

Functional Context of Scent-Marking in *Callithrix penicillata*

Danilo G.R. Oliveira Regina H. Macedo

Laboratório de Comportamento Animal, Universidade de Brasília, Brasília, Brazil

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Key Words

Black-tufted-ear marmoset · *Callithrix penicillata* · Chemical communication · Exudatory · Intergroup encounter · Reproductive signalling · Resource-labelling · Scent-marking

Abstract

Most mammals use olfactory signals for communicating identity, reproductive status and group-related dynamics. Callitrichids produce secretions as olfactory signals, the functional context of which is poorly known, especially in the wild. We analysed the functional significance of scent-marking in a free-ranging group of *Callithrix penicillata* in central Brazil. We recorded all occurrences of scent-marking according to context and conducted 10-min focal observations of adults and ‘scan sampling’ of the focal tree. We recorded the sex of scent-marking individuals and the location of occurrence within the home range, and found that there was no variation in rate of marking relative to either variable. However, females marked more along areas of contact with other groups in the home range and less in the core (non-contact) areas. Scent-marking in intergroup encounters, even when in agonistic contexts, was not associated with territorial disputes between groups. This suggests distinct functions for scent-marking for intra- versus intergroup communication. We also found a positive correlation between rate of scent-marking and height in the resource tree and between exudatory and air humidity.

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Introduction

Mammal olfactory signals can transmit information regarding sex, age, reproductive state, social status in the group, group membership, stress, maternal state and immunological condition of the individual [Ziegler et al., 1993; Heymann, 1998; Washabaugh and Snowdon, 1998; Smith et al., 2001; Palagi and Dapporto, 2006;

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Regina H. Macedo
Laboratório de Comportamento Animal, Departamento de Zoologia, ICC – Universidade de Brasília
Brasília, DF 70910-900 (Brazil), Tel. +55 61 3107 2915
Fax +55 61 3107 2922, E-Mail rhmacedo@unb.br

Smith, 2006; Macdonald et al., 2008]. Mammal chemical signals are produced by scent glands that are modified sebaceous or apocrine glands [Sutcliffe and Poole, 1978; Zeller et al., 1988; Pough et al., 1999]. Most callitrichids possess these glands in the sternal, lower abdomen and genital areas [Sutcliffe and Poole, 1978]. The organic compounds produced by these glands are deposited by the animal when it rubs the gland area over trunks or tree branches (hereafter called scent-marking), usually after gouging a hole in the tree or eating exudates [Coimbra-Filho, 1972; Stevenson and Poole, 1976].

The three central hypotheses concerning scent-marking [Heymann, 2006] suggest that this type of chemical signalling occurs (1) in a reproductive context within the group, (2) associated with territorial defence or (3) to communicate individual social status. Besides these, other functions proposed for primates include signals linked to aggregation, alarm, aggression, identity, spacing, orientation and optimization of foraging [Walraven and Elsacker, 1992; Lazaro-Perea et al., 1999].

The Callitrichidae family is comprised of small monkeys that live in a variety of habitats in Central and South America. They constitute territorial groups of 2–15 individuals that exhibit cooperative reproduction [Auricchio, 1995]. Although scent-marking in captive animals has been well studied in this family [Epple, 1973; Sutcliffe and Poole, 1978; Barrett et al., 1993; Washabaugh and Snowdon, 1998; Smith et al., 2001; Sousa et al., 2006], there are few systematic studies of this behaviour in the wild [Lazaro-Perea et al., 1999; Heymann, 2000; Miller et al., 2003]. Callitrichids may use these chemical signals in several contexts.

Unfortunately, studies of callitrichids in the wild are scarce, and none of the above hypotheses explaining scent-marking can be suggested as the most likely one at the present time. In *Callithrix jacchus*, scent-marking by the dominant female may contribute to the physiological limitation of reproduction of subordinate females, in addition to exerting behavioural control over reproduction [Stevenson and Rylands, 1988; Abbott et al., 1993, 1998; Barrett et al., 1993]. During intergroup encounters in one study with *C. jacchus* there was an increase in marking and non-aggressive interactions by subordinate females, maybe to signal receptivity and to attempt copulation with males of other groups [Lazaro-Perea, 2001]. For *Saguinus mystax*, no difference was found in rates of scent-marking between exclusive and overlap areas with other groups [Heymann, 2000], which suggests that scent-marking may not function in the context of territorial defence. And finally, although scent-marking has been associated with exudativory (i.e. consumption of plant exudates) in previous studies [Coimbra-Filho, 1971, 1972; Coimbra-Filho and Mittermeier, 1976; Lacher et al., 1981; Lazaro-Perea et al., 1999], it remains unknown whether this chemical communication is also used to label other types of resources.

