UNIVERSIDAD AUTÓNOMA DE MADRID

FACULTAD DE PSICOLOGÍA
Departamento de Psicología Biológica y de la Salud
Programa de Doctorado.- Comportamiento animal y humano: una perspectiva etológica

TESIS DOCTORAL

Functions of olfactory communication in wild saddleback tamarins, *Saguinus fuscicollis*

Yvan Lledo Ferrer
Madrid, 2010

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Presentada en el Departamento de Psicología Biológica y de la Salud de la Universidad Autónoma de Madrid para la obtención del Grado de Doctor con mención Doctor Europeo por:

Yvan Lledo Ferrer

Directores de la Tesis: **Dr. Fernando Peláez del Hierro**
Dr. Eckhard W. Heymann

El Dr. Fernando Peláez del Hierro, Profesor Titular, y el Dr. Eckhard W. Heymann, Profesor Visitante, ambos del Departamento de Psicología Biológica y de la Salud de la Facultad de Psicología de la Universidad Autónoma de Madrid

CERTIFICAN: Que el trabajo titulado "Functions of olfactory communication in wild saddleback tamarins, *Saguinus fuscicollis*", que presenta Don Yvan Lledo Ferrer para obtener el título de Doctor, ha sido realizado bajo su dirección, y se haya en condiciones para su presentación y defensa ante el Tribunal Calificador.

Madrid, a 12 de abril de 2010

VºBº   Los Codirectores

Fdo. Dr. Fernando Peláez del Hierro   Fdo. Dr. Eckhard W. Heymann

A mis padres, por todos los desvelos que he dado
Y por los que todavía daré

Y a Deborah,
por las distancias insalvables

Je voudrais pas crever
Avant d'avoir connu
Les chiens noirs du Mexique
Qui dorment sans rêver
Les singes à cul nu
Dévoreurs de tropiques
Les araignées d'argent
Au nid truffé de bulles
Je voudrais pas crever
Sans savoir si la lune
Sous son faux air de thune
A un coté pointu
Si le soleil est froid
Si les quatre saisons
Ne sont vraiment que quatre
Sans avoir essayé
De porter une robe
Sur les grands boulevards
Sans avoir regardé
Dans un regard d'égout
Sans avoir mis mon zobe
Dans des coinstots bizarres
Je voudrais pas finir
Sans connaître la lèpre
Ou les sept maladies
Qu'on attrape là-bas
Le bon ni le mauvais
Ne me feraient de peine
Si si si je savais
Que j'en aurai l'étrenne
Et il y a z aussi
Tout ce que je connais
Tout ce que j'apprécie
Que je sais qui me plaît
Le fond vert de la mer
Où valsent les brins d'algues
Sur le sable ondulé
L'herbe grillée de juin
La terre qui craquelle
L'odeur des conifères
Et les baisers de celle
Que ceci que cela
La belle que voilà
(...)

Boris Vian

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Chapter 1.
GENERAL INTRODUCTION

Animal communication, although intuitively clear, is nevertheless an extremely elusive concept. It can be defined as any action or trait produced by one animal, the sender, that provides information used by another animal, the receiver (Palagi et al. 2004). However, this picture gets easily complicated (Fig. 1), and no definition includes all forms of communication (Wyatt 2003).

Among all possible modes of signal transmission (visual, auditory, electroreception…), olfactory signals are possibly the most common way of communication in animals, from insects to mammals. It is substantially different from other ways of communication. Even if the sender controls the information included in the message and where and when it is deposited, some other features are beyond its control (Kappeler 1998). Scent marks are deposited on the substrate, and can be detected –if ever- long after deposition, even in the absence of the sender. Moreover, scents may need direct investigation by the receiver in order for the message to be effectively transmitted. Finally, the information content of the signal may be altered by countermarking (Ferkin & Pierce 2007), or simply deteriorated by time or weather conditions (Epple et al. 1980). This poor directionality of the signal makes it particularly susceptible to unintended receivers, shall them be conspecifics or predators (Koivula & Korpimäki 2001). Given these handicaps, it is surprising to find this way of communication so widespread among mammals (Gosling & Roberts 2001a).

Compared to rodents or other mammals, this channel of communication has received little attention in primates. One reason is the false belief that primates are essentially visual animals (Laska et al. 2003). Another reason is probably related to the difficulties it entails for a human observer (Epple 1985, 1986; Heymann 2006a), as well as methodological problems like the poor technical developments for its study and limitations specific to the study of primates, like their long life-histories. Thus, our knowledge about primate chemical communication is far behind from other modes like the visual or acoustic channel (Epple & Moulton 1978; Heymann 2006a).

Another problem in the study of chemical communication lies in the lack of a comprehensive theoretical framework (Kappeler 1998). Until recently, studies of chemical signals were more interested in the description of the signal and its variations (e.g. Epple 1985; Epple & Smith 1985) than in its ultimate function. However, the study of

communication from a functional viewpoint, identifying its influence on the lives of animals, seems more accurate (Zeller 1986).

Figure 1. Basic elements of the communication system (Endler 1993)
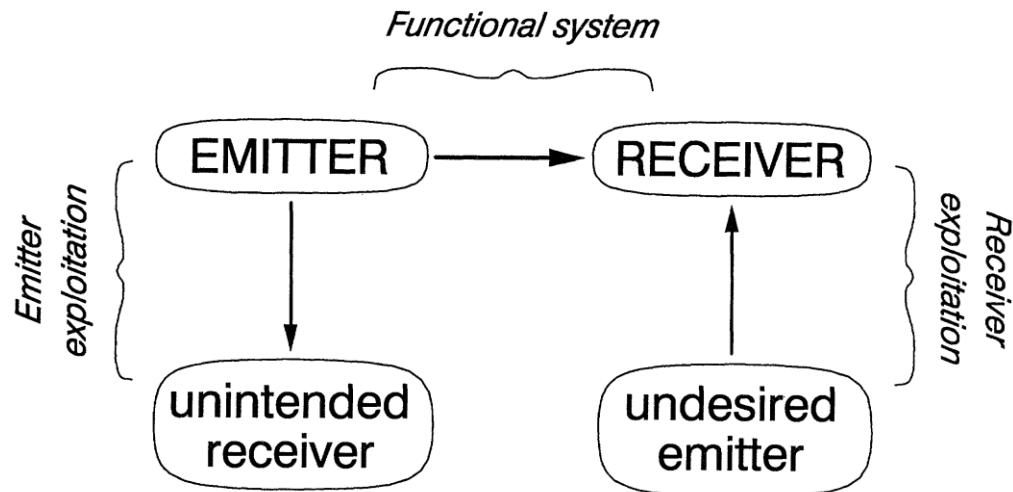
Rediscovered in the 1970s, Darwin's (1871) sexual selection theory has provided a very fruitful framework for the study of primate behaviour, morphology, development or reproductive strategies (see contributions in Kappeler & van Schaik 2004), and for the study of communication (Kappeler 1998; Snowdon 2004).

Sexual selection is a form of natural selection that acts differently on the two sexes (Clutton-Brock 2004). Some traits are selected because they confer a reproductive advantage to the bearer, even if they might represent a handicap for survival (Zahavi 1975). Sexual selection can be split in intersexual competition, or mate choice, and intrasexual competition, where same-sex individuals compete upon access to mates. Referring to chemical communication, Darwin (1871) stated that the development of elaborate odour glands in mammals is "intelligible through sexual selection, if the most odoriferous males are the most successful in winning the females, and in leaving offspring to inherit their gradually perfected glands and odours" (Darwin 1871, p. 281).

In the Primate order, olfactory communication is well-developed among strepsirrhines and among New World Primates (Platyrrhini), especially of the subfamily Callithrichinae (Albone 1984; Epple 1985, 1986). This family comprises the genera *Callimico*, *Callithrix*, *Mico*, *Callibella*, *Cebuella*, (Rylands et al. 2000a), which can be further split into marmosets (*Callimico*, *Callithrix*, *Mico*, *Callibella* and *Cebuella*) and tamarins (*Saguinus* and *Leontopithecus*).

The Callithrichinae possess some special reproductive characteristics. They undergo unusually high reproductive costs: a long gestation period in relation to their small body size (Ziegler et al. 1987); they give birth to dizygotic twins (Hershkovitz 1977) that represent 16-20% of the mother's body mass (Tardif et al. 1993); and they exhibit a post-partum oestrus 12 to 32 days after giving birth (Lunn & McNeilly 1982). The transport of infants has also been shown to be a costly activity which causes a loss of body mass on carriers, even under captive conditions (Achenbach & Snowdon 2002; Sanchez et al. 1999; Sanchez et al. 2005). Thus, the costs of pregnancy, lactation and infant carrying can occur simultaneously. In order to overcome these high costs, callitrichids have developed a cooperative breeding system in which all group members, related or not to the infants, participate in infant carrying (Emlen 1991; Solomon & French 1997). Indeed, one single pair could hardly raise infants (Goldizen 1987a, 1990; Goldizen & Terborgh 1989; Tardif 1997; Tardif et al. 1993).

Although callitrichids live in groups with several adults of each sex, reproduction is restricted to a single female (Snowdon & Soini 1988). This has led to the assumption that callitrichids were monogamous (Hershkovitz 1977), but field studies have challenged this view (Goldizen 1987a, 2003; Savage et al. 1997; Savage et al. 1988), the most common system being functional polyandry (Sussman & Garber 1987). The dizygotic twins may be sired by different males, this is rarely the case (Huck et al. 2005).

Callitrichines are a good model for the study of olfactory communication, as they possess a series of cutaneous glands distributed in the anogenital, suprapubic and sternal regions (Fig. 2), with which they deposit scent marks on the substrate (Fig. 3), combined with urine and probably vaginal secretions in females (Epple 1985, 1986; Epple et al. 1993; Epple & Smith 1985). These chemical signals contain a large number of volatile and non-volatile compounds and convey information about species, sub-species, sex, status and individual identity of the sender (Epple 1978; Epple et al. 1993; Smith et al. 1985). Besides, callitrichines possess a well-developed vomeronasal organ and main olfactory system (Epple 1985, 1986; Epple & Moulton 1978; Epple & Smith 1985; Evans 2003, 2006).

It has been proposed that different scent glands fulfil different communicative functions (Lemuridae: Palagi & Norscia 2009; Callithrichinae: Belcher et al. 1988; Epple et al. 1993; Epple & Smith 1985; French & Snowdon 1981). In *Saguinus fuscicollis*, the suprapubic gland is said to reflect high levels of arousal (Epple & Smith 1985), but there appears to be no functional distinction according to Belcher (Belcher et al. 1988), while in *Saguinus oedipus* it has been argued that anogenital marking is used in sociosexual context, while suprapubic in situations of aggressive arousal (French & Cleveland 1984; French & Snowdon 1981).

Figure 2. Suprapubic (S) and anogenital (CP-L) glands of male (a) and female (b) *Saguinus fuscicollis*. Taken from Zeller et al. (1988)
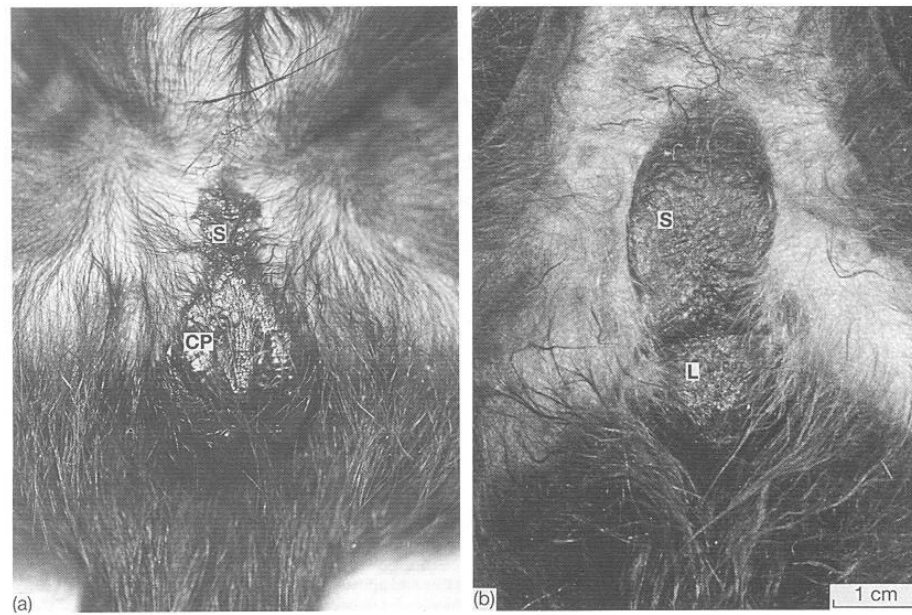
Instead of marking the substrate, the animals may also mark each other, a behaviour known as allomarking (Epple 1974, 1975; Heistermann 1995; Heymann 2001), and is said to be associated to environmental changes and aggressive encounters (Epple 1975). Collective scent marking, in which up to 5 individuals mark sequentially at the same place, has been described in *Saguinus fuscicollis* but not in *Saguinus mystax* (Heymann 2001).

Finally, the scent can be deposited over a previously deposited scent, which is known as *overmarking* or *countermarking* (Smith & Gordon 2002).

However, little is known about the function of these chemical signals, and only recently, some studies of wild populations have finally addressed this issue (Heymann 2006b; Lazaro-Perea et al. 1999; Miller et al. 2003). In his excellent review, (Heymann 2006b) highlights three functional hypotheses for scent marking in New World Primates: 1) territorial function; 2) regulation of social and reproductive dominance; and 3) mate attraction.

Territorial defence is probably the most discussed function of scent marking in mammals (Gosling 1982) as well as in callitrichids (e.g. Bartecki & Heymann 1990; Heymann 2000b; Izawa 1978; Lazaro-Perea et al. 1999; Miller et al. 2003; Rylands 1990; Yoneda 1984). In captivity, tamarins increase their scent-marking behaviour when confronted with strangers (French & Snowdon 1981), and the scent of the stranger elicits the same aggressive response as the stranger itself (Epple 1973). However, a closer look at the spatial

patterns of scent marking in the wild failed to reveal a consistent pattern (Heymann 2000b, 2006b): either there is no difference in the rates of scent marking between exclusive and overlap areas (e.g. Heymann 2000b; Lazaro-Perea et al. 1999; Miller et al. 2003), or the difference is related to range use (Bartecki & Heymann 1990; Rylands 1990). Gosling & Roberts (2001b) claimed that indeed tamarins were marking feeding resources, irrespective of their location in the territory, although this explanation is problematic (see chapter 3). Anyway, according to the existing evidence, a function of olfactory communication in territorial defence seems unlikely (Heymann 2006b).

Figure 3. Branch marked by a *Saguinus fuscicollis*. Notice the rests of urine (Photo Y. Lledo-Ferrer)

According to the second hypothesis, scent marks are a way of maintaining reproductive dominance within the group. As mentioned earlier, just one female per group is able to successfully reproduce. In captivity, it has been shown that dominant females mark more than subordinates (Epple et al. 1993; French & Cleveland 1984), and their olfactory cues contribute to the reproductive suppression[1] of subordinates (*Callithrix jacchus*: Abbott 1984; *Saguinus fuscicollis*: Epple & Katz 1984 ; *Saguinus oedipus*: French et al. 1984 ; Savage et al. 1988). However, such suppression is not so severe in the wild, where several females may present ovarian activity in the same group (Löttker et al. 2004), and multiple pregnancies can occur simultaneously (Smith et al. 2001 and personal observation). Moreover, dominant

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[1] We use the term reproductive suppression because of its wide use in the literature, although we do not mean that the reproduction of subordinates is being controlled by the dominants.

animals do not always mark more. In *Callithrix jacchus* dominant and subordinate females marked at equal rates, except during intergroup encounters, where subordinates marked more (Lazaro-Perea et al. 1999). In *Leontopithecus rosalia*, dominant females marked more than subordinates during intergroup encounters (Miller et al. 2003). Heymann (1998; Heymann 2006b) reports one group where the dominant female marked more, another with no differences, and a third one with the two subordinate females marked more than the dominant. Thus, the relationship between reproductive dominance and scent marking is contradictory.

