The role of scent marking in the social communication of wild golden lion tamarins, *Leontopithecus rosalia*

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The role of scent marking in the social communication of mammals is widely variable. One reason for this variation is that the function of scent marking may vary with different ecological and social conditions. The purpose of this study was to test four nonexclusive hypotheses explaining the role of scent-marking frequency in different ecological and social contexts for wild golden lion tamarins. Relative to ecological contexts, we compared scent-marking frequency during seasons of abundant and scarce food resources. Relative to social contexts, we compared scent-marking frequency when groups were isolated and when groups were in the presence of neighbouring groups. We found that the tamarins used scent marking to mark the location of food resources. Additionally, males used scent marking to communicate intrasexual dominance within their groups, while females did not. Our results also indicate that alpha females increased their scent-marking frequency to communicate to members of other groups, while the presence of members of other groups did not elicit a similar response by alpha males. We did not find evidence for a territorial function of scent marking in golden lion tamarins.

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Olfactory communication is an important part of the social behaviour of many mammals (Eisenberg & Kleiman 1972; Johnson 1973). Scent marking, one form of olfactory communication, may be defined as the deposition of odour by urination, defecation or the release of glandular secretions (Kleiman 1966). The majority of research on scent marking has been conducted in canids, mustelids, ungulates, rodents and primates (see reviews by Johnson 1973; Müller-Schwarze 1983; Brown & MacDonald 1986; Halpin 1986; MacDonald et al. 1990). Scent marking may communicate information regarding social status, stress, age, sex, reproductive state, group composition, individuality, maternal state and current motivational state (Brown 1979; Epple & Smith 1985; Halpin 1986; Smith et al. 1997, 2001; Penn & Potts 1998). The wide variation in proposed functions suggests scent marking may have different functions in different social and ecological contexts (Lazaro-Perea et al. 1999). For example, function may depend on whether or not a social group is isolated from or in contact with another group,

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or may vary with the seasonal availability of resources. The functions of scent marking relative to natural variation in social and ecological contexts of wild animals have not been fully explored (Lazaro-Perea et al. 1999).

Several hypotheses have been proposed to explain why animals scent-mark. First, scent marking may facilitate relocation of food resources and thus improve foraging efficiency (Henry 1977). A variety of animals including common marmosets, *Callithrix jacchus*, foxes, *Vulpes vulpes*, golden lion tamarins, *Leontopithecus rosalia*, wolves, *Canis lupus*, coyotes, *Canis latrans*, and otters, *Lutra lutra*, mark food resources (Box 1977; Henry 1977; Mack & Kleiman 1978; Harrington 1981, 1982; Kruuk 1992). Second, marking may function to communicate dominance status among group members, thus reducing the need for costly fights (Snowdon & Soini 1988). Marking for this purpose is seen in wildebeest, *Connochaetes taurinus* (Estes 1969) and several primate species including common marmosets, saddle-back tamarins, *Saguinus fuscicollis*, and cottontop tamarins, *Saguinus oedipus* (Epple 1970; Epple et al. 1979; French & Cleveland 1984). Third, animals may scent-mark for the purpose of defending food resources or territories, thereby reducing fights with conspecifics (sifaka, *Propithecus verreauxi*: Jolly 1966; Johnson 1973; Kruuk et al. 1984; Eurasian beaver, *Castor fiber*: Rosell et al. 1998; aardwolves, *Proteles cristatus*: Sliwa & Richardson 1998). Scent marking in common marmosets and saddle-back tamarins is frequent during

interactions between resident and intruder animals (Epple 1970; French & Snowdon 1981; Harrison & Tardif 1989). Finally, animals may mark to communicate other information among conspecifics. Communication among conspecifics may function to advertise social status and thus facilitate immigration, attract mates, guard mates or protect a social position within the group against immigrants. In a study of wild common marmosets, subordinate females marked more frequently than dominant females, possibly to advertise their social status for the purpose of attracting mates (Lazaro-Perea et al. 1999). Subordinate females may attract mates for the purpose of extragroup copulations or for the purpose of finding dispersal partners (Lazaro-Perea 2001).

