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*Original article*

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**Sex differences in olfactory communication in a primate, the moustached tamarin, *Saguinus mystax* (Callitrichinae)**

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**Abstract** This study examines the hypothesis that sexual selection has shaped patterns of olfactory communication in wild moustached tamarins, *Saguinus mystax*. Do sex differences exist in frequencies and in the intensity of scent marking, in the use of different scent-marking types, and in behavioural responses to scent marks? Scent marking (anogenital, suprapubic, sternal) and behavioural responses (sniffing and overmarking) were recorded in four groups (ten adult and subadult males, seven adult and subadult females in all groups combined) in north-eastern Peru. Frequencies and intensity of scent marking were significantly higher in female tamarins. Males and females did not differ in the use of anogenital marking, but suprapubic marking was employed significantly more often by females. Only 10% of scent marks were monitored by another group member, and only 5% were overmarked by another group member. Most sniffing of scent marks was done by males, and males sniffed at marks produced by females significantly more often than at marks produced by males. Both sexes overmarked scent marks with similar frequency, but females overmarked scent marks produced by males significantly more often than those produced by females. An increase in frequencies of scent marking was observed in two females of one group after the death of the reproducing female, but frequencies of scent marking remained the same in the males of this group. The female-biased rates of scent marking are consistent with predictions made by sexual selection theory for species with substantial male care for offspring and strong reproductive competition between

females. However, a decisive test of the proposed role of sexual selection will only be possible with more field data on patterns of olfactory communication in other callitrichine species.

**Key words** Olfactory communication · Scent marking · Competition · Sexual selection · *Saguinus mystax*

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**Introduction**

Whenever the sexes differ in morphological, physiological or behavioural traits that are not directly related to survival or to the basic requirements of reproduction, sexual selection is invoked as an explanation (Darwin 1871; Reynolds and Harvey 1994). Displays, ornaments or weapons that serve to attract mates or that are used in intrasexual contest may be either exclusively or more strongly developed in the sex that competes more strongly for access to mates (Darwin 1871; Andersson 1994). In mammals, it is usually the males that compete for access to females and, accordingly, exhibit such traits (Darwin 1871; Lincoln 1994; Clutton-Brock and Albon 1979).

Considerable attention has been paid to the role of sexual selection in shaping patterns of visual and vocal communication (e.g. Ryan 1985; Andersson 1994). However, although it was already suggested by Darwin (1871, p. 313) that “odoriferous glands [have] been acquired through sexual selection”, little attention has been paid to the role of sexual selection in shaping patterns of olfactory communication in mammals (see also Blaustein 1981; Arnold and Houck 1982). Blaustein (1981, p. 1007) suggested that in small mammals, odours “are probably functionally equivalent to secondary sexual characteristics” and that “sexual selection should act upon these odours just as it acts upon visually conspicuous characters”. This reasoning is extended here to include the behaviours that are associated with the dispersal of scents.

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Dedicated to Dr. Gisela Eppe, pioneer of research on callitrichine behavioral biology, on the occasion of her 60th birthday

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Scents play a significant role in the social and sexual communication of mammals (for reviews see Ralls 1971; Eisenberg and Kleiman 1972; Mykytowycz 1972; Johnson 1973; Brown 1979; Brown and Macdonald 1985). Scents of specific glands (or other sources of odour such as urine, faeces, or saliva) are often deposited on a substrate (or a conspecific) through highly ritualised behaviours (e.g. Ewer 1968; Mykytowycz 1972). Examples have been provided for sexual dimorphism in the development of scent gland organs, the frequency of scent-marking behaviour and the chemical composition of the odoriferous substances (e.g. Schultze-Westrum 1965; Payne and Swanson 1970; Goodrich and Mykytowycz 1972; Jannett 1986; Thompson and Fadem 1989; Koprowski 1993).

Scents are also important in the social and sexual communication of the Callitrichinae, the marmosets and tamarins (e.g. Epple 1974; Epple et al. 1986). These small (100–650 g) New World primates possess various patterns of scent marking involving glands in the anogenital, suprapubic and sternal region of the body (Epple et al. 1986). In captivity, sex differences in the frequency of scent marking have been identified, with females usually marking more often than males, particularly in species of the genus *Saguinus* (e.g. French and Cleveland 1984; Epple et al. 1986). So far, predictions derived from sexual selection theory have not been applied to examine patterns of scent marking in callitrichines. However, callitrichines show characters in their reproductive biology which would make such an approach particularly useful.