The influence of the context (e.g. occurrence of intergroup encounters) suggests that, instead, scent marking could serve to exchange reproductive information between groups. Scents could be a way of attracting and competing for mates or, in other words, these could be sexually selected traits. In order for a signal to be sexually selected, it has to meet several criteria (Snowdon 2004):

1) The signal has to be sexually dimorphic, as it is the case in the genus *Saguinus*. Dimorphism is found in the size of the glands, in the scent-marking behaviour, and in responses to scents (Heymann 1998, 2003; Smith & Gordon 2002).

2) There has to be variation within same sex individuals in the signal. We have already discussed the variations between dominant and subordinate females, especially during intergroup encounters. Frequency of scent marking did also vary after the disappearance of the breeding female in the group (Heymann 1998).

3) Conspecific discrimination and preference. Male marmosets are able to distinguish between scents from periovulatory and anovulatory females (Smith & Abbott 1998), and tamarins are capable of discriminating a familiar from an unfamiliar scent as well as the reproductive status of an unfamiliar female (Washabaugh & Snowdon 1998).

4) Expression of preference in the context of reproduction or mating. Scents from ovulatory females are not only preferred, but they also activate brain areas responsible for sexual behaviour, like the anterior hypothalamus and the preoptic areas (Snowdon et al. 2006), and increase testosterone levels in non-reproductive males (Ziegler et al. 2005).

5) Differences in the signal related to reproductive success. This last requisite has not been tested yet, as it is extremely difficult to measure reproductive success in a primate species.

Thus, there is growing evidence and good theoretical reasons to consider that olfactory communication in callitrichids may have been shaped by sexual selection.

The aim of this thesis is to determine the function of olfactory communication in wild saddleback tamarins, *Saguinus fuscicollis*. The study species will be presented in more detail in chapter 2. Each of the following chapters deals with one of the functions proposed in the literature for scent marking. The specific methods used to answer each research question are presented in the corresponding chapter. Although closely related, each chapter can be read and understood independently, since they are presented in form of scientific papers. The only difference with the submitted or published papers lies on the homogenous formatting applied for this Thesis. Chapter 3 and 4 address the contribution of scent marking in the territorial behaviour of the species. Chapter 3 analyses the spatial distribution of scents in the home range, while chapter 4 investigates the role of olfactory communication during intergroup encounters. Chapter 5 investigates sexual dimorphism in the deposition of the scents, but also in the response by other individuals. Chapter 6 evaluates the role of olfactory communication during competition over access to mates during mate guarding. Finally, chapter 7 offers a short discussion on the results of this Thesis, as well as considerations about its limitations and further research perspectives. References have been put together at the end of the Thesis.

Chapter 2.

STUDY SPECIES

Saddleback tamarins, *Saguinus fuscicollis*, are the most widely spread species of its genus (Hershkovitz 1977). Hershkovitz (1977) identified 14 sub-species, although modern classifications recognise 12 of them (Groves 2001; Rylands et al. 2000b), 7 from which are present in Peru (Soini 1990). They occupy almost the whole upper Amazonian basin, from the Ecuadorian and Peruvian Andes in the West, to the Rio Purus in Brazil, and from Rios Manoré-Apurimac in Bolivia to the Rio Caquetá, northern from the Putumayo in Colombia (Rylands et al. 1993). It is the tamarin species that has been most extensively investigated in the wild (Bartecki & Heymann 1990; Goldizen et al. 1996; Soini 1987; Terborgh 1983; Yoneda 1984). The sub-species studied in this Thesis at the Estación Biológica Quebrada Blanco is *Saguinus fuscicollis nigrifons* (I. Geoffroy, 1850), known as "pichico común" in Peru.

Saddlebacks are the smallest of all tamarins, with a body mass of about 350g (Table 1). Although there is no obvious sexual dimorphism, females are slightly larger and heavier than males (Heymann 2003; Soini 1990). They inhabit tropical lowland humid forests, but can also be found in seasonally flooded forests, patches or secondary forests (Snowdon & Soini 1988). It is the only tamarin for which vertical displacement between trunks is common (Garber 1991; Soini 1987; Terborgh 1983).

Saddleback tamarins are mainly frugivorous, but their diet also includes plant exudates and nectar, as well as animal prey like arthropods, amphibians or reptiles (Knogge & Heymann 2003; Nadjafzadeh & Heymann 2008). Due to their small body size, tamarins are in turn subject to a high predation pressure by a variety of animals, like ground mammals (Goldizen 1987b; Moynihan 1970), snakes (Heymann 1987; Shahuano Tello et al. 2002), but mostly raptors (Lledo-Ferrer et al. submitted; Oversluijs Vasquez & Heymann 2001; Terborgh 1983). For this same reason, they are not hunted by humans.

The mean group size is 5.1 individuals (Heymann 2001), although numbers may vary from 2 to 10 (Goldizen 1987b; Goldizen et al. 1996; Soini 1987). The modal mating system is monogamy, but polyandrous and polygynous groups are also common (Heymann 2001). There is a birth peak in the early half of the rainy season, between December and March (Snowdon & Soini 1988).

The group is cohesive throughout its territory (Smith et al. 2005), although the spread can be significant during intergroup encounters (Soini 1990). Saddleback tamarins, like all tamarin species studied so far, defend aggressively their territory against neighbours and strangers (Goldizen 1987b). However, not all intergroup encounters are aggressive, and

extragroup copulations may even take place (*Saguinus mystax*: Garber et al. 1993b; *Saguinus fuscicollis*: personal observation).

The groups are active from short after dawn (between 0515 h and 0600 h), and active for about 10 h a day, after what they retire to a sleeping tree or palm (Heymann 1995). Their main daily path length is about 1800 m (Soini 1990).

At the EBQB study site, saddleback tamarins form mixed-species troops with another callitrichid species, *Saguinus mystax* (Heymann & Buchanan-Smith 2000), with which they spend up to 80% of their time (Heymann 1990). There is a vertical segregation between the two species, with saddleback tamarins being mostly found at 10-15 m height, and moustached being higher in the canopy (Heymann & Buchanan-Smith 2000). Scent marks are deposited at a mean height of 5.8 m, on (in order) horizontal, inclined and vertical substrates, like lianas, branches, and stems (Heymann 2001).

Further information about the biodiversity at the study site can be found at http://www.soziobio.uni-goettingen.de/Peru/Biodiversity.html and in Heymann et al. (2010).

Table 1. Main characteristics of *Saguinus fuscicollis* spp.

Variable		References
Morphological variables		
Body mass	342-362 g	Hershkovitz 1977; Heymann 1997, 2003; Soini 1990
Body size (body and tail)	20.9 + 32.6 cm	Heymann 1997; Soini 1990
Dimorphism index	0.96	Heymann 2003
Reproductive variables		
Mating system	MG>PA>PG[1]	Heymann 2001
Cycle length	18 days	Hrdy & Whitten 1987
Gestation period	149 days (145-152)	Harvey et al. 1987
Newborns body mass	40 g	Harvey et al. 1987
Inter-birth interval	242 days	Harvey et al. 1987
Sexual maturity	23 months	Goldizen 1987b
Socioecological variables		
Mean group size	5.1	Heymann 2001
Individuals per group	3-8	Heymann 2001
Home range size	16-120 ha	Garber 1993
Home range overlap	21-79%	Garber 1993
Population density	13-22 ind.km^{-2}	Heymann 2001
Adult males per group	1.6	Heymann 2001
Adult females per group	1.5	Heymann 2001
Intergroup encounters per day	0.69	Heymann 2001
Olfactory communication		
Anogenital gland (AG)	yes	Epple 1985
Suprapubic gland (SP)	yes	Epple 1985
Sternal gland (ST)	yes	Epple 1985
Dimorphism in AG	females	Epple 1985; Heymann 2003
Diferential function of AG and SP	no	Belcher et al. 1988
Compounds found in scents	16	Smith et al. 1985
Allomarking	yes	Epple 1975, 1986; Heymann 2001
Combination of scent marks	yes	Epple et al. 1993; Heymann 2001
Collective scent marking	yes	Heymann 2001
Use of scent glands	AG>SP>ST	Heymann 2001

[1]MG=monogamy; PA=polyandry; PG=polygyny

Chapter 3.

THE EQUIVOCAL RELATIONSHIP BETWEEN TERRITORIALITY AND SCENT MARKING IN WILD SADDLEBACK TAMARINS, *Saguinus fuscicollis*

ABSTRACT

Scent marking has often been assumed to serve a territorial function in callitrichines, as seen in many other mammals. We studied three free-ranging groups of saddleback tamarins, *Saguinus fuscicollis*, in mixed-species troops with moustached tamarins, *Saguinus mystax*, in the Amazonian rainforest of Peru from May 2007 to June 2008. We recorded and located on GPS scent-marking events and their intensity, overmarking, olfactory inspections, intergroup encounters, and visits to feeding trees. Tree density and diameter at breast height were also recorded. We compared the distribution of scent marks between overlap, exclusive, encounter and tree areas with General Linear Mixed Models, and the distribution of feeding resources. The tamarins used a border marking strategy, marking more on the periphery of their territory, and resources were homogeneously distributed. However, feeding trees in overlap and encounter areas received more scent marking but were still visited by neighbouring groups, and intergroup encounters occurred more often than expected. It rather seems that the tamarins optimise signal transmission by depositing their scents where the probability of detection by neighbours is higher. Thus, saddleback tamarins may use shared areas of the territory to exchange information with neighbouring groups, perhaps gathering information about reproductive vacancies.

INTRODUCTION

Olfactory communication is substantially different from other forms of communication. Scent marks are deposited on the substrate, even in the absence of the potential receiver, and can be detected long after they were deposited, even in the absence of the sender (Gosling & Roberts 2001a). One of the most discussed functions of scent marking in mammals is territorial defence. By scent matching, neighbours and intruders may be able to assess territory owners without incurring the costs of direct confrontations (Gosling 1982; Gosling 1990; Gosling & McKay 1990). However, a territory holder must maximize the probability of its scents being detected by potential intruders, while reducing the costs of their deposition (Gorman & Mills 1984; Roberts & Lowen 1997). In economically defensible territories, animals should mark along the borders (e.g. *Canis latrans*: Gese & Ruff 1997), while in large territories, a hinterland marking strategy is more efficient (e.g. *Suricata suricatta*: Jordan et al. 2007).

Marmosets and tamarins are small-bodied New World Primates that live in the dense canopy of the Amazonian rainforests, and possess a well developed olfactory communication system. Their scent marks convey information about species, sex, reproductive condition and individual identity (Epple et al. 1993). These peaceful cooperative breeders (Caine 1993) are nonetheless intolerant towards neighbours or strangers (French & Snowdon 1981; Goldizen 1987b) and all group members participate in contests against neighbours (Lazaro-Perea 2001; Peres 1992). However, the intensity of the intergroup interaction varies greatly from severe aggression to peaceful (Buchanan-Smith 1991; Lazaro-Perea 2001), and extragroup copulations may happen (Digby 1999).

Although all callitrichid species studied so far possess defensible territories (Heymann 2000b), their home ranges overlap extensively with each other (Garber et al. 1993b). The possible function of scent marking in territorial defence is not clear for callitrichids (reviewed in Heymann 2006). Apart from *Mico intermedius* (Rylands 1990), no other species shows a clear border marking pattern (Heymann 2000b; Lazaro-Perea et al. 1999; Miller et al. 2003). Saddleback tamarins, *Saguinus fuscicollis*, marked the periphery of their home range more than the core area, but overall, rates of scent marking were related to patterns of range use (1990). The same was observed in moustached tamarins, *Saguinus mystax*, where expected and observed rates of scent marking in peripheral and core areas did not differ (Heymann 2000b). The latter study concluded that scent marks do not fulfil a territorial function in this species. This conclusion was challenged by Gosling & Roberts (2001b), who argued that the spatial pattern of scent marking should be determined by the distribution of resources in the territory. Indeed, marmosets usually mark gouging holes where they feed on exudates (e.g. Lacher et al. 1981; Lazaro-Perea et al. 1999), although a territorial function is unlikely (Rylands 1985). On the other hand, intergroup encounters in mixed species troops of tamarins take place in the vicinity of major feeding trees, so a resource defence function has been suggested (Garber 1988). Feeding trees can also serve as landmarks for the deposition of the signal (Macdonald 1985).

Therefore, in this study we re-examined the territorial function of scent marking in a tamarin species, taking the criticism by Gosling and Roberts (2001b) into account. Our study is based on the following predictions: (1) Since saddleback tamarins have defensible home ranges, scent marking should be concentrated in peripheral areas (border-marking strategy). (2) If scent marking serves a territorial function in the sense of defence of specific resources, a boundary marking strategy should be found if resources are homogeneously distributed. If resources are heterogeneous, scent marking should be associated to the resource and depend

on their size or importance. (3) If scent marking is a way of reducing the costs of territorial contests by allowing scent matching, intergroup encounters should happen by chance.

METHODS

Study Site & Study Groups

This study was conducted at the Estación Biológica Quebrada Blanco (EBQB) in the Amazonian lowland rainforest of north-eastern Peru (see Heymann 1995 for details of the study site). From May 2007 to June 2008 we followed three well-habituated groups of *Saguinus fuscicollis* (see Table 1 for group composition and mating system) forming mixed-species troops with *Saguinus mystax*. Each saddleback group was observed about six consecutive days per month, from exiting a sleeping site (between 0515 h and 0600 h) to retiring to a sleeping site (between 1530 h and 1635 h). All animals were individually recognizable through natural marks (e.g., genital pigmentation, shape of the tail, etc.). Additionally, eight neighbouring, less habituated groups were also followed for a period ranging between 10 and 30 days from February to September 2008.

Table 1. Composition and mating system of the study groups (MG=monogamous; PA=polyandrous; PG=polygynous; PGA=polygynandrous)

	Group 1	Group 2	Group 3
Male, adult	2	4	1
Female, adult	2-1[a]	2	2
Infant	-	-	0-1[b]-2[c]
Total	4-3	6	3-4-5
Observation time (hours)	550,4	306,4	505,8
Mating system	PGA-PA[a]	MG	PG

[a] One female disappeared between the 21st December 2007 and the 5th January 2008, while the group was not being observed. The group changed the mating system accordingly
[b] One infant born between the 20th November and the 1st December 2007, and disappeared between the 8th December 2007 and the 21st January 2008
[c] Two infant born between the 7th and the 10th March 2008

Data Collection

We recorded scent marking and olfactory behaviour (Table 2) with the behaviour sampling method (Martin & Bateson 1993). We noted the identity of the individual that scent marked, and if the scent received any kind of response from other group members. Responses to scent marks were usually recorded in the 5 minutes following deposition, since afterwards

the group had definitively abandoned the area and thus the scent could not receive any further response from other group members (see Heymann 1998 for a similar approach).