Callithrix penicillata is a small callitrichid (300–450 g) that is abundant in the savannah (Cerrado) biome of central Brazil. This species forms groups ranging from 2 to 15 individuals, usually including adult helpers, and twice yearly the dominant female gives birth to twin infants [Rylands et al., 1993; Miranda and Faria, 2001; Vilela and Faria, 2004]. Plant exudates constitute one of the most important food sources for callitrichines (*Saguinus*, *Cebuella*, *Mico*, *Callithrix*, *Leontopithecus*), and groups tend to explore the exudates of only a few trees over a long period of time, gouging holes in the trunk to extract the exudates [Fonseca and Lacher, 1984].

Exudates comprise saps, resins, latexes and gums, and supply these small-bodied primates with carbohydrates, calcium, magnesium and phosphate. Xylem sap,

which contains water, hormones, minerals and nutrients, flows unidirectionally from the roots toward the leaves, and is influenced by the plant's transpiration, which induces sap flow [Perämäki, 2005]. Transpiration is driven mainly by environmental factors such as soil water supply and atmospheric vapour pressure deficit [Moore et al., 2010]. Phloem sap, on the other hand, contains sugar in addition to other substances and flows bidirectionally, from the leaves to the non-photosynthetic parts of the plant, such as roots and bulbs [Perämäki, 2005].

Some studies have shown that temporal patterns of exudate consumption by tamarins are not evenly or randomly distributed throughout the day [Heymann and Smith, 1999]. Some specialized exudate feeders, such as the slow loris (*Nycticebus bengalensis*), exhibit a high selectivity for certain tree species as well as show seasonal variation [Swapna et al., 2010]. One possible explanation for these patterns is that exudate exploration may be associated with the productivity and quality of exudates, and this may be a function of the plant species [Nash and Whitten, 1989; Yezep et al., 2005]. It has also been posited that exudates may vary in chemical composition and water content in different seasons [Stewart et al., 1973], and that both chemical composition and exudate flow rate may be affected by climatological variables [Anderson and Pinto, 1980; Bearder and Martin, 1980; Geiger and Servaites, 1994; Corbesier et al., 2001].

In this study, our main objective was to identify patterns of scent-marking behaviour in a wild group of *C. penicillata* to determine functional context. We thus evaluated rates of scent-marking relative to the contexts of territorial defence, sexual category and interaction and in association with resource use. We expected that if scent-marking is used for determining territorial boundaries, then it should occur more frequently in areas of intergroup contacts in the group's home range. Alternatively, if scent-marking is used for resource labelling, it should be more frequent in core areas of the group's home range and more closely associated with trees being used as resources. We tested the relation between scent-marking and reproduction by comparing rates and contexts of markings conducted by males and females. We expected to find no difference between the sexes in rates of scent-marking or placement of these marks if marking is used exclusively for labelling resources. An additional objective was to determine patterns of scent-marking relative to different parts of the focal exudate tree as well as in relation to climatological variables. The savannah region of Brazil where this study was conducted has marked seasonal variation, and a previous study indicates that marmosets rely more heavily upon exudates during the dry season [Vilela and Faria, 2002]. This study was conducted during the transitional phase from dry to rainy season, thus allowing the observation of possible changes in patterns of exudate consumption.

Methods

Study Group and Study Site

The study group was habituated to the researchers and was composed of 13 individuals (table 1), which were captured and marked with picric acid in different parts of their body to allow identification. We used a multi-entrance trap with food to capture individuals. Age was estimated by physical characteristics, and social status was based on behavioural interactions among group members determined in another study of the same group [Decanini and Macedo, 2008a]. The hierarchy structure analyses performed in that study used a dominance-directed

Table 1. Individual identification of members of the *C. penicillata* group studied in the Botanical Garden of Brasília, Brazil

Individual	Sex	Age	Social status
TST ¹	male	adult	partially dominant
CMN	male	adult	partially dominant
CMRC	male	adult	partially dominant
BC ²	male	adult	partially dominant
PM	male	adult	subordinate
PTRS	male	adult	subordinate
RPRD ¹	female	adult	dominant
CT	female	adult	subordinate
RB ³	female	adult	subordinate
BRÇ ⁴	female	adult	subordinate
BCRB ⁴	female	adult	subordinate
CCL	male	subadult	subordinate
CESC	female	subadult	subordinate

The dominance hierarchy was established by Decanini and Macedo [2008a].

