during that period was considered ''pre-retirement.'' If the observation period began more than 60 min prior to the group's entry into its sleeping site, the behavior was deemed ''baseline.'' If the time of entry into the sleeping site was not known for a particular day, any scent marking noted during an observation period that commenced before 1400 hr was considered baseline, since GLTs rarely enter their sleeping site before 1500 hr (Dietz, unpublished).

In order to evaluate the effect of season and time of day on scent-marking rates, we discarded observations that occurred during intergroup encounters with conspecifics. We eliminated these observations because a previous analysis of these data demonstrated that alpha females significantly increased their rate of marking during encounters with conspecific groups [Miller et al., 2003]. In addition, we discarded all 15-min observations on individuals that were less than 1 year of age. We justified this exclusion after modeling scent-marking frequency as a function of age (see details of the repeated-measures analysis below). We found that individuals less than 1 year of age marked at a rate of 0.15 marks/hr (mean ± 1 SE = 0.08, 0.28)[1], while individuals 1 year or older marked at a rate of 2.53 marks/hr (mean ± 1 SE = 2.25, 2.85) with observations on all 49 individuals included in the model, including observations at any time of day or during intergroup encounters. This difference was significant ($t_5 = 4.58$, $P = 0.006$). Finally, for the analysis of time of day and seasonal effects, we removed individuals that were not observed at least once in both the pre-retirement and baseline categories. We removed these individuals because they did not contribute any information for the comparison of baseline vs. pre-retirement scent marking, and their inclusion in the model altered the adjustment for unequal replication. After all these exclusions were made, 26 individuals were included in the subsequent analyses (see Table I for a list of individuals and number of observations per season and time category).

Since we repeated 15-min observations of individuals throughout the study, we used a generalized linear model (GLM) repeated-measures analysis to determine the effect of time of day and season on scent-marking frequency. The exponential, autoregressive, and compound symmetry repeated-measures structures, which allow for uneven spacing in time, were considered. The repeated-measures correlation was small, and goodness-of-fit statistics indicated that the compound was the best-fitting of these structures. We used a generalized linear mixed model with the GLIMMIX macro (SAS version 9.1; SAS Institute

[1]The standard errors of the means are asymmetrical because the original data distribution is asymmetrical; counts of scent marks that fit an overdispersed Poisson distribution.

TABLE I. Distribution of 15-Minute Observation Periods Over the Two Seasons and Two Times of Day

Tamarin ID	Age (years)	Sex	Rank	Dry season observations		Wet season observations	
				Baseline	Pre-retirement	Baseline	Pre-retirement
750	3.5	F	A	15	1	46	1
721	4.2	F	A	47	3	35	0
703	4.5	F	A	20	1	31	1
651	5.0	F	A	20	1	5	0
524	5.5	F	A	36	2	63	6
663	5.5	F	A	1	1	24	0
436	7.1	F	A	21	0	20	1
291	10.5	F	A	9	0	23	1
704	3.7	F	S	5	1	0	0
603	4.2	F	S	16	3	17	1
720	4.4	F	S	29	0	46	3
695	1.8	M	?	14	1	0	0
226	12.5	M	?	2	0	18	1
690	2.4	M	A	16	1	16	0
649	3.6	M	A	18	0	38	2
716	4.1	M	A	32	1	43	1
600	4.3	M	A	15	2	33	1
592	4.6	M	A	22	2	47	1
517	5.2	M	A	17	3	15	0
481	6.5	M	A	49	4	49	3
310	10.1	M	A	10	1	22	1
733	1.1	M	S	0	0	12	1
727	1.5	M	S	0	0	34	2
698	2.3	M	S	21	1	33	1
715	3.9	M	S	39	1	14	0
434	7.6	M	S	16	1	39	2

Inc., Cary, NC). The distribution was defined as Poisson, and a log link was used because the data were counts of scent marks. This macro also accounts for overdispersion as compared to a Poisson distribution. When data are overdispersed (i.e., the variance exceeds the mean), Poisson regression models underestimate variance. The GLIMMIX macro calculates a coefficient of overdispersion and increases the variance to account for the overdispersion [Littell et al., 1996].