We explored the functional significance of scent-marking frequency in golden lion tamarins, a member of the primate family Callitrichidae. In the current study, we focused on scent marking that was the result of the deposition of odour from scent glands as opposed to faeces or urine. Scent-marking behaviour in golden lion tamarins is described in Kleiman et al.'s study (1988). Relative to other anthropoid primates, callitrichids have well-developed vomeronasal organs and scent glands and have high rates of scent marking, suggesting that chemical communication is important in this group of primates (Epple & Moulton 1978; Maier 1981; Epple & Smith 1985; Epple et al. 1993; Lazaro-Perea et al. 1999).

The four nonexclusive hypotheses stated above were used to generate the following predictions. One, if scent marking functions to communicate the location of resources among members of the same group, we predicted that the tamarins would mark fruit trees more frequently than nonfruit trees. Also, we predicted that they would mark fruit trees more frequently during the dry season when fruits are typically scarce and therefore hard to find, compared with the wet season when fruits are more abundant. Two, if scent marking functions to communicate social status among members of the same group, we predicted that dominant animals would mark more frequently than subordinate animals, outside of encounters with other groups. Three, if scent marking is used to communicate territory defence, we predicted that the tamarins would mark more frequently in areas of territorial overlap compared with areas of exclusive use. Scents placed in areas of territorial overlap may serve to communicate territory ownership to neighbouring groups. Four, if scent marking functions to advertise an animal's social status to members of other groups, we predicted that the tamarins that were most likely to emigrate (subordinates) or most threatened by immigrants (alpha females) would mark more often during intergroup encounters than outside of encounters. Alpha males may also mark more during encounters for the purpose of mate guarding or mate attraction. In the population of golden lion tamarins at Poço das Antas, females have a much lower rate of successful immigration than males (Baker & Dietz 1996). This lower rate of successful immigration is due to the fact that dispersing females can only enter a group if the reproductive (alpha) female's position is vacant (Baker & Dietz 1996). Dispersing females have not been observed to enter a

group by replacing the subordinate female. Alpha females may protect their position in the group by communicating their presence to conspecifics in other groups. In contrast, male immigrants may enter a group as alpha males or subordinate males, resulting in less of a threat to the alpha male's position compared to that of the alpha female.

Table 1. Average group compositions, infants not included (May 1998–April 1999)

Group	All males: all females	Adults:subadults: juveniles
BO	1:2	3:0:0
SA	4:2	3:1:2
FA	3:1	3:1:0
PP	2:1	3:0:0
BA	2:1	3:0:0
2F	2:3	4:0:1
2M	2:2	3:0:1
GF	4:1	4:0:1

METHODS

Study Site and Subjects

The study was conducted from May 1998 through to April 1999 in Poço das Antas Biological Reserve (22°30–33′S, 42°15–19′W), Rio de Janeiro State, Brazil. The reserve is a 6300-ha remnant of the Atlantic Coastal rainforest having a mixture of secondary swamp forest and early successional forest (Dietz & Baker 1993; Dietz et al. 1997). Topographic relief varies from 20–200 m above sea level. The climate in the reserve is seasonal (Dietz et al. 1994). During this study, dry season months included May–August 1998 and April 1999, during which precipitation and temperature were minimal, and wet season months included September 1998–March 1999.

The study animals included 34 wild golden lion tamarins in eight reproductive groups. Group compositions are summarized in Table 1. We observed all animals but infants (0–3 months of age) and two adults that were transient and not habituated to the presence of human observers. Group size averaged 4.6 and ranged from two to eight individuals. Most groups contained one reproductive female, one or two non-natal adult males and one to two litters of offspring. Most fertile copulations took place during May–July and births occurred in October and November. Groups occupied territories averaging 44.5 ha (Miller 2002). The tamarins consumed fruit, insects, small vertebrates, nectar and occasionally tree exudates. They slept in tree holes and occasionally in bromeliads or vine tangles.