First, there is strong reproductive competition between callitrichine females. Breeding is habitually monopolised by one female in each group (French 1997; contributions in Mittermeier et al. 1988), although there is increasing evidence from wild *Callithrix* spp. for sequential or simultaneous breeding by two females (Digby and Ferrari 1994; Ferrari et al. 1996). Female reproductive competition may be severe, even leading to female-induced infanticide (Digby 1995; Kirkpatrick-Tanner et al. 1996). This competition is probably caused by the need for helpers to successfully rear the heavy twin offspring (Digby 1995).

Second, there is substantial male investment in the offspring (Baker 1991; Goldizen 1986, 1988; Rylands 1986; Heymann 1990a). This point is particularly relevant in the context of sexual selection theory. Extensive male care is likely to restrict the reproductive rate of males (Clutton-Brock 1991) and thus to shift the ratio of female potential reproductive rate:male potential reproductive rate towards equality or towards higher female rates. This, in turn, should increase mate competition among females (Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992; see also Gwynne 1991). One should therefore expect traits in callitrichine females that have been shaped by sexual selection.

Moustached tamarins (*Saguinus mystax*) are the largest member of its genus (for body mass data see Snowdon and Soini 1988; Heymann 1997a,b). They live

in groups of 3–12 individuals (mean group size:  $5.5 \pm 0.2$ ), which usually include 2 (or more) adult males and 1–2 adult females (Soini and de Soini 1990). Only one female breeds in each group (Soini and de Soini 1990). Social relationships are characterised by very low levels of agonistic behaviour (Heymann 1996). Olfactory behaviours include three types of scent marking (anogenital, suprapubic, sternal), urine washing, muzzle rubbing, sniffing of substrates or group members, licking of marked substrates, and rubbing the cheeks in urine of other group members (Heymann 1985, 1995a, 1997a; Heymann et al. 1989).

In this paper, the olfactory communication, specifically the patterns of scent marking and responses to scent marks in wild moustached tamarins are examined in the light of sexual selection theory. First, I address the question of sex differences in frequencies of scent marking. Second, since studies in captivity also suggest sex-specific use of scent-marking types (e.g. French and Cleveland 1984), I examine whether similar differences exist in the wild. Finally, I examine responses to scent marks, in order to elucidate whether communication by scents is primarily addressed to the same or to the opposite sex, a feature which is relevant for the discussion as to whether inter- or intrasexual selection or both are operating.

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## Methods

### Study site

Data presented here were collected during field studies at two different sites in north-eastern Peru, the Estación Biológica Quebrada Blanco (EBQB) and the Estación Biológica Padre Isla (EBPI). EBQB is located at 4°21'S 73°09'W [this position was determined with a Garmin GPS-45 and differs from coordinates given in previous publications (4°40'S 73°W) that had been read from a map] on the right bank of Quebrada Blanco, a tributary of the Río Tahuayo. For details of the EBQB see Castro (1991) and Heymann (1995b). EBPI is located on Padre Isla, an 8-km<sup>2</sup> island formed by sediments of the Amazon some 70–80 years ago near Iquitos. For details of the EBPI site see Heymann (1990a), Encarnación et al. (1990) and Moya et al. (1990).

### Study animals

The subjects of the study were four groups of *S. mystax* (QB-1, QB-2 and QB-3 at EBQB, and PI on Padre Isla) whose compositions are shown in Table 1. These groups were studied between July 1985 and May 1986 (QB-1, 365.8 h of observation), between June and September 1990 (QB-2, 330.4 h), in August 1995 (QB-3, 160.8 h), and between October 1985 and June 1986 (PI, 318.2 h before + 62.0 h after the death of one adult female on 20 January 1986). Groups QB-1, QB-2 and QB-3 were living in interspecific association with groups of *Saguinus fuscicollis* (see Heymann 1990b). For further details of groups QB-1, QB-2 and PI see Heymann (1990a, 1996). Group QB-3 had been under observation since February 1994 (Knogge 1998; Smith 1997). All groups were habituated to the presence of human observers. Animals were identified using body size and natural markings, e.g. size and pigmentation of genitalia, and healed injuries (kink in tail, hole in ear lobe; see Heymann 1990a, 1996). Problems of individual identification resulted mainly