Table 2. Behavioural coding

Behaviour	Description
Scent-marking act	Marking with the anogenital (AG), suprapubic (SP) or sternal gland (ST)
Scent-marking event	Combination of scent-marking acts (Bartecki & Heymann 1990)
Overmarking	Marking over a previous mark from another individual
Scent inspection	Sniffing, muzzle-rubbing or licking a scent from other individual
Olfactory inspection	Sniffing, muzzle-rubbing or licking the substrate

Each scent-marking event was geo-referenced on a Garmin etrex GPS, with precision ranging from 10 to 20m. The location of the group was automatically recorded with the "TrackLog" option on the GPS.

Each feeding tree visited by the study groups was permanently marked with a numbered aluminium tag, geo-referenced, and its diameter at breast height (DBH) measured.

Whenever the focal group established visual contact with a neighbouring group, an intergroup encounter was said to begin. Encounters with isolated, wandering animals were not considered. We located the encounter on GPS, and classified the encounter as aggressive if chases and vigorous vocalizations took place. If the groups stayed in proximity without exchanging behaviours apart from few vocalizations, the encounter was considered as calm. We also recorded extra-group copulations and feeding behaviour during encounters.

Data Analysis

We analysed some derived measures from the direct observations: we calculated the density of scent-marking events (SME/Ha), the intensity of scent-marking (Heymann 2001), defined as the number of scent-marking acts per event (SMA/SME), and the number of olfactory inspections per hectare (OI/Ha). Overmarking (OM) and scent inspections (SI) were expressed as the proportion of scent-marking acts overmarked or inspected. We calculated feeding tree density (#trees/Ha); and as measures for the importance of the feeding resources, we calculated DBH density (sum of DBH of feeding trees/Ha), mean DBH per tree (sum of DBH of feeding trees/# feeding trees) and visits per tree (sum of visits to feeding trees/# feeding trees).

We defined home ranges using the Minimum Convex Polygon (MCP) approach on ArcView GIS 3.3, and identified the overlapping areas, defined as portions of the home range

used by more than one group. Overlap areas might be underestimated, since the neighbouring, less habituated groups may not have used their whole home range while being followed.

A 50 m-radius area was defined around each intergroup encounter, wherever two groups established visual contact. Another 15m-radius area around each feeding tree visited was also established.

We compared the density of scent-marking events, intensity of scent marking, proportion of scent-marking acts inspected and overmarked, and olfactory investigations between exclusive and overlap areas, encounter and overlap areas where no encounter took place, feeding trees in exclusive and overlap areas, feeding trees in encounter and overlap areas, and feeding trees in overlap areas against overlap areas excluding feeding trees. Data that did not meet the requirements of normality were square-root or log transformed. We used General Linear Mixed Models (GLMM), with individual identity nested within group as a random factor; sex, group and area as fixed factors, and Bonferroni adjustment for multiple comparisons. As one female disappeared from group 1 between December and January, data from this group after January 2008 were analysed separately.

The behaviour sampling method can bias the data towards more visible animals (Martin & Bateson 1993). In order to correct this bias, we conducted scan samples every 15 min, where the activity of each visible individual was recorded within 2 min. Since there were differences in visibility (expected vs. observed representation of individuals in scan samples) between individuals in Group 1 ($\chi^2{}_3 = 9.61$, $P < 0.03$) and in Group 2 ($\chi^2{}_5 = 20.87$, $P < 0.001$), individual scent-marking frequencies were corrected by dividing them by the proportion of scans where the respective individual was visible.

The distribution of food resources was compared between exclusive and overlap areas, as well as between encounter and overlap areas where no encounter had taken place, and analysed with a repeated measures ANOVA.

We calculated the probability of intergroup encounters with the Waser Gas Model (Waser & Wiley 1979). This model assumes that both groups move independently of each other, and that they can meet at any place in space, which is not the case for tamarins that have fixed territories and can only meet at overlap areas. Therefore we used the formula modified by Barret and Lowen (1998):

$$f = x \frac{4\rho v}{\pi} (s + d)$$

where

x = probability of finding the main study group in the overlap area (when resources are shared, $x = (o/2)/e + (o/2)$; o = proportion of overlap area and e = proportion of exclusive area)

ρ = density of other groups

v = group mean velocity

s = mean group spread

d = approach distance between groups

All tests were two-tailed and carried out on SPSS 16.0.

RESULTS

Home Ranges

The study groups differed in home-range size and in the proportion of home-range overlap (Table 3, Fig. 1). Group 1 had the smallest home range and shared 50% of it with neighbours, while Group 2 had the largest home range but only shared 21%.

Table 3. Home-range characteristics of the study groups

Group	Size (Ha)	Perimeter (m)	Overlap (Ha)	Overlap (%)
1	42.2	2397	21.3	50.4
2	80.6	3381	17	21.1
3	50.1	2590	17.4	34.6

Figure 1. Home ranges of the study groups and overlap areas
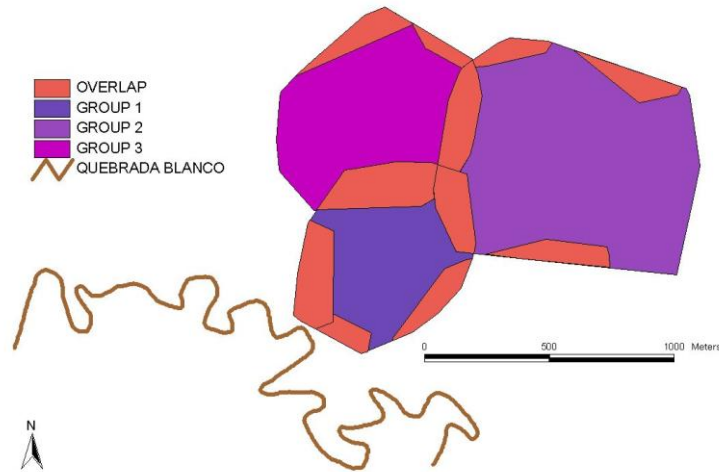
Distribution of Scent Marks

We found an increase in SME in overlap areas compared to the exclusively used ones (Fig. 2, see Table 4 for summary of results). Moreover, there was a significant interaction between sex and area (GLMM: $F_{1,8} = 16.48$, $P = 0.04$), where females marked more than males in exclusive areas, while males marked more in overlap areas. Following Heymann's (2000b) methodology, we found that the tamarins marked more in overlap areas than expected by the intensity of use (G1 2007: $G_1 = 56.29$, $P < 0.001$; G1 2008: $G_1 = 18.54$, $P < 0.001$; G2: $G_1 = 8.7$, $P < 0.004$; G3: $G_1 = 37.89$, $P < 0.001$).

Figure 2. Distribution of scent-marking events (Group 1)

27
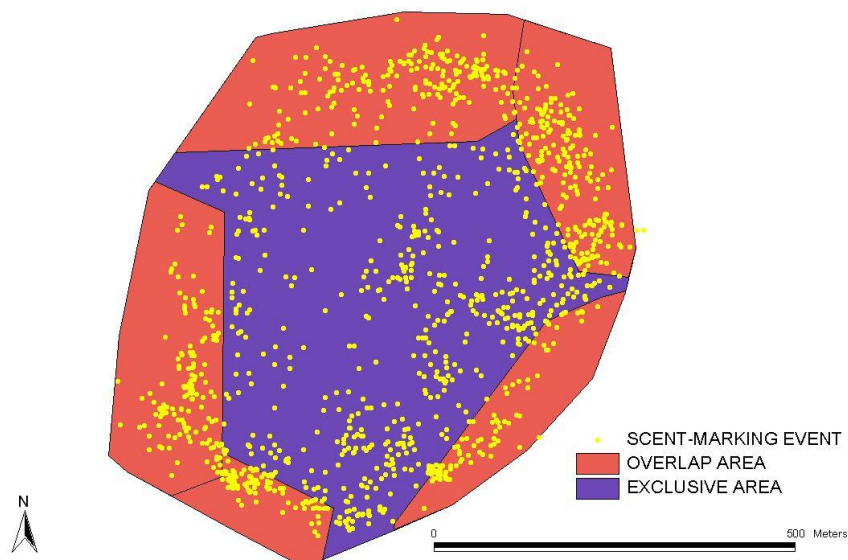
Table 4. Summary of results (GLMMs)

Comparison	SME	Intensity	Overmarking	Olfactory inspection
Exclusive vs. Overlap	**Overlap > Exclusive** $F_{1,8} = 53.98$, $P < 0.001$	**Overlap > Exclusive** $F_{1,8} = 102.95$, $P < 0.001$	Overlap = Exclusive $F_{1,15} = 1.4$, $P = 0.26$	**Overlap > Exclusive** $F_{1,8} = 24.16$, $P = 0.01$
Encounter vs. Overlap	**Encounter > Overlap** $F_{1,13.14} = 360.57$, $P < 0.001$	Encounter = Overlap $F_{1,15.66} = 1.6$, $P = 0.22$	Encounter = Overlap $F_{1,15.32} = 0.06$, $P = 0.81$	**Encounter > Overlap** $F_{1,15.39} = 8.69$, $P = 0.01$
Tree exclusive vs. Tree overlap	**Overlap > Exclusive** $F_{1,8} = 69.76$, $P < 0.001$	**Overlap > Exclusive** $F_{1,8} = 131.84$, $P < 0.001$	**Overlap ≥ Exclusive** $F_{1,15} = 3.88$, $P = 0.068$	**Overlap > Exclusive** $F_{1,8} = 26.05$, $P = 0.001$
Tree encounter vs. tree overlap	**Encounter > Overlap** $F_{1,8} = 179.02$, $P < 0.001$	Encounter = Overlap $F_{1,8} = 2.39$, $P = 0.16$	Encounter = Overlap $F_{1,15} = 1.04$, $P = 0.32$	**Encounter > Overlap** $F_{1,8} = 78.31$, $P < 0.001$
Tree overlap vs. overlap excluding trees	**Tree > Overlap** $F_{1,11.53} = 218.31$, $P < 0.001$	**Tree ≥ Overlap** $F_{1,17.19} = 3.16$, $P = 0.09$	Tree = Overlap $F_{1,14.54} = 1.94$, $P = 0.18$	**Tree > Overlap** $F_{1,10.97} = 48.65$, $P < 0.001$

The intensity of scent marking was higher in overlap areas compared to exclusive. There was also a significant interaction between sex and area (GLMM: $F_{1,11} = 16.04$, $P = 0.002$), with males marking more intensely in exclusive areas, whereas females mark more intensely in overlap areas.

Tamarins overmarked the same proportion of scents in exclusive and overlap areas, but inspected the substrate more often per hectare in overlap areas than in exclusive areas.

There were more scent-marking events in the area of intergroup encounters compared with overlap areas were no encounter took place, but intensity did not vary. The tamarins overmarked the same proportion of scents in encounter and overlap areas. However, the animals inspected the substrate more in encounter areas than in overlap areas.

Scent Marking and Feeding Trees

Trees in overlap areas received more SME than in exclusive areas and the animals scent-marked more intensely. The tamarins inspected the substrate close to trees in overlap areas more than in exclusive areas. We found a trend for higher proportion of overmarking in trees in overlap areas compared to trees in exclusive areas.

Trees in the encounter area received more SME than in the overlap area, but the intensity of scent-marking did not change. The tamarins performed more olfactory investigations in trees in the encounter area. There was no difference in the proportion of scent marks that were overmarked.

Trees in overlap areas received also more SME than overlap areas with no feeding trees in proximity, and there was a trend for higher intensity. The tamarins also inspected the substrate more often near feeding trees than in the rest of the overlap area, but there were no differences in the proportion of scents overmarked (results are summarized in Table 4).

Distribution of Resources in the Territory

There were no differences in tree density (ANOVA: $F_{1,4} = 1.23$, $P = 0.33$), DBH density (ANOVA: $F_{1,4} = 1.56$, $P = 0.28$), DBH per tree (ANOVA: $F_{1,4} = 0.31$, $P = 0.61$) or visits per tree (ANOVA: $F_{1,4} = 0.04$, $P = 0.85$) between exclusive and overlap areas. Moreover, there were neither differences between overlap and encounter areas in tree density (ANOVA: $F_{1,4} = 0.004$, $P = 0.95$), DBH density (ANOVA: $F_{1,4} = 0.016$, $P = 0.77$), DBH per tree (ANOVA: $F_{1,4} = 4.02$, $P = 0.12$) or visits per tree (ANOVA: $F_{1,4} = 0.35$, $P = 0.59$).

Intergroup encounters

We observed a total of 53 intergroup encounters. According to Waser's Gas Model, the probability of groups meeting each other was higher than expected if they had moved independently (Fig. 3; parameters given in Supplementary material). 41% of these were classified as calm and 59% as aggressive. Independently of the classification of the encounter, we saw males herding females from their own group right before or during the encounter in 65% of them. Three extra-pairs copulations were observed and three genital inspections that did not lead to copulation. Finally, on 7 occasions we saw animals feeding without interruption by the other group, during both calm and aggressive intergroup encounters.

Figure 3. Observed vs. expected frequency of intergroup encounters based on Waser's Gas Model
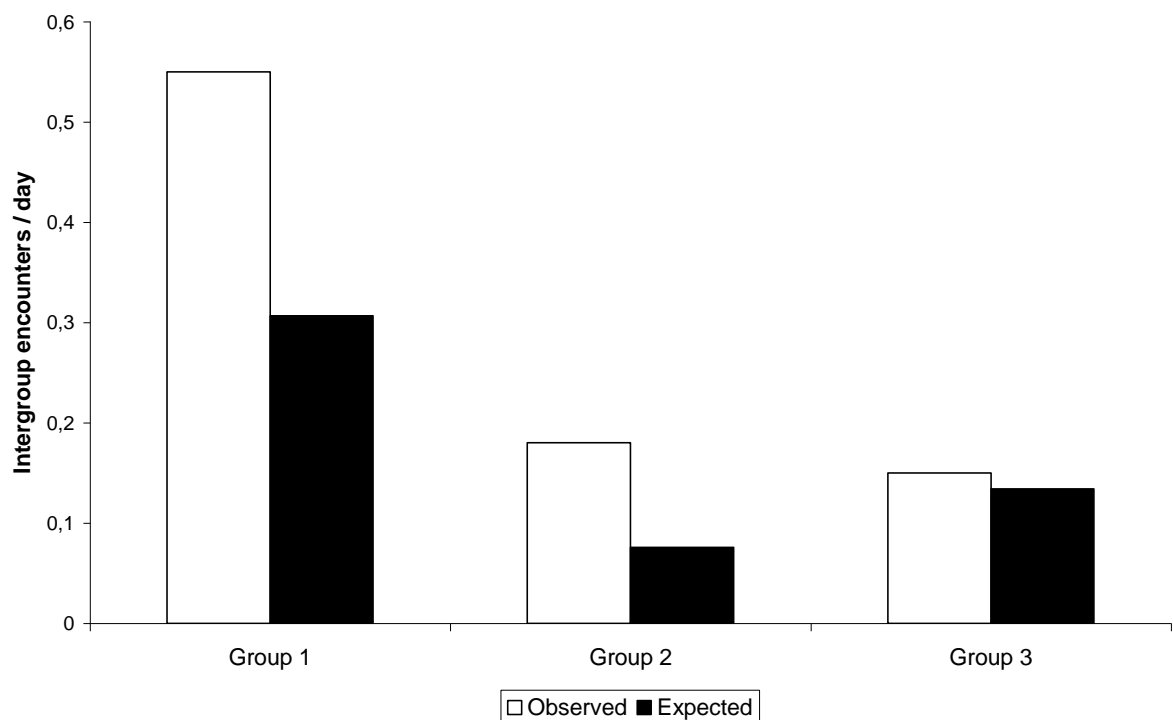
DISCUSSION

We have found a clear border marking strategy, which is consistent with an economically defensible home range. The tamarins deposited more scent marks and marked with higher intensity in overlap areas, and this marking pattern could not be explained by a higher intensity of use of these areas. These results are in line with Bartecki & Heymann (1990), whose saddleback tamarins marked more on the periphery at the same study site.