Data Collection and Analysis

We recorded all occurrences of circumgenital and sternal scent marks by the focal animal during 15-min focal periods during 125 days of observations. Forty-nine of the 125 study days were dawn to dusk, while the others

were half days of observations. We did not differentiate between circumgenital and sternal marks. Golden lion tamarins may circumgenital mark or sternal mark by dragging their bodies horizontally along a branch (Kleiman at al. 1988). Therefore, it was difficult to know whether one or both types of marking were taking place when individuals were horizontal. We noted whether the substrate marked was a fruit tree (i.e. a species fed upon by tamarins) or a nonfruit tree (i.e. a species never fed upon by tamarins). We compared the total number of scent marks in fruit trees (relative to the total time spent feeding on fruits) to the total number of scent marks in nonfruit trees (relative to the total time spent in nonfeeding activities), for each tamarin. We also compared the number of fruit trees marked relative to the time spent feeding on fruits in dry season months versus wet season months.

We noted the occurrence of all intergroup encounters. An encounter was said to begin when the nonfocal group was first heard or seen. An encounter was said to end when the nonfocal group was no longer in sight, nor vocalizing in response to the focal group. Intergroup encounters may serve several purposes, which confounds the function of scent marking during encounters. Therefore, we tested the hypothesis of territory defence by observing scent-marking frequency on days of no encounters (N_{days}=57). We compared each group's number of marks placed in overlapping areas of the territory to each group's number of marks placed in exclusive areas of the territory, relative to time spent in overlapping or exclusive areas, respectively. We recorded geographical coordinates (X, Y) every 20 min to determine territory sizes and the locations of areas of overlap. Territory area, as estimated from 95% contour areas, was calculated using the Adaptive Kernel method in ArcView (ESRI ArcView 3.1, Animal movement extension to ArcView 1.1, Hooge & Eichenlaub 1997).

We assigned age categories as follows: juvenile: 3–12 months; subadult: 12–18 months; adult: 18 months and older. In groups containing only two reproductive animals, both were considered the dominant animals. For groups that had more than one adult male and/or adult female, social status (dominant or subordinate) was assigned based on behaviours such as arch walking (Rathbun 1979), displacement at food sources and mate guarding.

We tested the hypotheses using two-tailed nonparametric statistical tests (GraphPad InStat 1998; SAS Institute 1999). Wilcoxon matched-pairs signed-ranks tests and Wilcoxon two-sample tests were used to compare scent-marking frequencies (Siegel 1956). We removed juveniles (N=4) from all analyses because their scent-marking frequency was very low, as it is for golden lion tamarins in captive studies (Kleiman & Mack 1980). The four juveniles scent-marked nine times during the course of the study. We omitted data on one adult female because she disappeared from the group 1 month after data collection began. We also omitted data on two adult males (father–son duo) from all comparisons that involved rank because it was unclear which male was dominant. Additionally, dominance ranks of six animals changed throughout the study. Therefore, we assigned either a dominant or subordinate rank to the six animals whose ranks changed, grouped them with the other animals of like rank and then compared scent-marking frequencies of dominant and subordinate animals. The animal's assigned rank was the rank that the animal maintained the longest during the study. When statistically comparing scent-marking frequencies for animals of the same rank on days of encounters to days of no encounters, we used data from all animals that held that rank during the time they held that rank.

We compared scent-marking frequencies of individuals when testing all hypotheses except those relative to territory defence and food resources. For the hypothesis regarding territory defence, groups were classified as being in areas of overlap or areas of exclusive use of their territories and therefore group means were compared. Additionally, for the hypothesis addressing the use of scent marking to mark food resources, we considered observations of individuals scent marking fruit trees to be independent of each other, while we considered observations of individuals visiting fruit trees (and consuming fruit) to be dependent on each other, since finding food is often a group effort. As a result, we compared scent-marking frequencies of individuals and numbers of visits to fruit trees by groups. We did not include time of day in our comparison of scent-marking rates on days with encounters to rates on days without encounters, because scent-marking rates across four time periods during the day (0600–0859, 0900–1159, 1200–1459, 1500–1800 hours) did not differ (K. Miller, unpublished data).

RESULTS

We recorded 1125 scent marks for 29 adults and subadults during 339.4 h in which animals were visible. Averages for 27 adults (not including the father–son duo whose ranks were unclear) were as follows: overall mean ($\pm$ SE)=2.3 $\pm$ 0.41 marks per animal/h visible, N=27; male=2.7 $\pm$ 0.63, N=15; female=1.8 $\pm$ 0.49, N=12; alpha female=2.4 $\pm$ 0.55, N=7; alpha male=4.1 $\pm$ 1.0, N=7; subordinate female=1.1 $\pm$ 0.91, N=5; subordinate male= 1.3 $\pm$ 0.50, N=8. Although we did not distinguish between the methods of scent transfer (horizontal dragging versus rubbing while sitting) or the type of mark deposited (circumgenital or sternal marks), our subjective impression was that the majority of scent marking was accomplished by horizontally dragging the body.