**Table 1** Composition of the study groups [age-class determination according to criteria provided by Soini and de Soini (1990)]

	QB-1	QB-2	QB-3	PI
Male, adult	2	2	2	2
Female, adult	1	1–2 <sup>a</sup>	2	1–2 <sup>b</sup>
Male, subadult	–	–	1	1
Female, subadult	–	–	–	1
Male, juvenile	–	–	1	2
Female, juvenile	–	1	1	–
Infant	–	–	–	0–1 <sup>c</sup>

<sup>a</sup> One female disappeared between 7 and 20 July 1990 while no observations were carried out

<sup>b</sup> One female killed by an anaconda on 20 January 1986 (see Heymann 1987)

<sup>c</sup> Infant born at beginning of December 1985; died on 23/24 January 1986 after death of mother

for adult males in groups QB-2 and PI, which in each case were essentially similar in body size and testes size, and for the two adult females in group QB-2, whose vulvas were the same size. The distinguishing feature in the QB-2 males – a stiff fifth finger on the left hand of one of the males – was often not visible during the short and rapid scent-marking events.

There are reasons to suppose that none of the individuals present in group QB-1 was still present in group QB-2, and that none of the individuals present in group QB 2 was still present in group QB 3. One of the adult males in QB-1 had a kink in the tail, while none of the adult males in QB-2 and QB-3 had such a kink. The female of QB-1 had extremely large labia majora throughout the study period, never seen again in any other female. One adult male in QB-3 had strongly asymmetric testes not seen in males in QB-1 and QB-2, and the other adult male of QB-3 was still subadult when the study by Knogge (1998) started in February 1994; one adult female was subadult and the other a juvenile at the beginning of Knogge's study. Therefore, we considered frequencies of each individual as a separate and independent data point.

#### Data collection

The study groups were usually observed for complete days, i.e. from the early morning when the tamarins left their sleeping site to the afternoon when the animals retired to a sleeping site. Scent-marking behaviour was recorded with a behaviour sampling method (Martin and Bateson 1993); whenever I observed scent marking, I recorded the number of scent-marking acts [= the completed rubbing movement involving one of the scent glands (anogenital, suprapubic, sternal)], the type of each act (anogenital, suprapubic, sternal), the individual or age-sex class involved, time of day, location within the home range, height in the forest and type and orientation of substrate, the behavioural context, and responses to scent marks. I could observe responses only if they occurred within a period of about 4–5 min, since after this period the group had usually moved on.

#### Data analyses

The analysis of sex differences in frequencies of scent marking is based on scent-marking events. A scent-marking event may either constitute a single act or an uninterrupted sequence of two or more successive acts of the same or of a different type. Differential use of scent-marking types was analysed by comparing the proportions of scent-marking events that included different types. As a measure for the intensity of scent marking, I used the number of acts per event.

For the analysis of sex differences, only adult and subadult animals were considered (scent marking was extremely rare in ju-

veniles). Subadults can be included in the analysis since their marking activity may approach that of adults (Epple et al. 1986). Individual scent-marking frequencies were calculated by dividing the number of scent-marking events per individual by the total number of observation hours for each group. The few events in which the identity of a female was not established were deleted from the analyses. However, events in which the identity of the male was not clearly established were too frequent to be deleted without biasing the result in favour of females. To make the analysis as conservative as possible, all these events were attributed to one male in each group, thus increasing the total variance and making it more difficult to obtain a significant difference between the sexes. To account for group differences in overall frequencies of scent marking, standardised frequencies were calculated by dividing individual frequencies by the group-specific mean frequency for adult and subadult animals. Both frequencies and standardised frequencies were subjected to a one-way ANOVA to test for sex differences. Differential use of scent-marking types and intensity of scent marking (defined as the number of scent-marking acts per event) were analysed with the Mann-Whitney *U*-test, since these data did not meet the assumptions for parametric tests.

For group QB-2, only data from the period after the disappearance of one adult female were used, since females were not readily distinguished before. For group PI, only data from the period before the death of one of the adult females were used in the analyses of sex differences. Data from both the period before and after the death of one of the adult females were used to examine changes in rates of scent marking in the remaining group members. For the analyses of differential use of scent-marking types and intensity of scent marking, one adult male in group QB-3 was excluded since it had not been observed marking.