However, our results contrast sharply with those of Heymann (2000b), who did not find a definite spatial pattern of scent marking in sympatric moustached tamarins, although they

invest more in boundary contests than saddlebacks (Peres 1992). This different pattern of scent marking cannot be accounted for by feeding ecology, as both species share between 75 and 90% of their vegetable diet (Knogge & Heymann 2003), and both studies were conducted at the same study site. Moreover, the limiting factor for tamarins is not the vegetable diet but the animal prey (Smith 2000). Indeed, animal prey is defended by depletion, and capture success in saddleback tamarins is significantly lower at the periphery of their home range (Peres 1992).

In our study, overlap areas received more scent-marking events than exclusive areas and the areas around intergroup encounters more than other shared areas where no encounter had taken place. However, as Gosling & Roberts (2001b, F7) put it: "it is difficult to ascribe a function to a signal without some direct indication of the benefits that accrue to the signaller". One possible benefit may be related to the exclusion of intruders. However, the large overlap between territories shows that scent marks are not effective in maintaining spatial exclusivity and preventing intrusions.

Another possible benefit might be related to the defence of especially valuable resources. Feeding trees in overlap areas received more scent-marking events and a higher scent-marking intensity than those in exclusive areas. When comparing the distribution of scents within the overlap area, we found that feeding trees received more scent-marking events, and a slightly higher intensity of scent-marking than the rest of the overlap area. Feeding trees in the encounter areas also received more scent-marking events, compared to feeding trees on other overlap areas where no encounter had taken place. This enhanced marking in food resources has also been reported in *Callithrix jacchus* (Lazaro-Perea et al. 1999), *C. penicillata* (Lacher et al. 1981), *Mico intermedius* (Rylands 1985), and *Leontopithecus rosalia* (Miller et al. 2003).

At first sight, this could be interpreted as an evidence for a resource defence strategy, since major feeding trees were located close to intergroup encounters according to Garber (1988). However, we found resources to be homogeneously distributed, so a boundary marking strategy would be more appropriate, with no need for a direct marking close to the resource. Anyway, this strategy does not seem to be effective, since we have observed different groups feeding on the same trees on different days, or during intergroup encounters. Moreover, overmarking other group members seems counterproductive, as it reduces the probability of the mark being detected compared to two separate marks.

One of the proposed functions of overmarking is signalling competitive ability of territory owners (Ferkin & Pierce 2007; Gosling & Roberts 2001a). By scent matching, the

intruder may be able to assess the competitive ability of the territory owner and decide whether to further intrude or not. This does not seem to be the primary function in saddleback tamarins. The perception of these overmarks does not restrain intruders from feeding, since animals do it even during intergroup encounters, without interference from the other group. Moreover, as intergroup encounters happened more often than expected by chance, the groups are certainly not avoiding confrontations. Thus, the tamarins may rather de using the information contained in the neighbours' scents in order to seek for them.

Chemical communication has been said to play an important role in the territorial agonistic behaviour of many mammals, from mice (Hurst & Beynon 2004) to antelopes (Gosling & Roberts 2001a) and to the conspicuous "stink fights" of ringtailed lemurs (Jolly 1966). Captive tamarins increase their scent-marking rates when confronted with intruders (Epple 1980; Epple & Alveario 1985; French & Snowdon 1981). In the wild, however, neighbours are not complete strangers but rather "dear enemies" (Temeles 1994), and 45% of the encounters are not aggressive. Moreover, we have found that rates of scent marking during intergroup encounters in saddleback tamarins did not differ compared to the marking rate at the same area when no neighbours were present (see chapter 4). It thus seems that the role of chemical communication in territorial defence in tamarins has been overestimated.

Most studies on territoriality have only considered deposition of the signal, neglecting its reception (although see Gosling et al. 1996a; Gosling et al. 1996b; Palagi & Norscia 2009), which gives an incomplete picture of the communication process (Kappeler 1998). Tamarins performed more olfactory inspections in overlap areas and close to feeding trees in these areas. These results are the logical counterpart of the increased scent density reported. If the neighbouring groups are also extensive and intensively marking these areas, the focal group could be trying to get as much information as possible by inspecting the substrate where other groups may have deposited a large amount of scents as well.

Our results suggest that rather than defending territories or resources, the tamarins are optimising signal transmission by marking where the probability of perception by other groups is higher, an economic strategy also described in antelopes (Brashares & Arcese 1999) and in ringtailed lemurs (Palagi & Norscia 2009). In contrast to terrestrial mammals, in the dense, humid, three-dimensional environment of callitrichid monkeys, the probability of detecting a scent from other group may be extremely low, and the signal may vanish quickly (Epple et al. 1980). The latter might be overridden by an enhanced intensity of scent-marking as seen in our study, while marking where the probability of finding an audience is higher may partially override the former .

Thus, feeding trees in overlap areas may be a bulletin board, where animals from different groups exchange information. A similar function was suggested for the gouging holes of common marmosets, but only in intragroup communication (Lazaro-Perea et al. 1997; Rylands 1985). The spatial pattern revealed by our study suggests, instead, that it serves for intergroup communication. Indeed, feeding trees in overlap areas may be visited by different groups within the same day, just as gouging holes in marmosets (Lacher et al. 1981). We observed several times the animals marking fruits from *Wettinia augusta* trees, without consuming them, which would have obliterated the message. However, they fed on those trees on previous and posterior days.

If overlap areas enable chemical information exchange between groups, it may be asked which kind of information is to be transmitted. The fact that the scent-marking pattern varies between males and females suggests that this information might be related to mating competition. Males deposited more scents in overlap areas than females, while females marked more intensely. In another study, we have found that scent-marking frequency correlates with copulations in males, while intensity of scent marking correlates with copulation in females (see chapter 5). It thus seems that both males and females perform scent marking in overlap areas in such a way that key features for mate choice might be detected by extra-group individuals. Indeed, extragroup copulations are quite common, which might explain the herding behaviour observed. Moreover, males overmark females and vice-versa (see chapter 5), which suggests that overmarking may be a way of concealment of chemical information like in antelopes (Brashares & Arcese 1999; Roberts & Dunbar 2000) rather than ensuring predominance for scent matching.

Reproductive constraints are extremely heavy on callitrichids. Not only do most males delay breeding in their groups (Goldizen & Terborgh 1989), but less than half of the females reach a reproductive position, as the number of adult females is higher than the number of reproductive positions (Goldizen et al. 1996). Thus, scent matching may not be a way to reduce the probability of a territorial contest, but to allow the animals to determine which neighbouring groups to meet and with what frequency in order to explore reproductive vacancies or to achieve extragroup copulations ("fight to learn", see Getty 1989). Even if further research (and bigger sample size) is needed to determine how group size, sex ratio and mating system influence scent-marking behaviour, our results are not likely to represent group idiosyncrasies. First, our results are in line with Bartecki and Heymann's (1990), whose saddleback tamarins marked more on the periphery at the same study site. Second, our study groups represented all possible mating systems (Table 1).

If scent marks are intended to exchange reproductive information between groups, the differences in the patterns of olfactory communication between *S. fuscicollis* and *S. mystax* may reflect subtle yet important differences in the mating system of the species (Heymann 2001). Huck et al. (2005) found a high within group relatedness in moustached tamarins at the EBQB study site, but mating partners were not closely related and one extragroup paternity was detected. Moreover, partners usually did not share the same haplotype (Huck et al. 2007), which suggests that there is regular outbreeding. We hypothesize that relatedness among saddleback tamarins may be higher than among moustached tamarins, which would put a higher premium on the former to look for reproductive vacancies in neighbouring groups.

ACKNOWLEDGEMENTS

Appendix 1. Parameters used for calculation of Waser's Gas Model

Parameters	Group 1	Group 2	Group 3
ρ (groups.km^{-2})	1.78	1.91	1.8
v (m.h^{-1})*	355.83	292.38	280.72
s (m)**	8.35	8.35	8.35
d (m)	50	50	50
x	0.76	0.24	0.44

* in the formula, v was multiplied by the mean observation time per day and group
** calculated from Smith et al. (2005)

Chapter 4.

CHEMICAL COMMUNICATION AND INTERGROUP INTERACTIONS IN WILD SADDLEBACK TAMARINS

ABSTRACT

Chemical communication plays an important role in intergroup encounters in many mammals, including primates. Captive studies in callitrichids also point to a relationship between scent marking and encounters with intruders. We studied three wild groups of saddleback tamarins, *Saguinus fuscicollis*, in the Amazonian rainforest of Peru for 13 months. During a total of 45 intergroup encounters, we recorded scent-marking events, scent-marking intensity, use of each scent gland, responses to scents, and olfactory inspections of substrate. We took two control periods: 24h after the encounter and when the group was using the same area, but no encounter was taking place. Data were analysed with General Linear Mixed Models. We found that the increase in scent-marking frequency was related to the use of an overlap area and not to the presence of the other group. Scents received even less inspections during encounters, and almost never from the other group; and there were no differences in scent-marking intensity or overmarking. These results suggest that, in contrast with captive settings, olfactory communication does not seem to play an important role in intergroup encounters in wild saddleback tamarins. Indeed, wild animals may be dear enemies with a long history of interactions, while captive animals were presented to complete strangers.

INTRODUCTION

Wild primate groups are rarely isolated from each other and interaction between groups is a common feature. Although usually agonistic, there is considerable variation both between and within species (Cheney 1987).

Chemical signals have been shown to play an important role in maintaining territorial integrity and spacing (Gosling 1982). Scent marks may convey information about competitive ability (Hurst & Beynon 2004), and thus scent matching should allow intruders to assess residents without direct confrontation, and to avoid the costs of escalating conflicts (Gosling & Roberts 2001a). In many species, scent marking is a conspicuous part of the aggressive display. Popartz (1968) found that aggression in swiss albino mice was mediated by olfactory cues, since a reduction of aggression occurred when the natural odours were masked by scent, and anosmic mice did not display any kind of aggressive behaviour. Male rabbits (*Oryctolagus cuniculus*) and male house mice (*Mus domesticus*) whose scents are present in

an experimental arena are more likely to win fights (Gosling & McKay 1990; Mykytowycz et al. 1976).

Scent marking is also part of the aggressive display in the ringtailed lemur, *Lemur catta* (Gaspari & Crockett 1984). When groups meet, two males may anoint their own tails with their own scents, face each other and wave their tales at one another, which has received the illustrative name of "stink fights" (Jolly 1966).

Olfactory communication is an important feature of the social life of marmosets and tamarins. They posses a well-developed olfactory communication system, with specialised glands in the anogenital, suprapubic and sternal region (Epple et al. 1993) and a functional vomeronasal organ (Evans 2003). They can perceive information about species, sub-species, sex, and individual identity in the sender's scent marks (Epple et al. 1993), and females also inform about their reproductive condition through their scents (Washabaugh & Snowdon 1998; Ziegler et al. 1993).

Scent-marking has been said to play a role in territorial behaviour in callitrichids (Walraven & van Elsacker 1992, but see Heymann 2006b). In captivity, scent marking is enhanced when animals hear long-call vocalizations from other groups (*Saguinus oedipus*: Snowdon et al. 1983; McConnell & Snowdon 1986; *Leontopithecus rosalia*: Mack & Kleiman 1978; Walraven et al. 1992).

During aggressive encounters, saddleback tamarins, *Saguinus fuscicollis*, scratch their chest and suprapubic area, which might stimulate the secretions from the sternal and suprapubic gland, and pervade the animal's fur (Epple 1975), scent-marking frequency is also increased (Epple 1980), and the scent of the stranger elicits the same aggressive response as the stranger itself (Epple 1973). Adult female intruders in *Leontopithecus rosalia* receive more olfactory investigations from the residents than other individuals. Female cottontop tamarins, *Saguinus oedipus*, increased their anogenital and suprapubic marking frequencies when confronted with strangers (French & Snowdon 1981; Harrison & Tardif 1989).

It has been argued that anogenital marking is used in sociosexual context, while suprapubic marking is performed in situations of aggressive arousal (French & Snowdon 1981). However, no functional distinction has been found between the different glands in saddleback tamarins (Belcher et al. 1988). The increase in scent-marking frequency is maintained even after the intruder is removed, at least for *Callithrix jacchus* (Epple 1970). Epple (1975) interpreted this enhanced scent marking by residents as a "triumph ceremony". However, little is known about the aggressive function of scent marking in the wild. Rylands (1990) reported that scent marking in *Mico intermedius* was more frequent during intergroup

encounters than any other context, a result replicated in common marmosets (Lazaro-Perea et al. 1999). On the other hand, Bartecki & Heymann (1990) did not find any increase in scent-marking frequency when comparing days with and without encounters, or intergroup encounters with the rest of the day. However, these results are based on a relatively small amount of observations.

By definition, an intergroup encounter can only take place in areas of overlap between the home ranges of different groups, and these areas receive more scent marking than core areas of the home range (see chapter 3). Therefore, it is important to determine if increases in scent-marking frequencies are related to the presence of the neighbour group, or just to the use of an overlap area.

If intergroup encounters allow the exchange of chemical information between groups, then scent-marking frequency should be enhanced in this context. Moreover, scents should also receive more responses in this case.

METHODS

Study Site & Study Groups

This study was conducted at the Estación Biológica Quebrada Blanco (EBQB) in the primeval Amazonian lowland forest in north-eastern Peru (see Heymann 1995 for details of the study site), from May 2007 to June 2008. We followed three well-habituated groups of *Saguinus fuscicollis* (see Table 1 for group composition) forming mixed-species troops with *Saguinus mystax*. As one female disappeared from Group 1 between December and January, we considered this group as a distinct social unit from January 2008 and thus their data were analysed separately.

Table 1. Composition of the study groups

	Group 1	Group 2	Group 3
Male, adult	2	4	1
Female, adult	2-1[a]	2	2
Infant	-	-	0-1[b]-2[c]
Total	4-3	6	3-4-5
Observation time (hours)	550,4	306,4	505,8

[a] One female disappeared between the 21st December 2007 and the 5th January 2008, while the group was not being observed
[b] One infant born between the 20th November and the 1st December 2007, and disappeared between the 8th December 2007 and the 21st January 2008, while the group was not being observed
[c] Two infant born between the 7th and the 10th March 2008

Each group was followed about six consecutive days per month, from exiting a sleeping site (between 0515 h and 0600 h) to retiring to a sleeping site (between 1530 h and 1635 h). All animals were individually recognizable through natural marks (e.g., genital pigmentation, shape of the tail, etc.).

Data Collection

An encounter was said to begin when two groups were in visual contact. However, the behaviour of the group is likely to be influenced by the proximity of other groups before and after the encounter itself. Therefore, we included the data from two buffer intervals. The first interval begins when the presence of a neighbouring group was noticed by the human observers, or since the monkeys started emitting series of long-calls, which are usually a prelude to an encounter (Garber et al. 1993b; Lazaro-Perea 2001; Terborgh 1983). The second interval includes all data until the group stops emitting long-calls (Miller et al. 2003), rests or abandons the area.

We observed a total of 53 intergroup encounters. Encounters with solitary animals were discarded, since these interactions were extremely brief and aggressive, with the intruder fleeing immediately. Successive encounters that were separated by less than 30 min. were considered as a single encounter in the analysis (Lazaro-Perea 2001).