Hypotheses Tested

Hypothesis 1: scent marking is used to communicate the location of food resources within groups

Golden lion tamarins marked fruit trees more frequently than nonfruit trees, relative to the time they spent feeding on fruits and engaged in nonfeeding activities, respectively (Wilcoxon matched-pairs signed-ranks test: T=320.0, $N_{individuals}$=29, P=0.03; Fig. 1). There was also a significant difference in the number of scent marks on fruit trees relative to time spent feeding on fruits
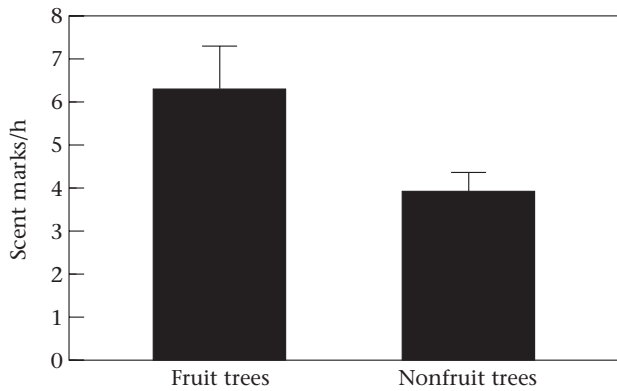
Figure 1. Mean number (+SE) of fruit trees and nonfruit trees scent-marked/h visible by golden lion tamarins, relative to the time they spent feeding and engaged in nonfeeding activities, respectively.
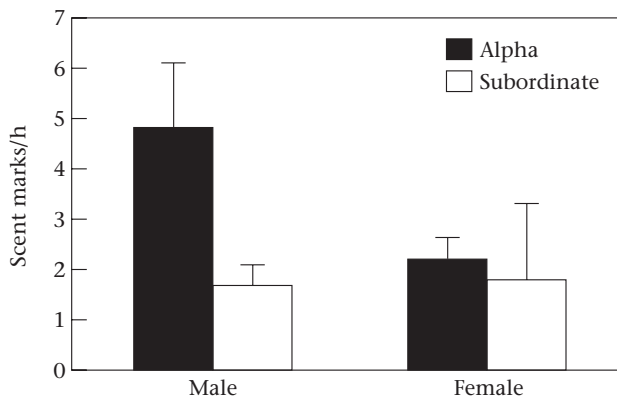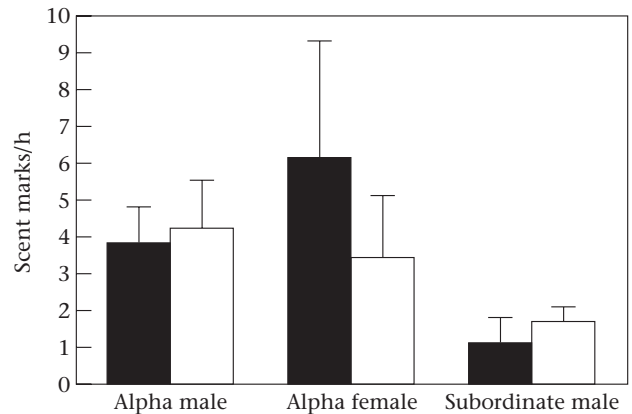

Figure 2. Mean number (+SE) of scent marks deposited/h visible by golden lion tamarins on days without intergroup encounters.

between the wet season and dry season (T=48.0, $N_{individuals}$=29, P=0.003). The tamarins marked more fruit trees during the wet season than in the dry season, which did not support our prediction that marking would be more frequent in the season of fewer resources. To further understand this result, we looked for seasonal differences in the number of fruit trees visited (and fed from) during days in which the groups were observed for 8 h or more. Significantly more fruit trees were visited and eaten from each day in the wet season than in the dry season (T=1.0, N_{groups}=8, P=0.02).