The fixed portion of the model contained the effects of season, time of day, the interaction of these two effects, and the time an animal was visible during the 15-min observation period as a covariate. The random portion of the model contained the animal as a block effect, the experimental error was defined as the interactions of an animal with season and time of day, and the residual was variation among 15-min periods (samples) within animal, season, and time of day. Using this model we evaluated the difference in the means of pre-retirement scent marking in the wet and dry seasons. We performed this analysis for males only and with both males and females included together in the model. There were too few observations of females for us to evaluate this relationship for females alone.

Although inclusion of the interaction term was needed to compare the means of pre-retirement scent marking in the wet and dry seasons, we excluded the interaction of season and time of day for the evaluation of main effects (season and time of day). We excluded the interaction term because it was not significant

and its inclusion would make the analysis nonorthogonal due to unbalanced replications among individuals. All other model terms remained the same. We performed this analysis for males only, females only, and both genders together.

RESULTS

Relative to baseline levels, the GLTs increased their rate of scent marking just prior to retiring. The mean rate of scent marking less than 30 min prior to retiring was 3.76 scent marks/hr (mean ± 1 SE = 2.92, 4.85). The baseline rate of scent marking was 2.03 (± 1 SE 1.76, 2.35). The difference between pre-retirement and baseline rates was statistically significant ($t_{58} = -2.46$, $P = 0.017$). When only males were included in the model, the baseline rate of marking was 1.91 scent marks/hr (± 1 SE 1.56, 2.33) while the pre-retirement rate of marking was 5.13 scent marks/hr (± 1 SE 3.83, 6.87). This difference was significant ($t_{32} = -3.51$, $P = 0.001$).

Conversely, there was no difference in the baseline and pre-retirement frequencies of marking by females ($t_{23} = 0.67$, $P = 0.51$). Their baseline rate of marking was 2.06 (± 1 SE 1.65, 2.57) and their pre-retirement rate was 1.36 (± 1 SE 0.74, 2.49; Fig. 1).

GLTs increased their rate of scent marking during the wet season ($t_{58} = -4.61$, $P < .0001$). The mean rate of scent marking across all time categories was 4.38 marks/hr ($\pm$ SE 3.68, 5.21) in the wet season and 1.75 (± 1 SE 1.42, 2.16) during the dry season. The seasonal difference remained significant when either of the two sexes was evaluated alone. Males marked at a rate of 1.87 marks/hr (± 1 SE 1.43, 2.43) during the dry season and 5.23 marks/hr (± 1 SE 4.21, 6.50; $t_{32} = -4.09$, $P < 0.001$) in the wet season. Females marked 1.10 (± 1 SE 0.73, 1.67) and 2.52 (± 1 SE 1.77, 3.60) times/hr during the dry and wet seasons, respectively ($t_{23} = -2.16$, $P = 0.041$; Fig. 2).

The rate of scent marking before retirement in the wet season was 6.76 marks/hr (± 1 SE 5.07, 9.01). This rate was greater than the rate of scent
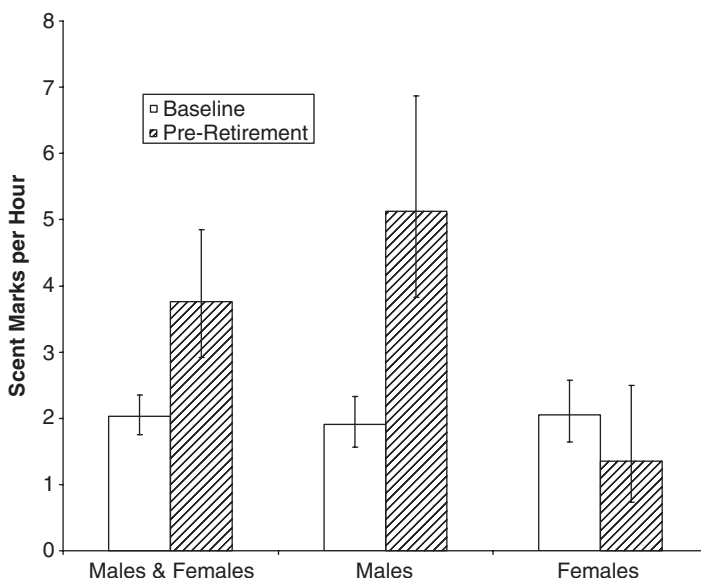