We recorded scent-marking behaviour and responses to scents (Table 2) with the behaviour sampling method. We noted the identity of the individual that scent marked, and if the scent received any kind of response from other individuals, belonging to the same group or not. Responses were recorded within 5 min. after deposition (Heymann 1998).

Table 2. Behavioural coding

Behaviour	Description
Scent-marking act	Marking with the anogenital, suprapubic or sternal gland
Scent-marking event	Combination of scent-marking acts (Bartecki & Heymann 1990)
Overmarking	Marking over a previous mark from another individual
Scent inspection	Sniffing, muzzle-rubbing or licking a scent from other individual
Olfactory inspection	Sniffing, muzzle-rubbing or licking the substrate

The behaviour sampling method can bias the data towards more visible animals (Martin & Bateson 1993). In order to correct this bias, we conducted scan samples every 15 min, where the activity of each identified individual was recorded within 2 min. Since there were differences in visibility (observed vs. expected representation in scan samples) between individuals in Group 1 ($G_3 = 9.93$, $P < 0.02$) and Group 2 ($G_5 = 18.5$, $P < 0.01$), individual

frequencies were corrected by dividing them by the proportion of scans where the animal was visible during intergroup encounters, or when no encounter was taking place.

Data analysis

Since scent marking is strongly influenced by the time of the day (Bartecki & Heymann 1990), we controlled this variable by recording the behaviour of the group 24 hours after the encounter. In cases where these data were not available (e.g., another encounter was taking place), we considered the 24 hours previous to the encounter.

Scent marking is also influenced by the area of the home range used (see chapter 3). Therefore, we recorded the behaviour of the group in the same area and at the same time of the day, but when no encounter was taking place, within the same time window as the encounter.

We calculated individual frequencies by dividing the observed frequencies by the observation time for each phase (encounter, next day, and same area). Overmarking and scent inspections were expressed as proportion of scent-marking acts overmarked or inspected. We also calculated the proportion of scent-marking acts deposited with each epidermic gland.

Data were modelled using General Linear Mixed Models, with individual identity nested within group as random factor, and sex, group and phase as fixed factors. Multiple comparisons were conducted with the Bonferroni adjustment. Data that were not normally distributed were log transformed.

All tests were carried out on SPSS 16.0.

RESULTS

Frequency and duration of encounters

Group 1 had 35 encounters (0.55 encounters per day), Group 2 had 7 (0.18 per day), and Group 3 was involved in 9 (0.15 per day). The mean duration of encounters was 14 min ($\pm$ 17), with a minimum duration of 1 minute and a maximum of 86.

Scent-marking frequency and intensity

Phase had a significant effect on the frequency of scent-marking events (GLMM, $F_{2, 28}$ = 6.14, $P = 0.006$; Fig. 1). Post-hoc comparisons revealed that scent-marking frequency was higher during encounters than the next day ($P = 0.007$), but did not differ from the same area (p=1). Females tended to mark more than males in all phases ($F_{1,14} = 3.2$, $P < 0.10$).

The use of the different scent glands did not differ between phases (proportion of AG: GLMM, $F_{2,24} = 0.21$, $P = 0.11$).

The intensity of scent marking was independent of phase (GLMM, $F_{2,28} = 0.03$, $P = 0.97$) and sex (GLMM, $F_{1,14} = 0.00$, $P = 0.99$).

**Figure 1.** Scent marking frequency (** indicates $P < 0.01$)
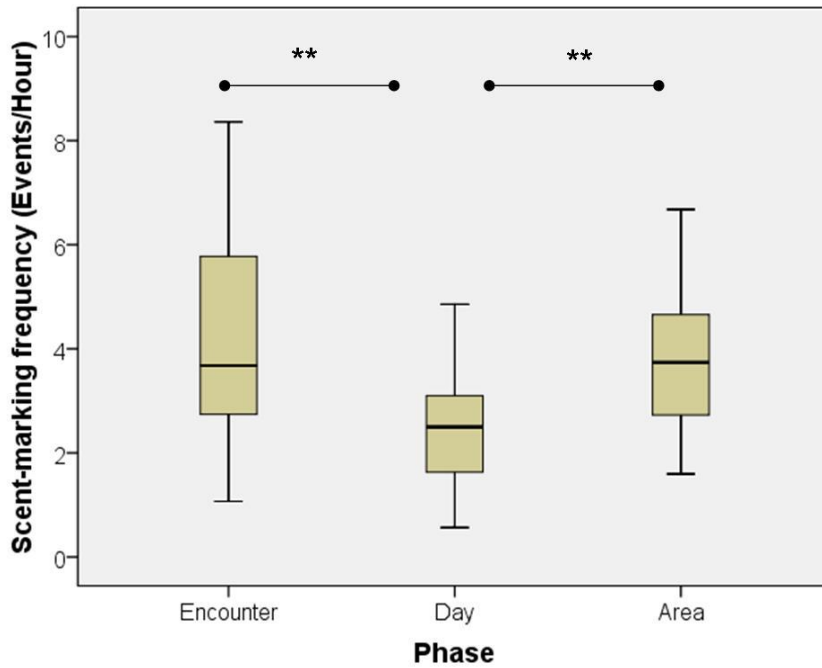
Responses to scent marks

Phase had a significant effect in the proportion of scents inspected by group mates (GLMM, $F_{2,30} = 3.6$, $P = 0.04$). Post-hoc comparisons revealed that a lower proportion of scents were investigated during intergroup encounters, compared to the same area (Bonferroni $P = 0.59$; Fig. 2). There was no difference in the proportion of scent-marking acts that were overmarked by group mates (GLMM, $F_{2,22} = 0.01$, $P = 0.99$).

We only observed four times a scent receiving a response from a member of the neighbouring group during an intergroup encounter.

Figure 2. Scent inspections
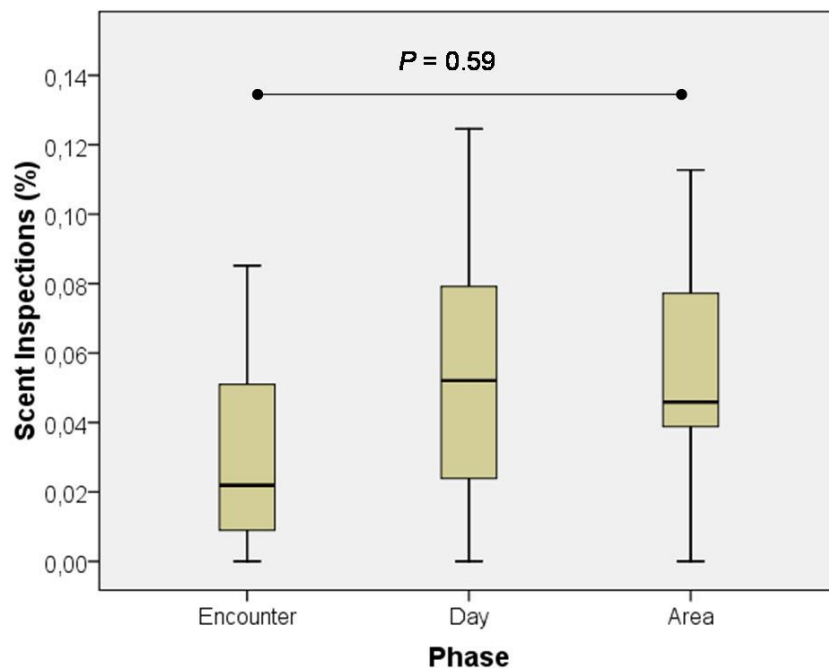
Olfactory inspections of substrate

Phase had a significant effect in the frequency of olfactory inspections (GLMM, $F_{2,28} = 6.96$, $P = 0.004$). It was significantly higher during intergroup encounters compared to the next day (Bonferroni $P = 0.005$; Fig. 3), but not compared with the use of the same area (Bonferroni $P = 1$).

Figure 3. Olfactory inspections (** indicates $P < 0.01$)
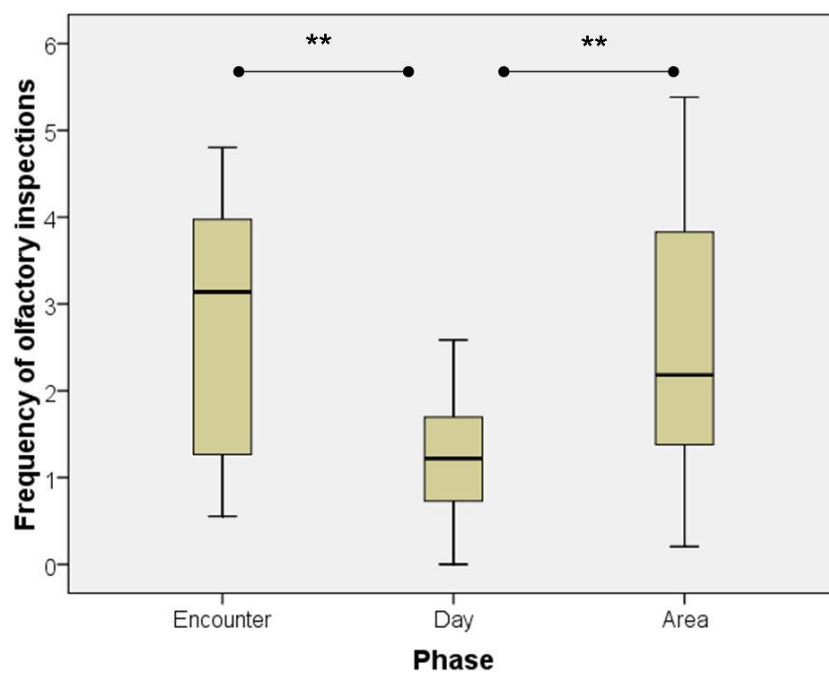
DISCUSSION

Intergroup encounters are common at home-range boundaries, happen more often than expected (see chapter 3) and may last up to 90 min. These encounters entail high costs in terms of energy expenditure (fights, chases), risk of injury, and time lost for foraging and feeding (Peres 1989, 1992). Thus, these encounters should bring other benefits to the animals, like an enhanced detection of chemical signals by neighbouring groups (e.g. Palagi & Norscia 2009), and neighbour assessment (Lazaro-Perea 2001).

All groups increased their scent-marking frequency during intergroup encounters, compared to 24 hours later. However, this increase is not related to the encounter with another group *per se*, as we found no difference in scent-marking frequency in areas of intergroup encounters and the same shared area of the home range, when no other group was present. Sifakas do not deposit the majority of their scents during intergroup encounters neither (Lewis 2006), although it is important to highlight that this study did not consider scent-marking frequency per context, but only the distribution of scent-marking events over contexts.

The use of scent glands did not differ across any of the phases, which indicates that saddleback tamarins are not transmitting different kinds of information by a differential use of the scent glands, a result consistent with captive studies (Belcher et al. 1988). This lack of differentiation in the use of scent glands contrasts with other primates like ring-tailed lemurs (Palagi & Norscia 2009) and cottontop tamarins (French & Snowdon 1981), which requires a satisfactory explanation. It could be possible that different combinations of scent-marking acts from different glands within an event do transmit a different message, but our data do not allow us to test this possibility.

During intergroup encounters the animals were less interested in their own group scents than in the same area when no other group was present. This may be explained by the nature of these intergroup encounters, where individuals spread over a large area, and are often aggressively chased by neighbours. Thus, actively monitoring group mates may be difficult in these conditions. But despite this decrease in scent inspections, the proportion of scents overmarked did not vary, which suggest that the animals nevertheless knew where the scents had been deposited, possibly via volatile cues. Since there is sexual dimorphism in the direction of overmarking (chapter 5), its function is likely to be related to the concealment of reproductive information.

One way to get the information transmitted by neighbours is by direct inspection of the substrate. Ideally, focal scent marks should be monitored, which was not possible in our

study. We only saw 4 scents receiving a response from the neighbouring group. Some other scents, unnoticed by the human observer may nevertheless have been inspected. An indirect way of evaluating this is by substrate inspection. Although the tamarins inspected the substrate with a higher frequency during intergroup encounters compared to the next day, this was again related to the use of an overlap area.

Taken together, these results suggest that olfactory communication does not seem to play a major role in the intergroup encounters of wild saddleback tamarins, in contrast to other mammals (Gosling & Roberts 2001a) and captive settings (Epple et al. 1993). Indeed, scent marking is not a very effective communication channel due to its poor directionality and slow transmission speed (Endler 1993). It is thus not well suited for intergroup encounters in callitrichids, which are characterised by vocal exchanges, chases and frenetic activity. Moreover, the detection of the signal in the canopy of a rainforest may not be as straightforward as for ground mammals.

Since chemical signals can be perceived in the absence of the sender (Gosling & Roberts 2001a), there may be no need to exchange this information while in direct, visual contact. As we have shown elsewhere (chapter 3), groups may already be constantly monitoring each other's scents at shared areas of their home ranges, so there may be no point in enhancing scent marking during actual encounters. Since scents provide information about reproductive condition, scent matching may allow the animals to decide whether to meet a neighbouring group, and which one of them. Intergroup encounters may then rather be the dénouement of this continuous monitoring and allow a visual, direct evaluation of neighbours (see Lazaro-Perea 2001 and the "fight to learn" hypothesis: Getty 1989).

The increase in scent-marking frequency during confrontations with strangers reported in captive studies may rather be an artefact of the captive setting. Since the intruders presented are usually complete strangers rather than "dear enemies" (*sensu* Temeles 1994), the residents have never had the chance to exchange information with them, which, combined with the spatial restrictions of the cage, makes olfactory communication much more efficient than in a tropical rainforest.

ACKNOWLEDGEMENTS

Chapter 5.

SEXUAL DIMORPHISM IN OLFACTORY COMMUNICATION IN WILD SADDLEBACK TAMARINS, *Saguinus fuscicollis*

ABSTRACT

Whenever there is strong competition for access to mates, sexual selection should favour the development of highly dimorphic traits like ornaments or weapons. Callitrichids are almost monomorphic in body size and lack weaponry, although competition over reproductive positions is strong, particularly between females. In this study we examined sexual differences in scent marking and in the responses to scents in wild saddleback tamarins in north-eastern Peru. We recorded scent-marking events, scent-marking intensity, and the proportion of scent-marking acts that received a response in form of inspection or overmarking, as well as allomarking behaviour. Females had higher scent-marking frequencies than males. Males with higher scent-marking frequencies copulated more with females, while for females only intensity of scent marking correlated with copulations. Females also inspected and overmarked a higher proportion of scents than males. Male scents were overmarked by females, and female scents were overmarked by males. Intersexual overmarking correlated with copulation frequency, as well as male intrasexual overmarking. Males performed more allomarking than females, and females received more allomarking than males. These results show that there is a clear sexual dimorphism in emission and reception of olfactory signals in saddleback tamarins, which suggests that both male and female choice may be mediated by chemical cues in this species.

INTRODUCTION

Sexual selection is a form of natural selection that acts differently on the two sexes (Clutton-Brock 2004). As female mammals invest more in offspring, they represent a limiting factor for males' reproductive success (Trivers 1972). Therefore, male mammals must attract females (intersexual choice) and at the same time compete over access to them with other males (intrasexual competition). This intense competition leads to the development of weaponry, ornaments, and other sexually dimorphic traits (Andersson 1994; Andersson & Iwasa 1996). On the other hand, female reproductive success is limited by the access to resources and the quality of parental care (Emlen & Oring 1977; Trivers 1972). Thus, females are expected to be choosy.