Hypothesis 2: scent marking is used to communicate social status within groups

Alpha males had significantly higher frequencies of scent marks (relative to the time visible) compared with subordinate males during days without intergroup encounters (Wilcoxon two-sample test: W=81.0, N_{alpha}=7, $N_{subordinate}$=8, P=0.01; Fig. 2). There was no significant difference in frequencies of scent marks between alpha females and subordinate females during days without intergroup encounters (W=24.0, N_{alpha}=7, $N_{subordinate}$=5, P=0.19; Fig. 2).

Figure 3. Mean number (+SE) of scent marks deposited/h visible by golden lion tamarins during intergroup encounters (■) and on days without intergroup encounters (□) for three rank/sex categories.

Hypothesis 3: scent marking is used in territorial defence

We found no significant difference in the average scent-marking frequencies of groups when they were in areas of overlap versus exclusive areas of their territories, during days without encounters (Wilcoxon matched-pairs signed-ranks test: T=17.0, N_{groups}=8, P=0.95).

Hypothesis 4: scent marking is used to advertise social status between groups

Alpha females had significantly higher scent-marking frequencies during encounters than on days without encounters (Wilcoxon matched-paris signed-ranks test: T=60.0, N=11, P=0.01; Fig. 3). There was no significant difference in the scent-marking frequencies of alpha males (T=16.0, N=8, P=0.84) or subordinate males (T=8.0, N=9, P=0.38; Fig. 3) during encounters compared to days without encounters. Data were insufficient to test for similar differences in subordinate females. Of the five subordinate females, only four had nonzero scent-marking frequencies during encounters and on days without encounters.

We found no significant difference in the scent-marking frequencies of alpha males and subordinate males during encounters (Wilcoxon two-sample test: W=71.5, N_{alpha}=7, $N_{subordinate}$=8, P=0.07; Fig. 4). However, scent-marking frequencies of alpha females were significantly higher than those of subordinate females during encounters (W=19.5, N_{alpha}=7, $N_{subordinate}$=5, P=0.04; Fig. 4).

DISCUSSION

Scent marking in wild golden lion tamarins apparently serves several functions. The high rate of scent marking on fruit trees suggests that marking is used to facilitate relocation of food resources among members of the same group. The lack of difference in scent-marking rates in areas of overlap and areas of exclusive use further suggests that marking fruit trees is used in intragroup communication. Mack & Kleiman (1978) found that captive golden
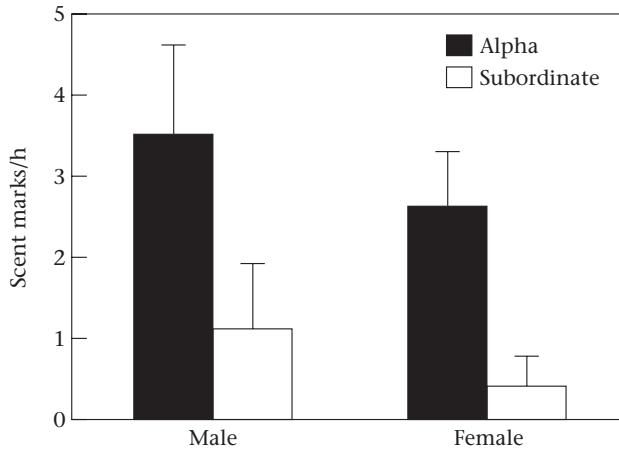
Figure 4. Mean number (+SE) of scent marks deposited/h visible by golden lion tamarins during intergroup encounters.

lion tamarins marked on pathways leading to and from feeding sites. In the current study, golden lion tamarins visited more fruit trees in the wet season than in the dry season. As a result, they encountered more unmarked fruit trees in the wet season than in the dry season, which could account for higher rates of scent marking in the wet season than in the dry season. Although we did not quantify the seasonal abundance of fruiting trees, another study conducted at Poço das Antas Reserve found greater fruit availability during the wet season than the dry season (Dietz et al. 1997). Alternatively, golden lion tamarins may mark trees more often in the wet season due to the increased rainfall, which may erode scents at a faster rate than during the dry season. Lazaro-Perea et al. (1999) found that common marmosets scent-mark at significantly higher rates during the rainy period than during the dry period of the fruiting season. Return rates to fruit trees previously marked versus unmarked would be useful to further examine this hypothesis.