Fig. 1. Mean rate of scent marking ($\pm$SE) observed during two different times of day.

marking before retirement in the dry season (1.75; ± 1 SE 1.10, 2.79, $t_{56} = -2.57$, $P = 0.013$). Males significantly increased their rate of pre-retirement scent marking in the wet season (9.02 marks/hr, ± 1 SE 6.45, 12.61) compared to the dry season (2.78 marks/hr, ± 1 SE 1.73, 4.48, $t_{31} = -2.15$, $P = 0.039$; Fig. 3).
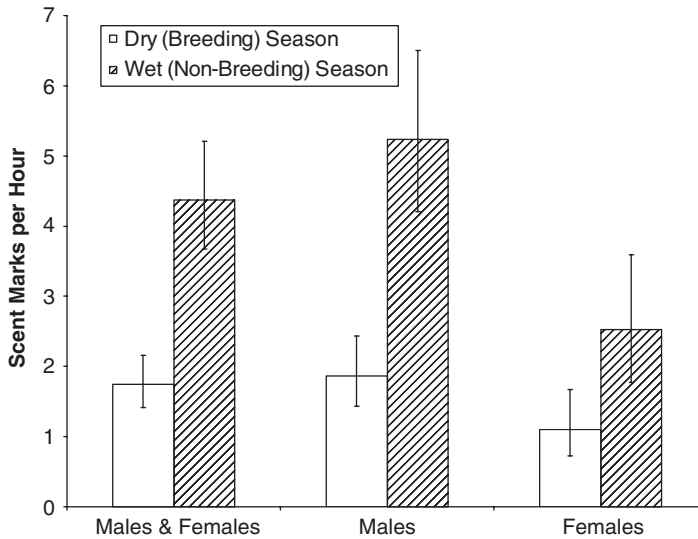

Fig. 2. Mean rate of scent marking ($\pm$SE) averaged over all times of day during the dry (breeding) and wet (nonbreeding) seasons.
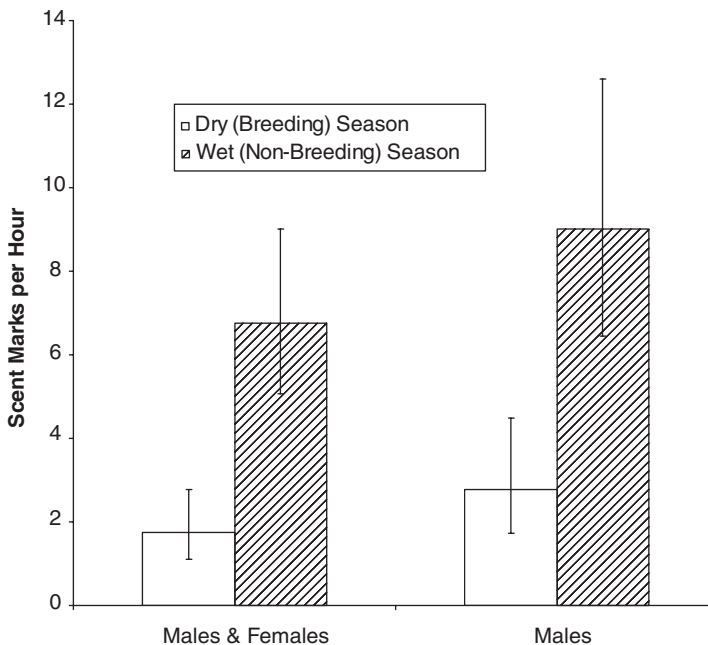

Fig. 3. Mean rate of pre-retirement scent marking ($\pm$SE) during the dry (breeding) and wet (nonbreeding) seasons.

DISCUSSION

These data indicate that GLTs do not attempt to mitigate predation risk by decreasing scent marking in the period before they retire. To the contrary, male GLTs significantly increased scent marking in the 30 min just before they entered their sleeping sites. These results are in apparent contrast to accounts of primates becoming quiet and behaving ''cryptically'' in and around sleeping sites (such behaviors are considered adaptations to avoid attracting predators) [Anderson, 1984; Caine, 1984, 1987; Heymann, 1995; Reichard, 1998].