Marmosets and tamarins, small New World primates from the sub-family Callithrichinae, represent an interesting exception to the general rule. Females give birth to heavy dizygotic twins (Tardif et al. 1993), but most infant care is provided by males (Goldizen 1987b). Indeed, infant carrying entails important costs for carriers (Achenbach & Snowdon 2002; Sanchez et al. 1999), and infant survival is related to the presence of helpers (Garber 1997). Long considered as monogamous, callithrichines show very flexible mating systems, from monogamy to polygyny, although functional polyandry is the most common in the wild (Goldizen 1987a; Goldizen et al. 1996; Sussman & Garber 1987). However, only one female per group is able to successfully raise infants (French 1997; Garber et al. 1993a; Goldizen et al. 1996; Savage et al. 1996), and even if multiple males may mate with the female, usually only one of them is able to monopolise most paternities (Huck et al. 2005). Thus, in tamarins males and females are a mutually limiting factor for reproduction. Both should then compete for reproductive positions, and both are expected to be choosy.

The application of sexual selection theory to primate communication has not been as fruitful as in other areas (Snowdon 2004). However, several species show clear sexual differences in scent-marking behaviour (e.g. *Lagothrix lagotricha*: Di Fiore et al. 2006; *Propithecus verrauxi*: Lewis 2005; *Mandrillus sphinx*: Feistner 1991). Tamarins posses a well-developed olfactory communication, with specialised glands in the anogenital, suprapubic and sternal region, whose secretions inform about species, sub-species, sex, and individual identity and about reproductive condition in females (Epple et al. 1993; Washabaugh & Snowdon 1998; Ziegler et al. 1993). Female odours attract males, and those of novel females induce sexual arousal in captive males (Heymann 1998; Ziegler et al. 1993; Ziegler et al. 2005), and activate brain areas responsible for sexual behaviour (Ferris et al. 2001; Snowdon et al. 2006), but also contribute to the inhibition of ovulation in subordinate females (Epple & Katz 1984; Savage et al. 1988).

Although tamarins are almost monomorphic and lack ornaments or weaponry, scent-marking frequency is female-biased in most tamarin species (Heymann 1998, 2003; Smith & Gordon 2002). Scent glands are much more developed in females than in males, and more than expected based on the degree of dimorphism in body size (Heymann 2003).

Heymann (1998) found that wild male moustached tamarins investigated more scents, and mostly those from females. In captivity, male red-bellied tamarins investigated more scents than females, and mostly those from females, while females did not investigate scents from their partners at all (Smith & Gordon 2002). However, the responses to scent marks can differ in a captive environment, where the ambient is likely to be saturated by scents.

Depositing a scent over a previous scent, or overmarking, is a common feature that may fulfil several functions (Ferkin & Pierce 2007). It has been suggested to inform about social rank or competitive ability (Fisher et al. 2003a; Rich & Hurst 1999), to attract mates (Heymann 1998; Kappeler 1998), or to guard them (Palagi et al. 2004; Roberts & Dunbar 2000). Male moustached tamarins received most overmarking (Heymann 1998), although this was not the case in red-bellied tamarins (Smith & Gordon 2002).

None of the studies that addressed sexual dimorphism in scent-marking behaviour has considered allomarking. This behaviour consists in depositing the secretion from the scent glands over the fur of another animal, instead of the substrate. Although described in several species of primates and other mammals (Brown & Macdonald 1985; Heymann 2001), its function remains unknown. It has been suggested to produce a group odour, like an olfactory membership badge, although the question is open whether individual relationships may also be recorded and broadcasted in that way (Buesching et al. 2003; Mueller-Schwarze 2006).

This study is aimed at detecting sexual differences in scent-marking behaviour and in responses to scent marks. If scent-marking behaviour plays a role in mate choice, it has to bring some reproductive advantages, like an enhanced copulation frequency, and responses to scents should depend on the sex of the emitter and the responder. If allomarking is intended to create a group odour, all individuals should be equally allomarked.

METHODS

This study was conducted at the Estación Biológica Quebrada Blanco (EBQB) in the primeval Amazonian lowland forest in north-eastern Peru (see Heymann 1995 for details of the study site), from May 2007 to June 2008. We followed three well-habituated groups of *Saguinus fuscicollis* (see Table 1 for group composition) forming mixed-species troops with *Saguinus mystax*. Each saddleback group was followed about six consecutive days per month, from exiting a sleeping site (between 0515 h and 0600 h) to retiring to a sleeping site (between 1530 h and 1635 h). All animals were individually recognizable through natural marks (e.g., genital shape and pigmentation, shape of the tail, etc.).

Data Collection

We recorded scent-marking frequency, scent-marking intensity, defined as the number of scent-marking acts per event (Heymann 2001), responses to scents and allomarking and

copulations (Table 2) with the behaviour sampling method. We noted the identity of the individual that scent marked, and if the scent received any kind of response from other group members. These responses were usually recorded in the 5 minutes following deposition, since afterwards the group had definitively abandoned the area and thus the scent could not receive any further response from other group members (see Heymann 1998 for a similar approach).

Table 1. Composition of the study groups

	Group 1	Group 2	Group 3
Male, adult	2	4	1
Female, adult	2-1[a]	2	2
Infant	-	-	0-1[b]-2[c]
Total	4-3	6	3-4-5
Observation time (hours)	550,4	306,4	505,8
Mating system	PGA-PA[a]	MG	PG

[a] One female disappeared between the 21st December 2007 and the 5th January 2008, while the group was not being observed. The group changed the mating system accordingly
[b] One infant born between the 20th November and the 1st December 2007, and disappeared between the 8th December 2007 and the 21st January 2008, while the group was not being observed
[c] Two infant born between the 7th and the 10th March 2008

Data analysis

The behaviour sampling method can bias the data towards more visible animals (Martin & Bateson 1993). In order to correct this bias, we conducted scan samples every 15 min, where the activity of each identified individual was recorded within 2 min. Since there were differences in visibility (expected vs. observed representation of individuals in scan samples) between individuals in Group 1 ($\chi^2_3 = 9.61$, $P < 0.03$) and Group 2 ($\chi^2_5 = 20.87$, $P < 0.001$), individual frequencies were corrected by dividing them by the proportion of scans where the animal was visible. As one female disappeared from Group 1 between December and January, the group changed its composition and mating system, and thus was considered as a new social unit after January 2008. Their data were then analysed separately.

Table 2. Behavioural coding

Behaviour	Description
Copulation	Mounting or being mounted with pelvic movements
Scent-marking act	Marking with the anogenital (AG), suprapubic (SP) or sternal gland (ST)
Scent-marking event	Combination of scent-marking acts (Bartecki & Heymann 1990)
Overmarking	Marking over a previous mark from another individual
Scent inspection	Sniffing, muzzle-rubbing or licking a scent from other individual
Allomarking	Rubbing a scent-gland over another animal

In order to account for intergroup differences in the overall frequency of scent marking, we calculated standardised frequencies by dividing individual frequency by the group mean, and compared them with the t-test. We calculated for each animal the proportion of female and male scents that were inspected or overmarked, and the frequency of allomarking. Data that did not meet the requirements of normality were square-root or log transformed. Data were modelled using General Linear Mixed Models, with individual identity nested within group as random factor, and sex, group and sex of the receptor as fixed factors. Multiple comparisons were conducted with the Bonferroni adjustment.

GLMMs were carried out on SPSS 16.0, other tests on Statistica 6.0 (StatSoft, Inc.).

RESULTS

Scent-marking frequency and intensity

Females marked more often than males (T test for independent samples, $T = 2.22$, $P < 0.05$; Fig. 1), but there were no differences in intensity ($T = 0.71$, $P = 0.49$). Individuals with higher scent-marking frequencies also performed more copulations ($R = 0.62$, $P = 0.011$). This was true for males (N = 9, $R = 0.72$, $P = 0.03$) but not for females (N = 7, $R = 0.54$, $P = 0.21$). However, intensity of scent marking correlated with frequency of copulations for females ($R = 0.83$, $P = 0.02$), but not for males ($R = 0.43$, $P = 0.25$).

**Figure 1.** Scent-marking frequency per sex ($P < 0.05$)

Scent-mark inspection

The tamarins inspected 4.2% of all scent-marking acts deposited. Females inspected a higher percentage of scents than males (5% vs. 3.5%, Log SI GLMM $F_{1,12.61} = 8.81$, $P = 0.01$), but percentage of received inspections does not differs between sexes (GLMM $F_{1,13.18} = 0.63$, $P = 0.44$).

Overmarking

The tamarins overmarked 9.4% of all scent-marking acts. Females tended to overmark a higher percentage of scent-marks than males (11% vs. 8%, GLMM $F_{1,12.26} = 3.9$, $P = 0.07$). Both sexes received the same percentage of overmarking (GLMM $F_{1,12.89} = 0.8$, $P = 0.39$). There was a significant interaction between the sex of the overmarker and that of the overmarked (GLMM $F_{1,13.03} = 25.06$, $P < 0.001$; Fig. 2): males overmark preferentially on females, while females overmark mostly on males.

Figure 2. Directionality of overmarking
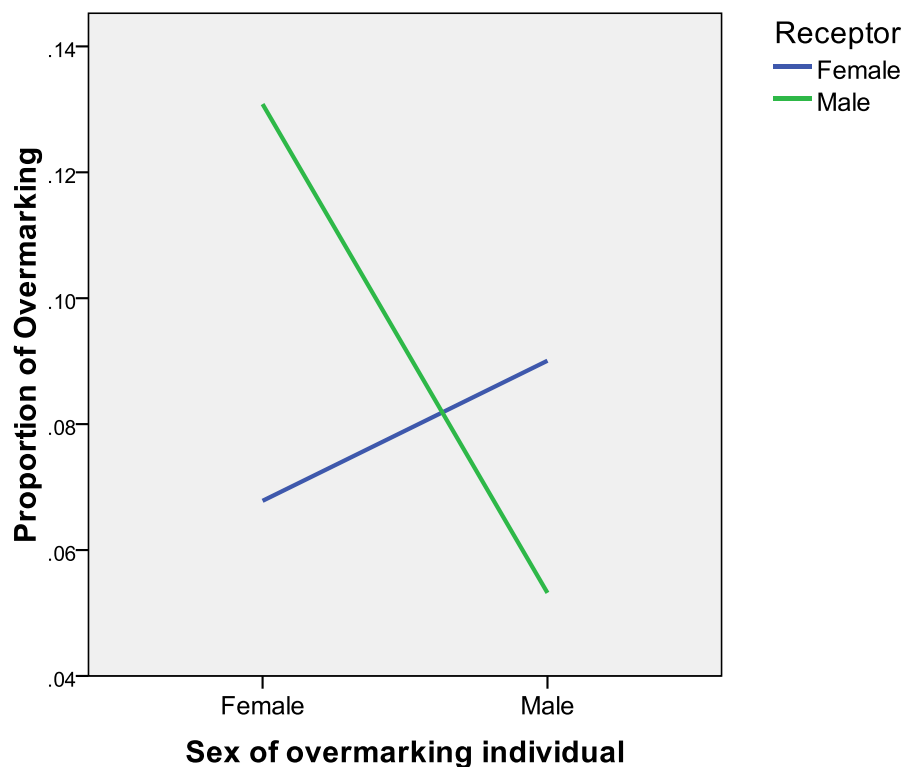
The proportion of overmarking performed by an individual correlated with its copulation frequency ($R = 0.66$, $P = 0.005$), which is true for females (N = 7, $R = 0.76$, $P = 0.05$), and possibly also for males (N = 9, $R = 0.64$, $P = 0.06$). Males that overmark same-sex

conspecifics perform more copulations ($R = 0.88$, $P = 0.004$), but this does not hold for females ($R = 0.72$, $P = 0.11$). Overmarking opposite sex individuals was also related to copulations ($R = 0.59$, $P = 0.016$), but no correlation was found when looking specifically at males overmarking females ($R = 0.59$, $P = 0.1$), neither females overmarking males ($R = 0.65$, $P = 0.12$).

Allomarking

We recorded 382 instances of allomarking, both animals being identified in 345 of them. Males performed allomarking at higher frequency than females (Sqrt AL GLMM $F_{1,8.64} = 13.3$, $P = 0.006$), and females received more allomarking than males (GLMM $F_{1,15.01} = 17.17$, $P = 0.001$), although the interaction between sex and receptor is not significant (GLMM $F_{1,8} = 3.46$, $P = 0.1$).

DISCUSSION

Our study shows that both deposition and reception of information by chemical means is highly dimorphic in saddleback tamarins. Female saddleback tamarins marked more than males, a result that matches previous studies (e.g. French & Cleveland 1984; Heymann 1998; Smith & Gordon 2002), but in contrast to moustached tamarins, intensity of scent marking did not differ. Males with higher scent-marking frequencies copulated more, which may be an indication of female choice. Scent marking is supposed to be costly (Gosling et al. 2000; Johansson & Jones 2007), as well as a reliable indicator of health and individual quality (Endler 1993; Penn & Potts 1998; Zala et al. 2004), although we still lack this kind of data for primates. Thus, females may prefer males able to scent mark at a high frequency, as they might be potential good quality individuals. On the other hand, males preferred to copulate with females that showed a higher scent-marking intensity, which is likely to make the stimulus more salient and also to entail production costs.

Thus, both male and female scents function for the attraction of mating partners. But as the relationship between copulation and conception is not straightforward, and there is sperm competition in tamarins (Garber et al. 1996; Heymann 2000a), we cannot prove that the individuals bearing these traits have a higher reproductive success. However, a higher copulation frequency is a good starting point, which has to be confirmed by paternity analyses.

Although we lack hormonal data and it was impossible to determine reproductive dominance -as only one of the 3 groups bred during the study period-, inhibition of subordinates by the reproductive female does not seem to be the primary function of female scent-marking. First, in Group 1, after the disappearance of the second female, the remaining female still had the highest scent-marking frequency in the group, although no competitor was present anymore. Similarly, Heymann (1998) observed even an increase of scent marking frequencies in two females after the reproductive female had died. Second, in Group 3, both females gave birth in a 3 month interval, which clearly indicates that no ovarian suppression was going on as seen in captivity (Löttker et al. 2004; Savage et al. 1988); although just one litter survived. Moreover, their scent-marking frequency was almost the same and the only male scent marked more than any of the females.

Females inspected a higher proportion of scents than males, which suggests that they are interested in the information transmitted by both sexes. Indeed, females have to compete with other females in order to get the only reproductive position available, but also to attract males. Thus, females may be simultaneously interested in monitoring male and female scents. Male intrasexual competition, on the other hand, seems to be more relaxed as it is common to see several males mating with the reproductive female in the group, and theoretically the dizygotic twins may be sired by different males.

As scent marks convey information about reproductive condition in callitrichids, and possibly also about individual quality and genetic distance (Charpentier et al. 2008a), excluding competitors from this information is a way of intrasexual competition (see also Palagi et al. 2004). Several species overmark opposite-sex conspecifics (see Ferkin & Pierce 2007 for a review), but as far as we know, no such interaction has been observed like in our study. It is still unclear if primates are able to mask the bottom mark as hamsters do (Johnston & Bhorade 1998; Johnston et al. 1994), although ring-tailed lemurs can nevertheless perceive the bottom scent (Kappeler 1998). Overmarking may also inform them about the overmarker's competitive ability (Rich & Hurst 1999). Indeed, male saddlebacks that overmark other males also perform more copulations. In an experimental approach, it has been shown that female pygmy lorises prefer overmarking rather than overmarked males as mates (Fisher et al. 2003a). Thus, overmarking may serve simultaneously as a way to attract mates and to inform rivals about costs of competition.