¹ Members of the reproductive pair.

² Died in March 2006.

³ Left the group in February 2006.

⁴ Entered the group in February 2006.

tree technique that allows complex and non-linear hierarchies [Izar et al., 2006]. By dominance analysis, we determined partially dominant individuals as being hierarchically superior to subordinate females and/or infants and dominant ones as superior to almost all others and not subordinate to any others [Decanini and Macedo, 2008a].

The study was conducted in the Brasília Botanical Garden, Distrito Federal, Brazil (15°51'42'' S, 47°49'41'' W), in savannah areas that included mesophytic forest and dense savannah, where about half of the trees have a canopy height of 4–10 m [Miranda, 1997]. The weather in the region is seasonal, and the study occurred during the transition from dry to rainy season and until the end of the rains. Other intermittent observations during the dry season indicate that the marmosets do not maintain use of the focal tree on a regular basis, probably because the resources in this tree become reduced.

Data Collection

After several weeks of habituation of the animals, the data for this study were collected from October 2005 to April 2006, totalling 106 h of contact. An observer (D.G.R.O.) followed the group 2 days each week for periods of 6 h, once during the morning (6.00–12.00 h) and once in the afternoon (12.00–18.00 h, or until the animals retired to the sleeping tree). The group's home range (areas visited routinely by the group) was approximately 16 ha and was roughly divided into areas where contacts with other groups occurred frequently (hereafter called peripheral: approx. 11 ha) and areas where contacts never occurred (hereafter called core: approx. 5 ha). Visual landmarks (e.g. trails, trees) were used to designate boundaries between the areas. The study group regularly came into contact with two other groups in the peripheral area, one of which had 14 members (10 adults, 4 juveniles). A third group also occurred in the area but was rarely seen. We were unable to identify the composition of two of the groups.

During observations, all occurrences of scent-marking were recorded, whether during focal scan sampling or not (see details below). For this study we considered scent-marking as

events resulting in the deposition of secretions from scent glands on any substrate. We conducted focal scan samples on adults for a period of 10 min with 10-min intervals between samplings. The order of sampling of individuals was determined randomly at the beginning of each day. For this group, most exudativory occurred at a single tree (*Anadenanthera macrocarpa*, Fabaceae), although occasionally individuals were seen gouging for exudates at other trees. However, since this occurred only rarely, we concentrated observations at the main tree and disregarded the occasional exudativory at other trees. When at least 2 group animals were at the main tree, we interrupted focal subject sampling and initiated focal tree sampling [Lazaro-Perea et al., 1997], which ended when all individuals left the tree. For this procedure, we used a diagram of the tree divided into vertical quadrants of 1 m, with branches classified as being at the front, back, right or left sides of the tree. Behaviour in the tree (scent-marking, exudativory, gouging, sniffing/licking, locomotion and inactivity) was recorded through instantaneous scan samples every 2 min [Martin and Bateson, 1993]. Scent-marking occurring out of the scanning period was also registered.

Whenever scent-marking occurred out of the focal tree context, we recorded the author of the marking and classified it according to the glands used. We also determined the area (i.e. peripheral vs. core) of the home range where the marking occurred and its behavioural context. The behavioural contexts wherein scent-marking was embedded were those for which behaviours had a longer duration and included 5 mutually exclusive categories: (1) exudativory (i.e. gouging for or eating plant exudates), (2) sexual interactions, which included attempted copulation or copulation, (3) aggressive responses, which included fights (pushes, bites), chases or presentation of genitalia to other animals, (4) locomotion (movement in any direction) or (5) inactivity. We also recorded subsequent interactions of other individuals (for 1 min) with the marked site (sniffing, licking or scent-marking in the same place).

In periods of intergroup encounters, we interrupted focal samplings and recorded all aggressive, sexual and olfactory (sniffing) interactions among members of different groups as well as any observed scent-markings. If more than one assemblage of individuals of different groups occurred during the encounter of two groups, we preferred to monitor the larger one.