Because group members often feed at a fruit tree together, golden lion tamarins may mark fruit trees simply because there is an increased likelihood that the marks and associated information are perceived by other group members. Rylands (1985) suggested that *Callithrix* species might mark gouged exudate holes because they are sniffed and licked by multiple group members. It is difficult to know whether tamarins also mark fruit trees to communicate fruit availability, because frequency of tree use and fruit availability are often interrelated. For example, large fruit trees may be marked preferentially because more group members can congregate in the trees and will perceive scent information, and because large trees generally offer more fruit than small trees. However, if fruit trees only serve as advantageous substrates for scent marking, because their frequency of use increases the likelihood that scent marks will be perceived, we would predict that any substrate tamarins used repeatedly would be marked preferentially. These substrates would include places where most group members congregate, and marking frequency would positively correlate with the amount of time the group spends in an area and how

close group members are to each other. Therefore, golden lion tamarins might also be expected to preferentially mark nonfood sites, such as nest sites, commonly used pathways in the territory and places where the entire group rests and grooms for extended periods.

Saddle-back tamarins recognize individuals' odours and discriminate between the odours of subordinate and dominant individuals (Epple 1973, 1974a, b). Dominant animals often scent-mark more frequently than subordinate animals (rabbits, *Oryctolagus cuniculus*: Mykytowycz 1965; Ralls 1971; capybara, *Hydrochaeris hydrochaeris*: Herrera & MacDonald 1994). The high frequency and chemical qualities of scent marks by dominant tamarins may also function to maintain dominance (Epple 1970; Epple & Smith 1985). In the current study, the dominant animals were always adults, whereas subordinate animals included adults and subadults. In Kleiman & Mack's study (1980) of scent marking in captive golden lion tamarins, males in their natal groups began to sternal-mark frequently at an average age of 10.6 months and females at an average age of 12.5 months. Therefore, by 12 months of age, subadult tamarins scent-mark at frequencies comparable to those of adults. As a result, in the current study, we did not regard any differences observed in scent-marking frequency between dominant and subordinate animals to be influenced by the age differences.

Our results are consistent with the hypothesis that male golden lion tamarins use scent-marking frequency to communicate intrasexual social status within their groups. Scent marking may play an important role in establishing and maintaining dominance among males by behaviorally suppressing subordinates males (Epple 1970). In contrast, scent-marking frequencies of alpha females and subordinate females did not differ on days without encounters, suggesting that alpha females do not use increased scent-marking frequency to communicate intrasexual social status within their groups. In a study of wild common marmosets, Lazaro-Perea et al. (1999) also found no difference in scent-marking frequencies of dominant and subordinate females. The researchers suggested that reproductive and social dominance may be more relaxed in natural environments where polygyny is occasionally observed and where subordinate animals are not forced to maintain close contact with dominant animals. Therefore, the pattern observed in captive studies of reproductive females marking more than subordinate females is not necessarily observed in wild studies. Although our study did not directly address the role of scent marking in the reproductive inhibition of subordinates, the fact that dominant females did not scent-mark more than subordinates suggests that scent marking may not be important in this context.

Variation in relatedness among group members may explain the observed difference between scent-marking frequencies of alpha females and alpha males on days without encounters. Because female immigration is rare in this population (Baker & Dietz 1996), the subordinate female in the group is often the daughter (or occasionally the granddaughter) of the alpha male in the group. As a result, the alpha female may not use scent-marking frequency to communicate her dominance to the

subordinate female because the subordinate female does not pose a threat (i.e. is unlikely to mate with her father/grandfather). In contrast, subordinate males in the group are often not sons of the alpha female, and thus, could potentially mate with her. Therefore, the alpha male may use scent-marking frequency to communicate his dominance to subordinate males, relative to the threat they pose. In the current study, two of the five groups that contained subordinate females included subordinate females that were unrelated to the alpha male (40%), whereas five of the six groups that contained subordinate males included males that were unrelated to the alpha female (83%). A comparison of scent-marking frequency across alpha females (and across alpha males) in groups having subordinates that vary in relatedness to members of the opposite sex would be useful in addressing the potential relationship between relatedness and the use of scent marking.