Although factors such as locomotion and foraging may complicate our comparison of pre-retirement rates of scent marking relative to all other times of day, inclusion of the time a GLT was visible as a covariate in the model corrects for differences in visibility. In addition, GLTs significantly increased their rate of travel in the 30 min prior to retirement compared to all other times of day (Franklin et al., 2006). Consequently, if locomotion had an effect on our analysis, it would artificially decrease estimates of pre-retirement scent marking.

Although our data are not appropriate to test for a link between increased scent marking near tamarin sleeping sites and increased predation risk at sleeping sites, we speculate that such a relationship exists. Few studies have described the hunting methods of mustelids; however, one study reported that mustelids preyed significantly more on voles in experimental plots where scent had been added [Koivula & Korpimaki, 2001], and tracking by scent appears to play a major role in predation by some species in this family [Ewer, 1973]. GLTs travel an average of approximately 129 m during the 30 min before they enter their sleeping site (Franklin et al., 2006). Consequently, the majority of scent deposited by tamarins during this time period is located within 100 m of their sleeping site, and we speculate that this proximity to the sleeping site may facilitate sleeping-site location by predators.

If a cost is incurred by scent marking near sleeping sites, why do GLTs increase marking and what might be the benefits of this behavior? We hypothesize two possibilities: First, GLTs increase scent marking near sleeping sites because marking plays a critical role in identifying or maintaining reproductive opportunities, the benefits outweigh the associated increase in predation risk, and focusing scent around sleeping sites enhances signal transmission. Second, scent marking along pathways to sleeping sites may decrease the likelihood of predation by helping tamarins quickly find their way to sleeping sites at dusk, when crepuscular predators are active.

Scent marking in numerous mammalian species is known to be an important means of transmitting information about dominance status and the stage of the female reproductive cycle, and suppressing reproduction of subordinate females by dominant females [Barrett et al., 1990; Brown & Macdonald, 1985; Epple, 1970; Epple et al., 1993; French, 1997; Gosling & Roberts, 2001; Kappeler, 1998; Kleiman & Mack, 1980; Sillero-Zubiri, 1998; Smith & Abbott, 1998; Ziegler et al., 1993]. If scent marking is important for transmitting information about reproductive status or suppressing reproduction of subordinates, individuals may concentrate their scent in a location where group members will likely encounter the signal [Rylands, 1985]. Since GLTs spend more time in their sleeping site than any other location [Miller 2002], marking near sleeping sites would be an appropriate location.

To test the hypothesis that scent marking near sleeping sites confers a reproductive benefit, we compared rates of scent marking just prior to entering

the sleeping site between the breeding (dry season) and nonbreeding (wet season) seasons. We expected that if scent marking plays a role in the reproductive process, then marking before entering sleeping sites would be greater during the dry season, when the majority of fertile copulations occur [Dietz et al., 1994]. In contrast to that prediction, we found that the frequency of scent marking by males prior to entering the sleeping site was greater in the nonbreeding season than in the breeding season (see Fig. 3). Over all times of day, scent-marking rates were greater in the nonbreeding season than the breeding season for both males and females (Fig. 2).

Scent is used by many mammals to identify ownership of territories [Johnson, 1973] and may be used to deter conspecifics from taking burrows or dens [Brady & Armitage, 1999; Goszczynski, 1990]. Primates have not been observed to use scent marks to deter competitors from usurping a sleeping site; however, callithrichids have been reported to mark other resources, such as gum or fruit trees, possibly to identify ownership [Bartecki & Heymann, 1990; Lazaro-Perea et al., 1999; Miller et al., 2003]. GLTs use tree cavities for sleeping [Rylands, 1985], and appropriate cavities may be limited [Coimbra-Filho, 1977], potentially leading to competition among groups [Radespiel et al., 2003]. In such situations, establishing ownership of sleeping sites may confer benefits to individuals by ensuring protection from predators or inclement weather. The data from this study are consistent with tamarin use of scent to safeguard their favored sleeping trees. However, predictions for alternative hypotheses also fit the observed pattern of scent marking and may be more feasible.