The proportion of scents that received a response in form of inspection or overmarking was comparable to that of moustached tamarins at the same study site (Heymann 1998), and extremely low compared to other primates like sifakas, where only 8% of female scents

escape from male's attention (Lewis 2005). It may be asked why tamarins do scent mark at all, given this poor success in signal transmission. However some information may be transmitted by volatile components, without direct inspection of the scent (Belcher et al. 1988). On the other hand, as suggested by Heymann (2003), only high quality individuals may be able to afford such a permanent chemical display for such a little result.

In our study allomarking also proved to be dimorphic, and thus no group odour can be created as in badgers (Buesching et al. 2003). Allomarking may instead be a way of overriding the poor efficiency of scent marking. An animal that is allomarked by another has no choice but to perceive its allomarker's odour, like any other animal approaching the allomarked individual. Female tamarins are the main receivers of allomarking, while males are the principal allomarkers. It can be hypothesized that males use allomarking to tighten their bonds to females, and to claim ownership or preferential access against other males (Gosling 1990).

Our results suggest that olfactory communication in saddleback tamarins serves simultaneously for intersexual and intrasexual competition, depending on the sex of the sender and the receiver. Thus, olfactory signals could be the chemical equivalent of a peacock's plumage (Penn & Potts 1998).

ACKNOWLEDGMENTS

Chapter 6.

CAN OVERMARKING BE CONSIDERED AS A MEAN OF CHEMICAL MATE GUARDING IN A WILD CALLITRICHID?

ABSTRACT

Mate guarding of fertile females is a male strategy to monopolize matings and thus to ensure paternity. Since in tamarins and other callitrichids, female reproductive status is advertised through scent-marks, one may expect mate guarding by chemical means. During a field study on the function of scent marking in saddleback tamarins (*Saguinus fuscicollis*) in north-eastern Peru, the opportunity arose to address this question during an episode of consortship observed in a polyandrous trio. We compared allomarking, scent-marking frequency, and overmarking before and during consortship. During consortship, the consort male was the only to allomark the female. While scent-marking frequency decreased for all individuals, the consort male marked more than the other male during consortship, while there was no difference in the previous period. The consort male overmarked female scents more often than during the control period, and more than the other male. During consortship, almost 50% of female scents were overmarked by the consort, and more than 56% of the consort's scent marks were employed to overmark female's scents. Therefore, the other male had limited access to female scent marks. These results suggest that mate guarding has a chemical component in tamarins, and that olfactory communication may play an important role in mating competition.

INTRODUCTION

Male mammals are expected to try to monopolise females and expel competitors, and this intrasexual competition usually leads to the development of highly sexually dimorphic traits as predicted by the sexual selection theory (Darwin 1871). However, copulation by itself does not ensure fertilisation.

Mate guarding is a means of increasing the likelihood of paternity by "the concealment of mates from intrasexual competitors" (Thornhill & Alcock 1983). This "concealment" usually takes the form of "persistent following of a female by a male that involves exclusion of other males from access to the female" (Alberts et al. 1996).

In polyandrously mating callitrichids, where some competition exists between males for access to the single reproducing female per group, "classical" mate guarding has been observed (e.g. Goldizen 1989; Huck et al. 2004). However, callitrichids haven't developed visible ornaments or weaponry, and they are almost monomorphic in body size.

The question arises whether in species where olfactory signals are important for broadcasting the fertile status of females, competition could take place at the chemical level. This could take the form of (a) overmarking of female scent marks if these contain relevant information on female fertility, in order to conceal it, and (b) allomarking the fertile female. In mammals, marking over a previously deposited scent may fulfil a mate guarding function, either by masking the information from female scents (Ferkin & Pierce 2007; Roberts & Dunbar 2000), or by informing about the male's competitive ability (Rich & Hurst 1999), or both.

Here we examine patterns of male overmarking and allomarking in *Saguinus fuscicollis* under the hypothesis that overmarking and allomarking represent a kind of "chemical mate guarding". The opportunity for retrospectively addressing this question arose during a study on the scent-marking strategies of *S. fuscicollis* when in one of our study groups "classical" mate guarding occurred, indicating a fertile phase of the female (Löttker et al. 2004).

METHODS

This study was conducted at the Estación Biológica Quebrada Blanco (EBQB) in the primeval Amazonian lowland forest in north-eastern Peru (see Heymann (1995) for details of the study site). The study group was being followed in the context of a broader study on olfactory communication since May 2007. In January 2008 one female disappeared and since then the group was composed by two males and one female. All animals were adults, individually recognizable through natural marks (e.g., genital pigmentation, shape of the tail, etc.). The group was followed about six consecutive days per month, from exiting a sleeping site (between 0515 h and 0600 h) to retiring to a sleeping site (between 1530 h and 1635 h), yielding a total of 28 complete days of observation (ca. 245 hours). One of the males was sticking to the female during 5 days (May/June 2008), which we interpreted as playing a consortship role at the descriptive level. That male will be referred to as the consort.

We compared the behaviour of the animals during the days before consortship (control period), to the 5 consortship days (consortship period).

Behavioural categories (see Table 1) were recorded on field notes with the behaviour sampling method (Martin & Bateson 1993). This kind of data can be biased towards more visible animals. In order to correct this bias, we also conducted scan samples every 15 min, where the activity of each visible individual was recorded within 2 min. There were neither differences in visibility between periods (Female: $\chi^2_{Yates} = 2.02$, $P < 0.16$; Males: $\chi^2_{Yates} =$

0.08, $P < 0.78$; $\chi^2_{Yates}=1.5$, $P < 0.22$) nor within periods (Control: $\chi^2_2 = 0.34$, $P < 0.84$; Consortship: $\chi^2_2 = 1.22$, $P < 0.54$).

Table 1. Description of behavioural categories

Behaviour	Description
Scent-marking act	Rubbing the anogenital, suprapubic or sternal gland on the substrate
Scent-marking event	Combination of scent-marking acts (Bartecki & Heymann 1990)
Overmarking	Marking over a previous mark from another individual[a]
Scent inspection	Sniffing, muzzle-rubbing or licking a scent from other individual
Allomarking	Depositing scent on another individual

[a] It was impossible in our study to see if the overmark completely covered the bottom mark

We compared the proportion of female scent-marking acts that were inspected or overmarked by males with the Z test for proportions and compared the proportion of the male's own marks devoted to overmarking the female for each male.

Under the null hypothesis of no difference between periods, expected frequencies were calculated as

(1) Expected frequency in period i = Total number of occurrences of behaviour * Observation time in period i / Total observation time

Under the null hypothesis of no difference between males within a given period, we calculated expected frequencies per male as

(2) Expected frequency per male in period i = Total number of occurrences of behaviour in period i/ Number of males (= 2)

We compared observed and expected frequencies with χ^2 test with Yate's correction for df=1. All tests were carried out on Statistica 6.0 (StatSoft, Inc.).

RESULTS

Frequency of scent marking

All individuals scent marked less than expected during consortship (Female: $\chi^2_{Yates} = 6.46$, $P < 0.02$; Consort: $\chi^2_{Yates} = 4.03$, $P < 0.05$; 2nd Male: $\chi^2_{Yates} = 31.75$, $P < 0.001$; Fig. 1). There was no difference between both males in the control period ($\chi^2_{Yates} = 0.22$, $P = 0.64$; Fig. 2), but the consort marked more than the other male during consortship ($\chi^2_{Yates} = 15.72$, $P < 0.001$; Fig. 2).

Figure 1. Observed vs. expected frequencies of scent marking during consortship (* $P < 0.05$; *** $P < 0.001$)
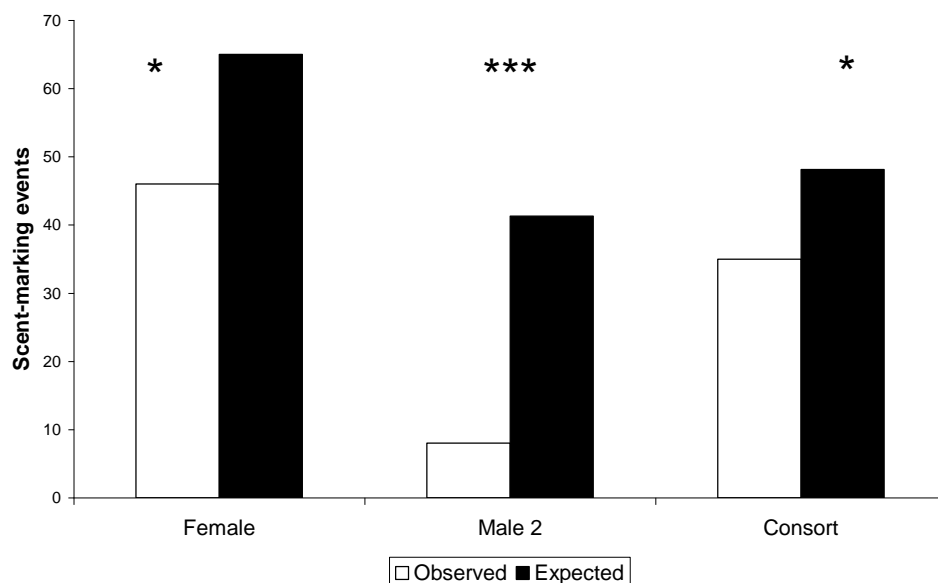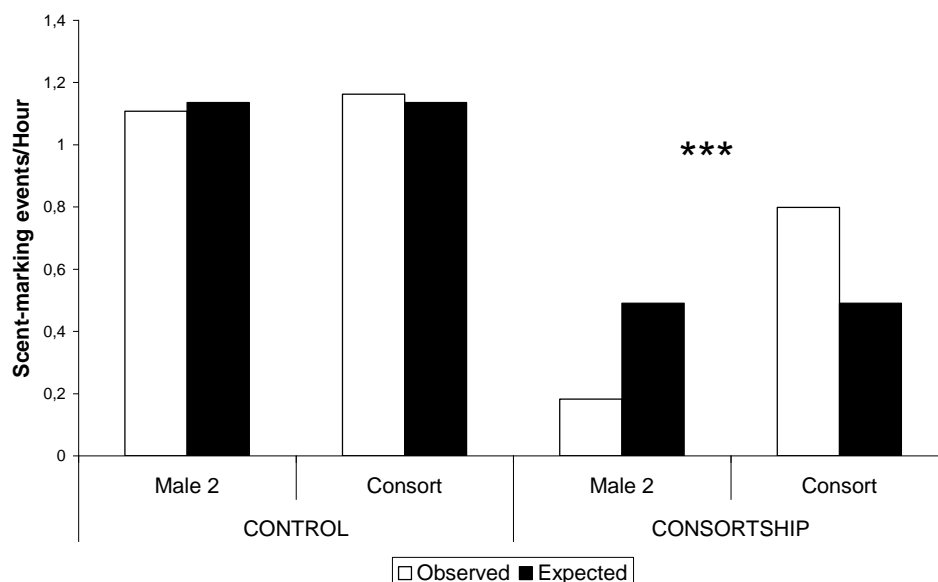

Figure 2. Observed vs. expected frequencies of scent marking by both males, by periods (*** $P < 0.001$)

Overmarking

During the control period, both males overmarked about 14% of female scents. During consortship, the consort increased the proportion of female scents overmarked to 48% ($Z =$ 7.9, $P < 0.001$) while the other male decreased it to 5% ($Z = 2.2$, $P < 0.03$). The difference in

the proportion of female scents overmarked was significant between both males during consortship ($Z = 7.07$, $P < 0.001$). During the control period, the female received 55% and 45% of overmarking from the consort and the other male, respectively. However, during consortship the female received 90% of overmarking from the consort alone. This increase was significant ($Z = 4.86$, $P < 0.001$). The consort performed 95% of his overmarking on the female during consortship, increasing the proportion in comparison to the control period ($Z = 4.3$, $P < 0.001$).

Scent marking budget

The consort devoted 23% of its own scent-marking acts to overmark the female during the control period, and the other male 17%. The consort increased this proportion up to 56%, which was significant ($Z = 6.54$, $P < 0.001$), and also significantly higher than the other male (21%, $Z = 3.03$, $P < 0.001$).

Allomarking

The consort was the only individual to allomark the female during consortship, and it did it more often than the other male during both periods (Control: $\chi^2_{Yates} = 9.52$, $P < 0.003$, Consortship: $\chi^2_{Yates} = 5.14$, $P < 0.03$; Fig. 3). The consort did not increase its allomarking frequency on the female during consortship ($\chi^2_{Yates} = 0.79$, $P = 0.37$), while was a trend for decrease in the other male ($\chi^2_{Yates} = 3.67$, $P < 0.06$).

Figure 3. Observed vs. expected frequencies of female allomarking by both males during consortship (* $P < 0.05$)
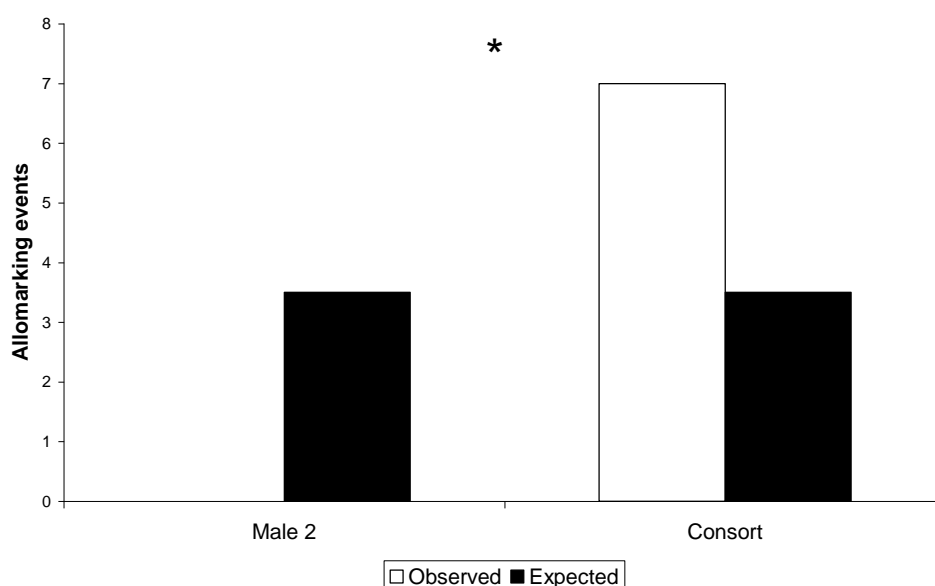
DISCUSSION

Information about the reproductive state of females can be perceived through scent marks (Washabaugh & Snowdon 1998; Ziegler et al. 1993). However, as shown in golden-headed lion tamarins, males may be able to detect the follicular period, but not the peri-ovulatory days (de Vleeschouwer et al. 2000). Thus scent marks could be the chemical equivalent to the sexual swellings of macaques, informing about the probability of ovulation (Huck et al. 2004).

In our study, all animals decreased their scent-marking frequency during consortship. This may be a way for the female to limit her chemical advertising during receptive periods, thus forcing the male to remain in close proximity and stimulating male-male competition over access to scents (de Vleeschouwer et al. 2000).

By allomarking, an animal deposits the secretion from its scent glands over the fur of another animal, instead of the substrate. It may create a shared, group odour; or inform about individual relationships (Buesching et al. 2003; Mueller-Schwarze 2006). In our study, the creation of a group odour seems unlikely, since female allomarking was monopolised by the consort during mate guarding. Rather, the function of allomarking may be related to the reinforcement of the ties between mates. It may also fulfil a mate guarding function, as the other male must perceive the consort's odour whenever approaching the allomarked female.