This study did not demonstrate a role for scent marking in territorial defence, contrary to studies of other species including, aardwolves, pikas, *Ochotona princeps*, and wolves (Peters & Mech 1975; Meaney 1990; Richardson 1990). Scent marking is often described as having a role in territorial defence, but in many cases, the relationship between marking and defence is not demonstrated or no relationship exists (Johnson 1973). Relative to the amount of time spent in areas of overlap and exclusive areas of the territory, golden lion tamarins did not scent-mark areas of overlap more frequently than exclusive areas, on days without encounters. Other studies of wild callitrichids have also found that scent marks are either concentrated in exclusive areas or distributed randomly throughout the territory (exclusive areas: saddle-back tamarins: Yoneda 1984; common marmosets: Lazaro-Perea et al. 1999; random distribution: black-mantled tamarins: *Saguinus nigricollis*: Izawa 1978). Heymann (2000) found that wild moustached tamarins, *Saguinus mystax*, scent-mark with equal frequency in the periphery and in areas of exclusive use, relative to the time they spend in these areas. Guimarães (1998) found that buffy-headed marmosets, *Callithrix flaviceps*, scent-mark most frequently in the most intensively used areas, regardless of the group's location in the territory. These results differ from those of Rylands' (1990) study of wild tassel-ear marmosets, *Callithrix humeralifer*, in which rates of scent marking were higher in the periphery of the territory than in the central areas of the territory, outside of encounters. Similarly, saddle-back tamarins scent-mark the periphery of their home range, where they spend more of their time, more frequently than central areas (Bartecki & Heymann 1990).

Two reasons for variation among these studies of wild callitrichids may be the degree of territoriality shown by each species and the way in which territoriality is maintained. Groups that do not maintain exclusive areas (e.g. those in low-density populations) are not expected to display behaviours, such as scent marking, that may function in defining territory boundaries. Wild golden lion tamarins maintain exclusive areas in their home ranges and frequently engage in encounters, averaging one encounter every 2 days (Miller 2002). But, animals that maintain exclusive areas may use various behaviours to maintain that exclusivity, including vocalizations, scent marking, physical encounters or mutual avoidance. Additionally, scent marks placed in exclusive areas or on the periphery of exclusive areas, rather than in overlapping areas, may communicate territory ownership (Gosling & Roberts 2001). This last possibility remains to be tested for wild golden lion tamarins.

The results of our study are consistent with the hypothesis that golden lion tamarins use scent marking during encounters to communicate information other than territory ownership. Intergroup encounters may serve as a way to exchange information for the purpose of mate selection, extragroup copulations and/or attracting immigration partners (see Hubrecht 1985; Garber et al. 1993; Lazaro-Perea 2001). Additionally, individuals (alpha females) in social positions that are most threatened by immigrating individuals may use scent marking to advertise their presence to potential immigrants and deter their immigration. In the present study, alpha females scent-marked more frequently during encounters versus on days without encounters, suggesting that they use scent marking to deter female immigrants and/or to communicate their presence to alpha females in other groups.

Ralls (1971) stated that mammals mark most often when they are dominant to and intolerant of conspecifics. Wild and captive studies of tamarins and lion tamarins demonstrate that reproductive females often show high levels of aggression towards female intruders (French & Snowdon 1981; Sutcliffe & Poole 1984; French & Inglett 1989; Harrison & Tardif 1989; Baker & Dietz 1996). Smith & Abbott (1998) found that common marmoset females deposited significantly more scent marks than males in response to test odours from female subjects. Previous studies demonstrate that male and female common marmosets do not show significantly different rates of scent marking in the absence of test odours (Epple 1970; Sutcliffe & Poole 1978). Female cottontop tamarins increase their suprapubic scent marking when confronted by unfamiliar animals, whereas males use threats and overt aggression (French & Snowdon 1981; French & Cleveland 1984). Studies of wild golden lion tamarins demonstrate that female residents show higher levels of aggression towards female intruders than male intruders (Baker & Dietz 1996). Reproductive female golden lion tamarins would not benefit from the immigration of an unrelated female (Dietz & Baker 1993) and should therefore resist female immigrants (Baker & Dietz 1996). Regardless of whether the female intruders are familiar (e.g. wild studies) or unfamiliar (e.g. many captive studies), resident females show heightened aggression, which may include scent marking.