Scent marking prior to retirement may assist a rapid return to "safe" sleeping sites. Unlike most other New World primates, including many species in the family *Callitrichidae*, GLTs almost exclusively use tree cavities for sleeping sites [Rylands, 1993]. Further, GLTs use relatively fewer sleeping sites on a more frequent basis compared to other callithrichids [Franklin, 2004]. Returning rapidly to a safe and unoccupied tree cavity as light fades may be the most effective way to avoid crepuscular predators that are active during the time GLTs approach their sleeping site, and nocturnal predators from which GLTs will be safe once they are inside an impregnable tree hole.

If scent marking is used to assist relocation of sleeping sites, one could hypothesize that scent marking should occur as individuals depart a sleeping site–not as they return to it [Braune et al., 2005]. However, if scent persists longer than the interval between repeated uses of a site, then scent marking while returning to a sleeping site could function in assisting relocation of that sleeping site on subsequent days. Since tamarins use few sites repeatedly [Franklin, 2004], scent that remains recognizable up to 72 hr after deposition [Epple et al., 1980] could provide waypoints to assist relocation of a sleeping site on ensuing days. Another nonexclusive hypothesis is that scent deposited by individuals leading the way to the sleeping site could form a trail for group members to follow minutes later, maintaining group cohesiveness at a time of rapid locomotion while minimizing the need for vocalizations that could attract predators. Increased GLT scent marking concurrent with increased locomotion lends support for this hypothesis, and has also been observed in wild common marmosets (*Callithrix jacchus*) [Lazaro-Perea et al., 1999].

Regardless of whether scent functions to assist relocation of a sleeping site days later or to maintain group integrity during rapid travel to the sleeping site, GLTs may increase the rate of marking during the nonbreeding season (wet season) in order to replenish scent that is washed away by rain [Lazaro-Perea et al., 1999]. We speculate that the strategy of marking pathways to

sleeping sites in order to quickly locate them at dusk, when predation risk is high, may become counterproductive when a predator "learns" how to excavate tree cavities and can exploit olfactory signals to locate sleeping sites at night.

ACKNOWLEDGMENTS

REFERENCES

Alonso C, Langguth A. 1989. Ecologia e comportamento de *Callithrix jacchus* (Primates: Callitrichidae) numa ilha de Floresta Atlantica. Rev Nordest Biol 6:105–137.

Anderson JR. 1984. Ethology and ecology of sleep in monkeys and apes. Adv Stud Behav 14:165–229.

Anderson JR. 1998. Sleep, sleeping sites, and sleep-related activities: awakening to their significance. Am J Primatol 46:63–75.

Barrett J, Abbott DH, George LM. 1990. Extension of reproductive suppression by pheromonal cues in subordinate female marmoset monkeys, *Callithrix jacchus*. J Reprod Fertil 90:411–418.

Bartecki U, Heymann EW. 1990. Field observations on scent-marking behaviour in saddle-back tamarins, *Saguinus fuscicollis* (Callitrichidae, Primates). J Zool 220:87–99.

Brady KM, Armitage KB. 1999. Scent-marking in the yellow-bellied marmot (*Marmota flaviventris*). Ethol Ecol Evol 11:35–47.

Braune P, Schmidt S, Zimmermann E. 2005. Spacing and group coordination in a nocturnal primate, the golden brown mouse lemur (*Microcebus ravelobensis*): the role of olfactory and acoustic signals. Behav Ecol Sociobiol 58:587–596.

Brown RE, Macdonald DW. 1985. Social odours in mammals. Oxford, UK: Clarendon Press. 568p.

Caine NG. 1984. Visual scanning by tamarins: a description of the behavior and tests of two derived hypotheses. Folia Primatol 43: 59–67.

Caine NG. 1987. Vigilance, vocalizations, and cryptic behavior at retirement in captive groups of red-bellied tamarins. Am J Primatol 12:241–250.

Caine NG. 1993. Flexibility and co-operation as unifying themes in *Saguinus* social organization and behaviour: the role of predation pressures. In: Rylands AB, editor. Marmosets and tamarins. Oxford, UK: Oxford University Press. p 200–219.

Cheney DL, Wrangham RW. 1987. Predation. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 227–239.

Coimbra-Filho AF. 1977. Natural shelters of *Leontopithecus rosalia* and some ecological implications. In: Kleiman DG, editor. The biology and conservation of the Callitrichidae. Washington, DC: Smithsonian Institution Press. p 79–90.