Our data suggest that overmarking in saddleback tamarins might be the chemical equivalent to physical mate guarding of females. During mate guarding, the guarder overmarked the female more often than expected, and more than the other male. Almost half of all female's scent marks (48%) were overmarked by the guarder. The female received less overmarking from the other male, as her scent marks had already been overmarked –and thereby monopolised- by the guarder. Thus, although there is no direct, aggressive competition between males over access to the female, mating competition may nevertheless take place at the chemical level.

Mate guarding is supposed to be a costly activity, entailing a decrease in energy intake and/or an increase in energy expenditure (Alberts et al. 1996). An animal can only deposit a limited quantity of scent, since scent marks are costly to produce (Gosling et al. 2000). The consort male modified its scent-marking budget, devoting most of its scent marks to overmarking the female during consortship. Thus, a male able to monitor and overmark a high proportion of female's scents over a long period of time is reliably indicating its competitive

ability as well as its individual quality, both to the female and to potential competitors (Johnston 2003).

Despite its limitations, our study is, to our knowledge, the first to have directly addressed the importance of chemical communication in mating guarding in a primate. It would be critical to know if primates are able to mask the bottom mark as hamsters do (Johnston & Bhorade 1998; Johnston et al. 1994), or if the female scent can nevertheless still be perceived after being overmarked, as suggested in ring-tailed lemurs (Kappeler 1998). Careful experiments, combined with detailed field observations will deepen our understanding of the role of olfactory communication in mating competition.

Chapter 7.

GENERAL DISCUSSION

As stated by Heymann (2006a), olfaction has been the "neglected sense" in primate research. Saddleback tamarins are one of the few species whose olfactory communication has been extensively studied, although mostly in captivity (e.g. Epple & Smith 1985, although see Bartecki & Heymann 1990; Heymann 2001). This project was aimed at elucidating the function of scent marking in wild saddleback tamarins, *Saguinus fuscicollis*. Our study has offered a new approach in the understanding of olfactory communication in this species, within the framework of sexual selection.

The detailed analysis of territorial scent marking using GIS (Geographic Information System) technology presented in chapter 3 revealed an equivocal relationship between territoriality and scent marking. Whereas scents were distributed along the periphery and close to feeding trees and areas of intergroup encounters, there were no obvious advantages in terms of territorial or resource defence. Rather, scents were deposited in an economic way which maximises the probability of signal transmission between groups. This is especially important considering the limitations of chemical communication like its poor directionality and high degradation rate. We thus hypothesized that this enhanced scent marking at territory borders may be a way of exchanging information between groups, in order to monitor possible breeding vacancies. Thus, territorial defence does not seem to be the primary function of scent marking in wild saddleback tamarins, and the existing evidence for other species (reviewed in Heymann 2006b) should be re-evaluated.

A key factor in determining if olfactory communication fulfils a territorial function is its role in direct territorial contests, as has been shown in multiple species. Captive studies have pointed out the role of scent marking in the aggressive response towards intruders in captive tamarins (Epple 1973; French & Snowdon 1981). However, our data in wild animals showed that this increase is related to the use of an overlap area, rather than to the presence of another group in proximity. As groups are already in olfactory contact throughout the boundaries, intergroup encounters may rather be the occasion for a direct assessment of neighbours (Lazaro-Perea 2001), based on the olfactory information gathered at the territorial borders. Results from captive studies might just be an artefact of the experimental setting, where animals are complete strangers instead of dear enemies (Temeles 1994).

But scent marking is not limited to the areas of home range overlap between groups, and is likely to function in intra-group communication as well. As any communication process, scent marking should be analysed taking into account both the deposition and the reception of

the signal (Kappeler 1998). Chapter 5 showed that this process is sexually dimorphic both in the deposition and in the reception of the signal. Although we lack hormonal data, the reproductive suppression of subordinates does not seem to be the main function of scent marking. Some features of the signal -frequency, intensity, and directionality of overmarking- were related to copulations, depending on the sexual identity of the sender and the receiver. This sexual dimorphism suggests that scent marking seems to have evolved through sexual selection in saddleback tamarins, and may play a role in mate selection and mating competition.

Mate guarding is an obvious form of direct mating competition. Chapter 6 investigated scent-marking behaviour during an episode of mate guarding. The consort male overmarked an important proportion of the female's scents during this period, which we interpreted as a way of preventing the other male from gathering the reproductive information encoded by the female, or showing its quality and competitive ability. Thus, overmarking may be the chemical equivalent to physical mate guarding.

Taken together, these results suggest that the main function of olfactory communication in wild saddleback tamarins might be related to the search, selection and competition for mating partners, may these be found inside or outside the group. Thus, as stated by Heymann (2003; 2006b), scent marking is likely to have evolved through sexual selection in tamarins.

LIMITATIONS

Nevertheless, we have to point out some limitations of the present study, which have to be considered for future research.

The first limitation, inherent to primate research, is related to sample size. Although 3 groups representing 13 animals is at the upper limit of what is feasible in field conditions, a bigger sample size would have allowed us to investigate not only male and female marking strategies, but also the influence of the group's mating system and the individual strategies (e.g. male subordinates, or differences within subordinates related to age). If scent marking allows the exchange of reproductive information between groups as hypothesized in chapter 3, then the marking strategy of each individual should be dependent on its reproductive position in the group, its age, group size, sex ratio etc. but also on the strategy of other group members. For instance, a non-reproductive female in a group with enough helpers may signal to find an outgroup partner, while in a group with scarcity of helpers her scents might be

overmarked by the dominants, in order to prevent her from getting in contact with extragroup individuals, even if she represents a potential competitor for the reproductive female.

The absence of infants in 2 out of 3 groups did not allow us to determine female reproductive dominance. The faecal samples collected throughout the study period could be analyzed in order to determine ovarian activity (Löttker et al. 2004), but this lay beyond the frame of this dissertation due to time constraints. However, it may me hypothesized that females do not undergo a reproductive suppression but a reproductive restriction. That is, scents from other males and females would allow them to evaluate their reproductive chances, and to decide when ovarian activity is worth, based on this assessment. This would be coherent with the proposed function of olfactory communication in mating competition, by allowing the animals to adapt their reproductive strategy to the strategies of the other members of the group.

A key factor in determining if olfactory signals are sexually selected is the reproductive advantages it entails for the bearer of the trait (Snowdon 2004). Given the slow life-history of primates, such a hypothesis can only be indirectly assessed. For this purpose, faecal samples were collected in order to perform genetic analysis to determine paternities and relatedness among our study animals. Unfortunately, DNA amplification failed despite all our efforts (e.g. Arandjelovic et al. 2009). Problems in sample storage likely resulted in a degradation and fragmentation of the DNA, whose quality is already low in faecal samples. Moreover, the primers used by Huck et al. (2005) in moustached tamarins may not be adapted for saddlebacks. As discussed earlier (chapter 3), relatedness within the group may determine the observed differences in marking behaviour between moustached and saddleback tamarins. Relatedness should also influence the patterns of intra-group communication identified in chapter 5.

FURTHER WORK

Although this thesis consists of 4 research papers, the data collected during the field season will allow us to investigate other aspects of olfactory communication.

We will try to place olfactory communication in the context of the social life of the animals. Scent-marking acts are not deposited on the vacuum, but on a stream of behaviour, preceded and followed by other kinds of behaviours. This conceptual approach will allow to calculate transitional probabilities between specific scent-marking acts or events, and other

behaviours, like specific responses to scent marks (sniffing, overmarking, etc.), or other kinds of behaviour (affiliative, sexual, etc.) which might be facilitated by the marking behaviour. Such information theory based analysis is common in the study of human vocal communication (e.g. Zipf 1949), and has also been applied to gestural communication in gorillas (Genty & Byrne 2010) and auditory communication in dolphins (McCowan et al. 1999). However, to our knowledge, it has never been applied to chemical communication in any mammal.

Finally, it would be possible to apply mechanistic home range models to analyze group movements. In this framework, different mathematical models can include different factors (both social and ecological) that are thought to influence group movements (distribution of resources, presence and density of neighbours, etc.). Each model represents a hypothesis that can be tested with empirical data. One of such models is the conspecific avoidance model generated for coyotes, *Canis latrans*, where scent marks from different groups are said to allow spacing between groups in order to avoid confrontations (Moorcroft & Lewis 2006). However, the mathematical abilities needed for such a modelling are far beyond our skills.

FURTHER PERSPECTIVES ON CHEMICAL COMMUNICATION IN TAMARINS AND OTHER PRIMATES

Our knowledge of primate chemical communication lies far behind that of other mammals like rodents (e.g. Hurst & Beynon 2004). Even if our work has deepened our understanding of chemical communication in a wild primate, some questions remain nevertheless unanswered.

Our study has pointed out some striking differences in the patterns of olfactory communication between tamarin species. Some of them might be related to the testing conditions (e.g. captive vs. free-ranging, see chapter 4), but some others are likely to reflect species idiosyncrasies, like differences in the spatial pattern of scent marking (*S. fuscicollis* vs. *S. mystax*, chapter 3), in the use of scent-marking glands (*S. fuscicollis* vs. *S. oedipus*, chapter 4) or in the reception of overmarking (*S. fuscicollis* vs. *S. mystax*, chapter 5). These are likely to reflect subtle differences in paternal investment (Heymann 2003) and/or in the mating system of the species (Heymann 2001). However, our current knowledge of tamarin social systems does not allow a detailed identification of these key features.

No function could be found for collective scent marking (Heymann 2001): its spatial pattern failed to reveal any territorial function and thus was not mentioned in chapter 3. This collective scent marking might also be linked to the mating system of the group, as it almost never happened in the polygynous group, but was common in the others (polygynandrous, polyandrous and presumed monogamous). On the other hand, it was obvious that the animals performed it on some specific substrates. It may be a way to anoint the body with some special substance present on the substrate at those places, and a botanical identification of them would be useful.

Our study has shed some light on some mechanisms poorly understood like overmarking. However, some other questions have arisen, particularly about its functional consequences. It would be critically important to determine whether primates are able to completely mask the bottom mark, or if both scents can nevertheless be perceived. In the latter case, discrimination might be based in the differences in age between the top and the bottom scent (Rich & Hurst 1999), or they spatial configuration (Johnston & Bhorade 1998). The overmarking individual may then be informing competitors about its competitive ability (Ferkin & Pierce 2007), as just good quality individuals would be able to monitor and overmark a high quantity of scents.

Indeed, chemical signals might be good indicators of health and individual quality (Endler 1993; Gosling et al. 2000; Zala et al. 2004). Mice have been found to discriminate scents from parasite infected individuals (Penn & Potts 1998). In primates, scents from ringtailed lemurs inform about heterozygozyty (Charpentier et al. 2008a), which is a predictor of health and survivorship (Charpentier et al. 2008b). Moreover, scents also inform about relatedness between individuals, although this information was only apparent during the breeding period (Charpentier et al. 2008a).

There is growing evidence that scents contain information related to the Major Histocompatibility Complex (MHC) in both rodents and humans (Penn & Potts 1999). In non-human primates, preliminary data suggest that the concentration of volatile compounds in the scent marks of ring-tailed lemurs, *Lemur catta*, is related to genes coding MHC (Knapp et al. 2006). Smith (2006) suggests that this could also be true in callitrichids. In fact, information about MHC is essential for mate choice, in order to ensure genetic variability (Wyatt 2003), and rodents prefer scent marks from individuals with a MHC profile different than their own (Penn & Potts 1998). Although still scarce in primates, there is considerable evidence that chemical communication is important in mate selection (Johansson & Jones 2007).

Last, but not least, the role of olfactory communication in primate conservation has received little attention, but offers interesting clues for the future. 14 out of the 60 callitrichid taxa are threatened and two of them, *Leontopithecus caissara* and *Saguinus oedipus*, are listed as Critically Endangered (IUCN 2009. IUCN Red List of Threatened Species. Version 2009.2. <www.iucnredlist.org>. Downloaded on 11 January 2010). Thus, the survival of these and other species may need captive breeding programs and re-introduction of captive bred animals. In captivity, it is nearly impossible to introduce a new animal on a pre-established group because of the aggression it receives (Rothe & Darms 1993). However, familiarity between animals reduces the aggressiveness (French et al. 1995; Koenig & Rothe 1994). One way of making animals familiar to each other is by exposing them to scent marks of other individuals, avoiding the stress of direct contact. The inclusion of olfactory management techniques in breeding programs could then reduce the number of non-breeding pairs in captivity and enhance genetic variability. This possibility has been successfully tested in another threatened primate, the pygmy loris, *Nycticebus pygmaeus* (Fisher et al. 2003b) and in giant pandas, *Ailuropoda melanoleuca* (Swaisgood et al. 2002; Swaisgood et al. 1999; Swaisgood et al. 2000).

SUMMARY

Olfactory communication is a distinctive trait of the Callithrichinae, which however remains largely neglected (Heymann 2006a), and its possible functions have been the matter of a certain controversy (Gosling & Roberts 2001b; Heymann 2000b, 2006b). In this thesis, we used the theoretical framework of sexual selection to investigate the functions of olfactory communication in wild saddleback tamarins, *Saguinus fuscicollis*, in the Amazonian rainforest of North-eastern Peru. The analysis of the spatial patterns of scent marking and its relation to feeding resources allowed us to discard a classical territorial function. Rather, scent marks would be deposited in order to allow the exchange of reproductive information between groups. Moreover, in contrast to findings in captivity, scent-marking frequency did not increase during intergroup encounters. Scent marking also showed to be sexually dimorphic, both in the emission and reception of the signal, and some of its features correlated with copulations. It thus seems that both inter- and intrasexual competition might take place at the chemical level. This was further suggested by the analysis of scent marking patterns during an episode of mate guarding, where female scents were monopolised by the guarder through overmarking. Taken together, these results suggest that olfactory communication in wild saddleback tamarins functions for mate attraction and mating competition. However, genetic analyses are needed in order to determine its reproductive advantages.

RESUMEN

La comunicación olfativa es una característica distintiva de los calitrícidos, que sin embargo ha recibido poca atención (Heymann 2006a), y sus posibles funciones han sido objeto de cierta controversia (Gosling & Roberts 2001b; Heymann 2000b, 2006b). En esta tesis hemos tomado la teoría de la selección sexual como marco para investigar las funciones de la comunicación olfativa en el pichico común, *Saguinus fuscicollis*, en condiciones de libertad en la selva amazónica del Noreste de Perú. El análisis de los patrones espaciales de marcaje y su relación con los recursos alimenticios nos permitió descartar una función territorial en su sentido clásico. Los marcajes más bien parecen ser depositados para permitir el intercambio de información entre grupos. Además, en contraste con estudios en cautividad, la frecuencia de marcaje no aumenta durante los encuentros intergrupales. Los marcajes también resultaron ser sexualmente dimórficos tanto en su emisión como en su recepción, y algunas de sus propiedades correlacionaron con la frecuencia de cópulas. Por lo tanto parece que tanto la competición inter- como intrasexual tienen lugar a través de la comunicación química. El análisis de los patrones de marcaje durante un episodio de *mate guarding*, durante el cual los marcajes de la hembra fueron monopolizados por uno de los machos a través del sobremarcaje, apoya esta hipótesis. En conjunto, nuestros resultados apuntan a que la comunicación olfativa en esta especie sirve para la atracción de pareja y la competición por la misma. Sin embargo, son necesarios análisis genéticos para determinar exactamente sus ventajas reproductivas.

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