We obtained climatological data (rainfall and air humidity) for the study period from the meteorological station of the Ecological Reserve of IBGE-RECOR. These data were used to test the existence of associations between climate conditions, scent-marking and exudativory behaviours.

Statistical Analyses

We used χ^2 tests to evaluate the frequency of scent-marking performed in different areas (periphery vs. core) of the group's home range (corrected for relative sizes of the two areas to determine expected frequencies) as well as to determine the existence of differences in this behaviour between males and females (corrected for numbers of each sex). χ^2 tests were also used to assess differences between the sexes regarding preferred places to scent-mark (corrected for both factors) and to evaluate the behavioural context in and out of intergroup encounters. To test the association between scent-marking rate and quadrant height in the focal tree, we used a Spearman correlation test. Similarly, to assess the relations between exudativory, scent-marking rates, air humidity and months (rainfall), we used Pearson correlation tests.

Results

A total of 201 scent-markings were recorded, excluding those during focal tree sampling, resulting in a mean rate of 1.9 ± 1.9 scent-marks/h. All but 2 records of scent-marking were circumgenital. We conducted 116 focal subject samplings with adult individuals and in these, 35 scent-markings were observed, resulting in a mean rate of 1.8 ± 1.0 scent-marks/h.

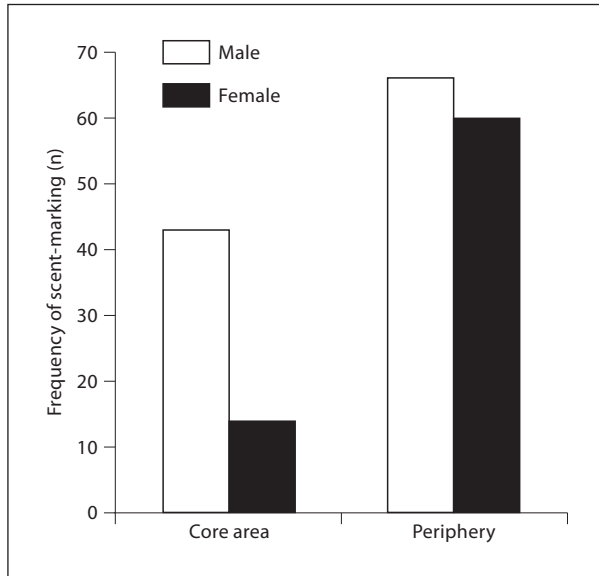


Fig. 1. Frequency of scent-marking according to the sex of the marker and the position of the marking in the territory.

Scent-Marking relative to Area

Of scent-markings recorded, 69.5% (140.0 = observed frequency; 139.6 = expected frequency) occurred in the periphery section and 30.5% (61.0 = observed frequency; 61.4 = expected frequency) in the core section, a statistically non-significant difference ($\chi^2 = 0$, d.f. = 1, $p = 1.0$). Of the 185 scent-markings where we identified the performer, 109 (58.9%) were conducted by adult males and 76 (41.1%) by adult females ($\chi^2 = 1.23$, d.f. = 1, $p = 0.27$; expected frequency for both males and females = 92.5), also exhibiting no statistical difference. Considering the placement of the markings in the territory relative to sex, we found that: (1) in the periphery, males marked 66 times (expected frequency = 75.4) and females 62 times (expected frequency = 52.6), and (2) in the core, males marked 43 times (expected frequency = 33.6) and females only 14 times (expected frequency = 23.4). There is a statistically significant association between sexes and location of scent-marking ($\chi^2 = 10.59$, d.f. = 1, $p < 0.01$, fig. 1), indicating that males and females have different rates of scent-marking that may depend upon their position in the home range.

Scent-Marking relative to Intergroup Encounters

During the study period, the animals were involved in intergroup encounters for 10 of 36 (28%) days where observations occurred, with accumulated time spent in encounters of 12.2 h (1.1 ± 0.7 h duration per encounter). Thirty-six scent-markings (of a total of 201, see above) occurred in periods of intergroup encounters, resulting in a mean rate of 3.0 ± 3.3 scent-marks/h during these events.