Correa HKH, Coutinho PEG. 1997. Fatal attack of a pit viper, *Bothrops jararaca*, on an infant buffy tufted-ear marmoset (*Callithrix aurita*). Primates 38:215–217.

Cushing B. 1984. A selective preference by least weasels for oestrous versus dioestrous urine of prairie deer mice. Anim Behav 32: 1263–1265.

Dawson GA. 1979. The use of time and space by the panamanian tamarin, *Saguinus oedipus*. Folia Primatol 31:253–284.

Day RT, Elwood RW. 1999. Sleeping site selection by the golden-handed tamarin *Saguinus midas midas*: the role of predation risk, proximity to feeding sites, and territorial defence. Ethology 105: 1035–1051.

Dietz JM, Baker AJ, Miglioretti D. 1994. Seasonal variation in reproduction, juvenile growth, and adult body mass in golden lion tamarins (*Leontopithecus rosalia*). Am J Primatol 34:115–132.

Dietz JM, Peres CA, Pinder L. 1997. Foraging ecology and use of space in wild golden lion tamarins (*Leontopithecus rosalia*). Am J Primatol 41:289–305.

Edmunds M. 1974. Defence in animals. New York: Longman Inc. 357p.

Emmons LH. 1987. Comparative feeding ecology of felids in a neotropical rainforest. Behav Ecol Sociobiol 20:271–283.

Endler JA. 1986. Natural selection in the wild. Princeton, NJ: Princeton University Press. 336p.

Epple G. 1970. Quantitative studies on scent marking in the marmoset (*Callithrix jacchus*). Folia Primatol 13:48–62.

Epple G, Alveario MC, Golob NF, Smith III AB. 1980. Stability and attractiveness related to age of scent marks of saddle back tamarins. J Chem Ecol 6:735–748.

Epple G, Belcher AM, Kuderling I, Zeller U, Scolnick L, Greenfield KL, Smith III AB. 1993. Making sense out of scents: species differences in scent glands, scent-marking behaviour, and scent-mark composition in the Callitrichidae. In: Rylands AB, editor. Marmosets and tamarins: systematics, behaviour, and ecology. Oxford: Oxford University Press. p 123–151.

Ewer RF. 1973. The carnivores. Ithaca, NY: Cornell University Press. 494p.

Ferrari SF, Lopes Ferrari MA. 1990. Predator avoidance behaviour in the buffy-headed marmoset, *Callithrix flaviceps*. Primates 31: 323–338.

Franklin SP. 2004. Predator influence on golden lion tamarin nest choice and pre-sleep behavior. M.Sc. thesis, University of Maryland, College Park, MD.

Franklin SP, Hankerson SJ, Baker AJ, Dietz JM. 2006. Golden lion tamarin sleeping-site use and pre-retirement behavior during intense predation. Am J Primatol 68:?–?.

French JA. 1997. Proximate regulation of singular breeding in callitrichid primates. In: Solomon NG, French JA, editors. Cooperative breeding in mammals. Cambridge, UK: Cambridge University Press. p 34–76.

Gosling LM. 2000. Life history costs of olfactory status signalling in mice. Behav Ecol Sociobiol 48:328–332.

Gosling LM, Roberts SC. 2001. Scent-marking by male mammals: cheat-proof signals to competitors and mates. Adv Stud Behav 30: 169–217.

Goszczynski J. 1990. Scent marking by red foxes in central Poland during the winter season. Acta Theriol 35:7–16.

Gould L. 2002. Adult male scent-marking in *Lemur catta* and *Eulemur fulvus* rufus. Int J Primatol 23:575–586.

Heymann EW. 1987. A field observation of predation on a moustached tamarin (*Saguinus mystax*) by an anaconda. Int J Primatol 8:193–195.

Heymann EW. 1995. Sleeping habits of tamarins, *Saguinus mystax* and *Saguinus fuscicollis* (Mammalia, Primates, Callitrichidae), in northeastern Peru. J Zool 237: 211–226.

Johnson RP. 1973. Scent marking in mammals. Anim Behav 21:521–535.

Kappeler PM. 1998. To whom it may concern: the transmission and function of chemical signals in *Lemur catta*. Behav Ecol Sociobiol 42:411–421.