A comparison of scent-marking frequencies of alpha females when they encounter groups that vary in the number of subordinate females (0 to 1) would be useful in addressing the issue of female intolerance and scent marking. But, many groups of wild golden lion tamarins do not have subordinate females. During most of the current study, five of the eight study groups had no subordinate females (K. Miller, unpublished data).

Therefore, we did not have sufficient data to statistically compare scent-marking frequencies of alpha females when encountering groups that had subordinate females versus those that did not. We were able to quantify scent-marking frequencies of alpha females in four groups that encountered neighbouring groups having varying numbers of subordinate females. Three of the four alpha females tended to scent-mark more frequently when encountering groups that had at least one subordinate female compared with groups having no subordinate females (K. Miller, unpublished data). Also, given that alpha females in the present study did not scent-mark more frequently than subordinate females outside of encounters, it is unlikely that alpha females use scent-marking rates to communicate to subordinate females within their own groups, during encounters.

Chemical signals may serve as repellents to animals of the same sex, while concurrently serving as attractants to animals of the opposite sex (Epple & Smith 1985). We cannot rule out the possibility that reproductive females use scent-marking frequency during encounters to attract mates. Sexual selection theory would predict female-biased rates of scent marking in a species with a high incidence of paternal care and intense intrasexual reproductive competition among females (Heymann 1998). Documenting scent-marking frequency for reproductive females during and outside of breeding months relative to encounter frequency would be useful in addressing this question. Documenting responses to scent marks such as sniffing and overmarking also would be useful in determining whether marking by females functions in intrasexual and/or intersexual communication (see Kappeler 1998).

Dixson (1998) postulated that intrasexual competition among females might have favoured the evolution of complex scent glands in female callitrichids. He cites saddle-back tamarins and cottontop tamarins as two exemplary species in which the females have well-developed circumgenital glands. These species are known to have complex mating systems in which competition between females is intense. Future research might address this hypothesis with female golden lion tamarins, since we observed a difference in scent-marking frequencies of dominant females during and outside of encounters. Areas of future research may also include measuring scent quantity, duration of scent marking and variation in the chemical composition of scents for wild tamarins. Dominant common marmoset females deposit a single circumgenital scent mark for 1.6 s, whereas subordinate females deposit a single scent mark for 0.4 s (Smith 1994). As a result, a dominant female's mark may contain more scent material than a subordinate female's mark. The complex chemical composition of scent marks has been noted for other callitrichid species (Belcher et al. 1989, 1990; Smith et al. 2001). Smith & Abbott (1998) found that common marmosets can distinguish between the periovulatory and luteal phases of the ovarian cycles of dominant females, showing a higher frequency and duration of investigative behaviour towards scents from females in the periovulatory phase than in the luteal phase. Therefore, quantitative and qualitative differences in the chemical composition of scent marks are probably important in understanding the function of scent marking in the social communication of callitrichids (Washabaugh & Snowdon 1998). In the current study, because scent marking was examined throughout the year, the function of scent marking very likely changed as a result of differences in male and female reproductive status. Quantifying responses to marking (sniffing, overmarking) by alpha females and males in addition to chemical analyses of golden lion tamarins' secretions would assist in determining whether marking functions in intrasexual or intersexual communication (see Kappeler 1998).

Although we observed no difference in scent-marking frequencies of alpha males and subordinate males during encounters, alpha males marked significantly more than subordinate males during days without encounters. These observations suggest that alpha males use scent-marking frequency to communicate with members of their own groups, rather than to attract new mates or guard their mates from members of other groups.

In summary, scent marking is a complex behaviour that varies in use and function depending on social and ecological contexts, both within and between groups. Our results demonstrate that variation in scent-marking frequency is influenced by ecological conditions such as fruit seasonality. Our data suggest that golden lion tamarins use scent marking to facilitate relocation of food resources within groups, but not for the purpose of territory defence. Our results also demonstrate that variation in scent-marking frequency is influenced by social conditions, such as whether groups are engaged in encounters or not. Our data suggest that males use scent marking for the purpose of intrasexual communication within groups, while females use scent marking for the purpose of intrasexual communication between groups.

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