Of the 36 scent-markings that occurred during intergroup encounters, none was performed by the reproductive pair of the group. Only 5 (13.9%) of the markings

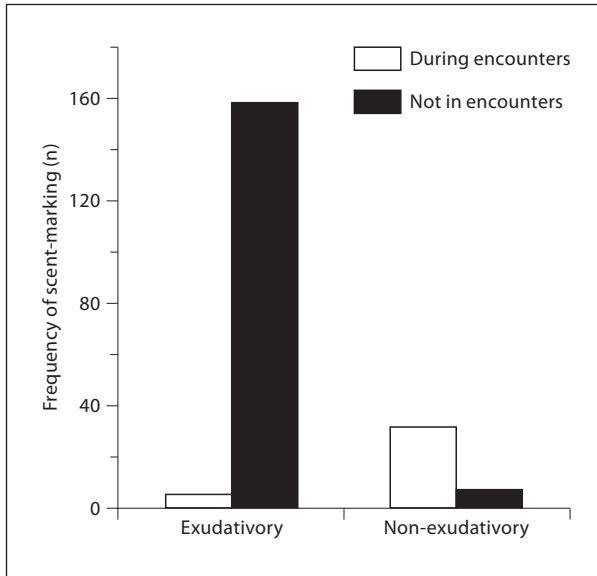


Fig. 2. Frequency of scent-marking according to its context (exudatory or not) and to the state of group interaction (in or out of intergroup encounter).

during intergroup encounters were associated with exudatory, while in periods without intergroup interactions we observed 158 (95.8%) scent-markings that occurred in the context of exudatory and only 7 associated with other contexts. Thus, of the 38 records of scent-marking unrelated to exudatory, 31 (81.6%) occurred during intergroup encounters. The association between rates of scent-marking and contexts of occurrence of the behaviour (exudatory or other) and the periods in which they were carried out (during intergroup encounters or not) were highly significant ($\chi^2 = 123.8$, d.f. = 1, $p < 0.0001$; fig. 2). These results indicate that during normal activities of the group, scent-marking was more likely to be associated with exudatory, while during intergroup encounters scent-marking was associated with other behavioural contexts, instead of foraging for exudates. During intergroup interactions, 63.9% of the scent-markings occurred in association with non-aggressive interactions between members of different groups (including 27.8% that occurred after copulation or attempted copulation), and only 19.4% of markings were linked to aggressive interactions.

Scent-Marking relative to Focal Tree

During focal tree sampling periods, 1,827 scent-markings were recorded ($91.3 \pm 60.7/h$), a much higher rate than that which occurred away from the focal tree ($1.9 \pm 1.9/h$). Marking frequency was distributed along the vertical quadrants of the focal tree as follows: 0 m = 4; 1 m = 84; 2 m = 212; 3 m = 269; 4 m = 231; 5 m = 384; 6 m = 643. There is a highly significant and positive correlation between height and frequency of scent marks (Spearman $r_s = 0.88$, $n = 7$, d.f. = 5, $p < 0.01$).