To analyse whether the sexes differ in their responses to scent marks, all groups had to be lumped together, because the figures would otherwise have been too low for statistical treatment. I compared the number of observed and expected responses of males and females with a *G*-test. Expected frequencies took into consideration that e.g. in a group of two males and one female, reactions to a male scent mark could come from one male and one female, those to a female scent mark from two males but not from a female.

The death of one adult female in group PI provided the opportunity to analyse potential changes in scent-marking frequencies in relation to the social change. Individual scent-marking frequencies before and after the death were compared with a *t*-test; the two adult males were lumped together for this analysis.

Behaviour sampling has the potential problem of incurring a sampling bias against individuals that are less habituated to the observer or that behave less obviously. I checked for such a bias by comparing observed and expected age-sex class and individual representation in scan sampling data with the *G*-test. No such bias was apparent in any of the groups except for the males of QB-3 (Table 2). However, this bias would not affect sex differences.

## Results

The sexes differed in the overall frequency of scent marking, the frequency of use of different types of scent marking, the intensity of scent marking and the response to scent marks.

### Frequency of scent marking

Frequencies of scent marking were significantly higher in females than males (ANOVA:  $F = 9.33$ ,  $df = 1, 15$ ,  $P < 0.01$ ; Fig. 1). The difference between the sexes becomes even more pronounced if the differences between the groups in overall frequencies of scent marking are

accounted for by standardising the frequencies (ANOVA:  $F = 14.76$ ,  $df = 1,15$ ,  $P < 0.005$ ). In each group, frequencies of all females except for the subadult female in group PI were higher than the frequencies of males.

### Use of scent-marking types

For males, the proportion of scent-marking events involving anogenital marking varied between 75% [QB-3; note however the very small number ( $n = 7$ ) of events in males, with only one event not involving anogenital marking] and 100% (median: 95.8%); for females the

proportion was 99–100% (median: 100.0%). The difference is not significant (Mann-Whitney  $U = 16.00$ ,  $N_1 = 9$ ,  $N_2 = 7$ , ns).

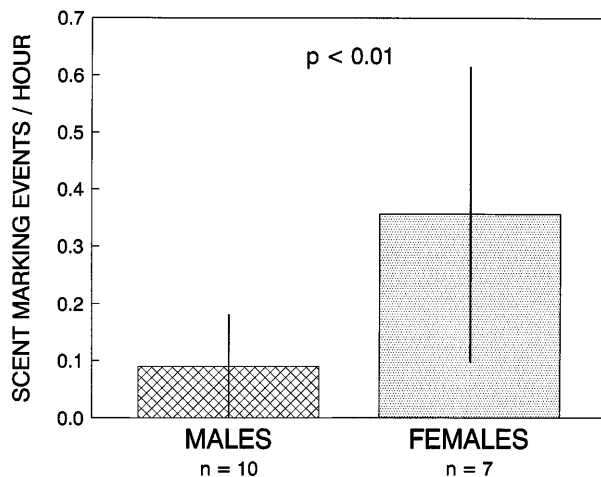
The proportion of events involving suprapubic marking varied between 0.0% and 4.7% (median: 0.0%) for males, and between 0.0% and 13.8% (median: 11.1%) for females. The difference between males and females is significant (Mann-Whitney  $U = 6.50$ ,  $N_1 = 9$ ,  $N_2 = 7$ ,  $P < 0.01$ ).

Events involving sternal marking were extremely rare. Of the ten events, six were observed in males, two in females, and in two cases, the individual was not clearly identified. The small number makes statistical testing unreasonable.

**Table 2** Statistics for the observed and expected representations of age-sex classes and individuals in the scan samples ( $G$ -test, values are  $G_{adj}$ )

	QB-1	QB-2	QB-3	PI
Age-sex class	0.512	2.828	1.078	1.469
$df$	1	1	1	1
Males	1.127	0.063	27.760*	–
$df$	1	1	2	–
Females	–	–	–	1.873
$df$	–	–	–	2

\* $P < 0.001$



**Fig. 1** Comparison of scent-marking frequencies (means  $\pm$  SD, unstandardised) of adult and subadult male and female *Saguinus mystax*

### Intensity of scent marking

A scent-marking event may involve a single act or two or more acts from the same or from different scent-marking types. Males and females differed in intensity, with females including on average more acts per event than males (females:  $1.274 \pm 0.103$ , males:  $1.126 \pm 0.098$ ; Mann-Whitney  $U = 11.00$ ,  $N_1 = 9$ ,  $N_2 = 7$ ,  $P < 0.05$ ). If differences between the groups in overall intensity are taken into account, the sex difference becomes even more pronounced (Mann-Whitney  $U = 8.00$ ,  $N_1 = 9$ ,  $N_2 = 7$ ,  $P < 0.02$ ). As with overall scent-marking frequencies, in each group the intensity of scent marking of all females except the subadult female in group PI was higher than the intensity of scent marking in males.