Kleiman DG, Hoage RJ, Green KM. 1988. The lion tamarins, genus *Leontopithecus*. In: Mittermeier RA, Rylands AB, Coimbra-Filho AF, Fonseca GAB, editors. Ecology and behavior of neotropical primates. Washington, DC: World Wildlife Fund. p 299–347.

Kleiman DG, Mack DS. 1980. Effects of age, sex, and reproductive status on scent marking frequencies in the golden lion tamarin, *Leontopithecus rosalia*. Folia Primatol 33: 1–14.

Koivula M, Korpimaki E. 2001. Do scent marks increase predation risk of microtine rodents? Oikos 95:275–281.

Lazaro-Perea C, Snowdon CT, de Fatima Arruda M. 1999. Scent-marking behavior in wild groups of common marmosets (*Callithrix jacchus*). Behav Ecol Sociobiol 46: 313–324.

Littell RC, Milliken GA, Stroup WW, Wolfinger RD. 1996. SAS system for mixed models. Cary, NC: SAS Institute. 633p.

Miller KE. 2002. Olfactory communication, feeding behaviors, and energy budgets of wild golden lion tamarins (*Leontopithecus rosalia*). Ph.D. dissertation, University of Maryland, College Park, MD.

Miller KE, Laszlo K, Dietz JM. 2003. The role of scent marking in the social communication of wild golden lion tamarins, *Leontopithecus rosalia*. Anim Behav 64: 1–9.

Moynihan M. 1970. Some behavior patterns of platyrrhine monkeys. II. *Saguinus geoffroyi* and some other tamarins. Smithsonian Contrib Zool 28:1–77.

Neyman PF. 1977. Aspects of the ecology and social organization of free-ranging cotton-top tamarins (*Saguinus oedipus*) and the conservation status of the species. In: Kleiman DG, editor. The biology and conservation of the Callitrichidae. Washington, DC: Smithsonian Institution Press. p 39–72.

Penn D, Potts WK. 1998. Chemical signals and parasite-mediated sexual selection. Trends Ecol Evol 13:391–396.

Pochron ST, Morelli TL, Terranova P, Scirbona J, Cohen J, Kunapareddy G, Rakotonirina G, Ratsimbazafy R, Rakotosoa R, Wright PC. 2005. Patterns of male scent-marking in *Propithecus edwardsi* of Ranomnafana National Park, Madagascar. Am J Primatol 65:103–115.

Radespiel U, Ehresmann P, Zimmermann E. 2003. Species-specific usage of sleeping sites in two sympatric mouse lemur species (*Microcebus murinus and M*. ravelobensis) in northwestern Madagascar. Am J Primatol 59:139–151.

Reichard U. 1998. Sleeping sites, sleeping places, and presleep behavior of gibbons (*Hylobates lar*). Am J Primatol 46:35–62.

Roberts SC, Gosling LM, Thornton EA, McClung J. 2001. Scent-marking by male mice under the risk of predation. Behav Ecol 12: 698–705.

Rylands AB. 1985. Tree-gouging and scent-marking by marmosets. Anim Behav 33: 1365–1367.

Rylands AB. 1993. The ecology of the lion tamarins, *Leontopithecus*: some intrageneric differences and comparisons with other callitrichids. In: Rylands AB, editor. Marmosets and tamarins. Oxford: Oxford University Press. p 296–313.

Sillero-Zubiri C. 1998. Scent-marking and territorial behaviour of Ethiopian wolves (*Canis simensis*). J Zool 245:351–361.

Smith TE, Abbott DH. 1998. Behavioral discrimination between circumgenital odor from peri-ovulatory dominant and anovulatory female common marmosets. Am J Primatol 26:265–284.

Stanford C. 1988. Chimpanzee and red colobus: the ecology of predator and prey. Cambridge, MA: Harvard University Press. 336p.

Sussman RW, Kinzey WG. 1984. The ecological role of the Callitrichidae: a review. Am J Phys Anthropol 64:419–449.

Terborgh J. 1983. Five New World Primates. Princeton, NJ: Princeton University Press. 260p.

Ziegler TE, Epple G, Snowdon CT, Porter TA, Belcher AM, Kuderling I. 1993. Detection of the chemical signals of ovulation in the cotton-top tamarin, *Saguinus oedipus*. Anim Behav 45:313–322.