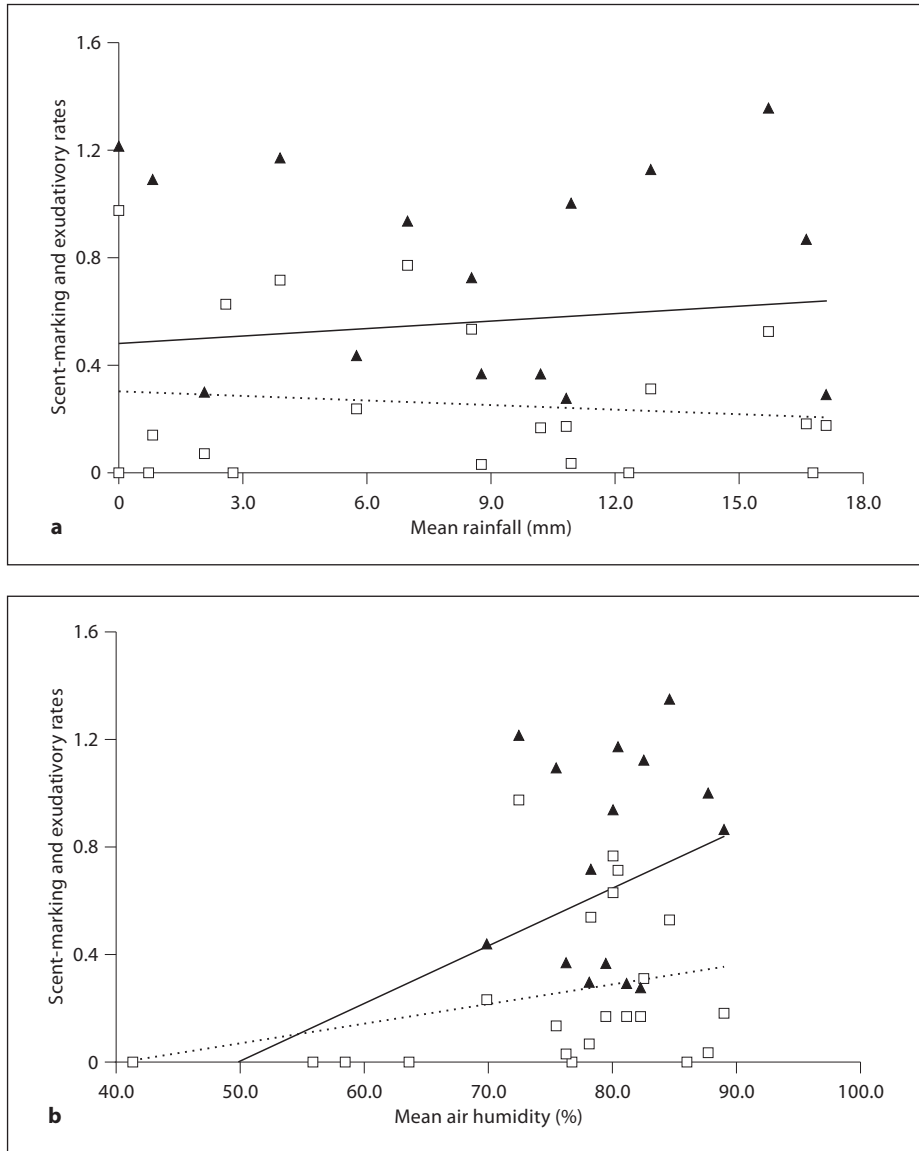


Fig. 3. Recorded variation of scent-marking rate (□) and exudatory (▲) during periods of focal tree sampling (a), and mean air humidity (□) and rainfall (▲) through the weeks (b).

We found a significant positive correlation between time (weeks) of the study period with both the rates of scent-marking (Pearson $r = 0.58$, d.f. = 20, $p < 0.05$) and exudatory (Pearson $r = 0.52$, d.f. = 20, $p < 0.05$) in the focal tree. There was also a significant positive correlation between rate of scent-marking and exudatory (Pearson $r = 0.71$, d.f. = 20, $p < 0.001$; fig. 3) indicating that this chemical communi-

cation is strongly associated with this type of foraging behaviour. Finally, we found that exudatory and air humidity are also positively correlated (Pearson $r = 0.52$, d.f. = 20, $p < 0.05$); however, the scent-marking rate was not directly correlated with any climatic variable.

Discussion

In our study the hypothesis that scent-marking has a territorial function was not sustained, because markings were not concentrated in areas of intergroup contacts in the home range of the group. It appears that for some callitrichids scent-marking may have a more important role in territorial defence than for *C. penicillata*. For example, *Saguinus fuscicollis* mark more in areas previously marked by animals of other groups, especially if they interact aggressively before the markings occur [Eple, 1973]. In the present study, scent-marking during intergroup encounters was not associated with territorial conflicts. Instead, scent-marking seemed to function in other types of intergroup communication that may involve the search for a viable sexual partner in addition to individual conflicts.

The hypothesis of involvement of scent-marking in the reproductive processes within the group was not supported in a straightforward manner either, because there were no differences in marking rate between males and females. However, we cannot exclude the sexual content of chemical communication, especially since sexual differences in the signals may be expressed qualitatively, and not quantitatively, and each scent mark may present a unique chemical bouquet. Although males and females in our study did not differ overall in frequency of scent-marking, our data point to a pattern in this behaviour that differs for the sexes relative to location of marking, although the function of this difference is not obvious. Females concentrated their markings in contact areas of the home range and males in the core, non-contact areas. Lazaro-Perea [2001] reported that subordinate females interacted more in a non-aggressive way during intergroup encounters, probably to assess potential reproductive opportunities in other groups. The increase in the olfactory signalling at the periphery by subordinate females may function to communicate and search for sexual partners outside their groups, since reproductive opportunities for them within their own groups are limited.

Our data support the hypothesis that scent-marking in *C. penicillata* is associated mostly with resource labelling when it occurs in core areas of the territory, especially relative to the trees used in exudatory. Our findings are similar to those reported by Lazaro-Perea et al. [1999], and it is clear that scent-marking is associated with exudatory, but not with other feeding activities such as foraging for fruits and insects, or access to sleeping trees. Since we rarely observed an animal from another group in the focal tree of the studied group, scent-marking behaviour seems to function as a signal for intragroup communication when associated with tree exudates.

Our results show a significant increase in scent-marking exclusively during intergroup encounters, not associated with exudatory, but occurring instead in sexual and aggressive contexts. Additionally, the agents of the behaviour were non-reproductive individuals. This latter finding differs from that of Lazaro-Perea [2001], who registered 21 and 50% of participation in scent-marking by the reproductive female and male, respectively, during intergroup encounters. Our study suggests that

scent-marking has different functions when targeted at individuals of different groups compared to how it is used within the group. It is probable that chemical communication during intergroup encounters is closely linked to reproductive factors, mainly the search for sexual partners in other groups.

Scent-marking in the focal tree did not vary significantly between quadrants, but varied relative to height. Possibly, animals choose the exudatory holes they label based on the height of the resource, with a preference for holes gouged at higher points on the tree. Additionally, scent-markings in the lower quadrants only occurred after the third month of the study period. Hence, it is plausible that the resource in the upper parts of the tree is of superior quality, is easier to access or is available earlier in the rainy season. An alternative explanation is that the animals spend more time at greater heights in the tree for a reason unrelated to the resource itself, and if they scent-mark at a fixed rate regardless of location, then scent-marking would occur at higher rates at the top of the tree. To discriminate between these two explanations, future studies should quantify the amount and quality of exudates available at different heights in the tree and throughout the seasons.

Scent-marking and exudatory rates were correlated. Previous studies have shown that there is a behavioural sequence during extraction of exudates that follows the order: exudatory, tree gouging and scent-marking [Silva, 2000]. Exudatory is associated with air humidity and scent-marking is associated with exudatory, hence the scent-marking rate is also indirectly associated with air humidity. Possibly, environmental factors such as air humidity influence the amount of exudates in the tree.

Some anecdotal observations in the field lead us to conclude that scent-marking in the resource tree may function to label gouged holes that are already empty or with little resource. First, we observed that the highest marking rates occurred during months with little rainfall. When the tree contained a large amount of exudates (dripping from the holes), individuals consumed these and rarely scent-marked. We also observed that when the extraction of the exudate seemed mechanically more difficult (gouging of the hole requiring movement of the whole body and the production of much sound), it was more likely that the marmoset would mark the hole. This signal could allow the animals to save time and energy in their search for exudates and to leave the marked areas of the tree without gouging for some time so that exudate renewal could occur, with the possible advantage of the tree surviving. This construal of foraging behaviour at the resource tree is analogous to the interpretations of another study of *C. penicillata* [Lacher et al., 1981].

It is important to emphasize that our study was conducted mostly during the rainy season, and resource availability during the dry season may cause variations in scent-marking strategies. A previous study conducted in the same region indicates that marmosets consume more exudates during the dry season, using many more tree species than during the rainy season [Vilela and Faria, 2002]. Possibly, the rains allow more focused exploitation of only a few trees.

In conclusion, we suggest that scent-marking in *C. penicillata* is used differently by individuals depending on whether the context is communication within the group or between groups. In the within-group context, scent-marking appears to be used mostly for resource labelling strictly associated with exudatory. The labelling of holes in the resource tree may allow an assessment of quantity and quality of exudates in the tree. Future studies should evaluate this hypothesis by analysing exudate

production and composition among holes gouged by the animals in different parts of the tree, and test these parameters relative to scent-marking. An alternative hypothesis, unrelated to exudate production, is simply that scent-marking may occur more frequently at gouged holes because these are more likely to be visited by many individuals and may also hold scent better than other sites [Rylands, 1985]. In the context of encounters between groups, scent-marking appears to be linked with sexual behaviour and may function to signal the reproductive receptivity of females to males of other groups.

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