### Response to scent marks

Response to scent marks may include sniffing, licking (usually only if urine was mixed with the mark), muzzle rubbing and overmarking. However, most scent marks did not elicit a response obvious to the observer and only about 10% and 5% of scent marks were monitored through sniffing and overmarking, respectively, within 4 min. Licking and muzzle rubbing were extremely rare.

Males sniffed at scent marks significantly more and females significantly less often than expected by chance (Table 3). Furthermore, males sniffed significantly more often at scent marks produced by females than at scent marks produced by other males than would be expected

**Table 3** Sniffing of scent marks

Scent mark made by	Number of marks	Number of marks sniffed by		Expected number of sniffs by males	
		Male	Female		
Males	146	2	1	13.7	$G_{adj} = 11.762$ $P < 0.001$
Females	452	54	4	42.3	
$\Sigma$	598	56	5		
Expected		37.2	23.8		

$G_{adj} = 14.982$   
 $P < 0.001$

**Table 4** Overmarking of scent marks

Scent mark made by	Number of marks	Number of marks overmarked by		Expected number of overmarks by males	Expected number of overmarks by females	Expected total number of overmarks
		Male	Female			
Males	146	6	11	4.4	3.4	7.8
Females	452	12	3	13.6	10.6	24.2
$\Sigma$	598	18	14			
Expected		19.5	12.5			
		$G_{adj} = 0.144$ ns				
				$G_{adj} = 0.349$	$G_{adj} = 8.814$	$G_{adj} = 5.977$
				ns	$P < 0.005$	$P < 0.05$

from the frequency of scent-marking events (Table 3). The number of sniffs by females was too small for statistical examination.

Frequencies of overmarking of scent marks in both sexes did not differ from expected frequencies (Table 4). However, scent marks of males were overmarked significantly more often and those of females significantly less often than expected (Table 4). While males overmarked male and female scent marks according to expected frequencies, females overmarked male scent marks more and female scent marks less than expected (Table 4). However, given the small numbers, these results should be treated with caution.

Licking of scent marks (probably when urine had been voided with the mark) was extremely rare and observed only in males, and was directed exclusively to marks produced by females.

It is highly unlikely that immediate responses occurred later than 4 min after the scent-marking event. The group usually had moved on within such a period.

#### Changes in scent-marking frequency after the death of an adult female

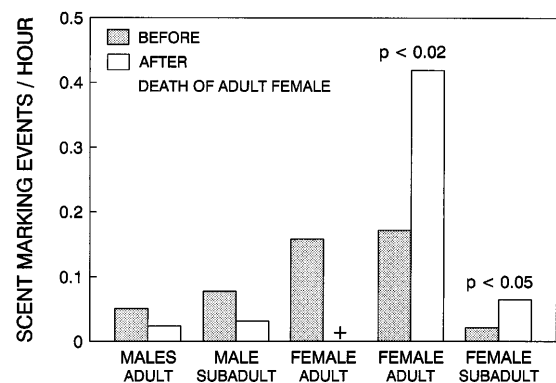
The adult reproductive female of group PI was killed by an anaconda on 20 January 1986 (Heymann 1987). Within a few days after this event, there was a notable increase in the size of the vulva of the second adult female, and later also in the subadult female. Both females showed a significant increase in scent-marking frequency, while no change was noted in the adult and subadult males (Fig. 2).

## Discussion

This study demonstrates for the first time sex differences in scent-marking behaviour of a wild callitrichine primate. Adult and subadult females show significantly more frequent, more diverse, and more intensive marking than adult and subadult males. This is in line with findings in different tamarin species in captivity (Box and Morris 1980; Coates and Poole 1983; French and Cleveland 1984; Heymann 1985; Castro 1990; Rohrhuber 1990; Buchanan-Smith and Jordan 1992; for review

see Epple et al. 1986) and confirms predictions made by the theory of sexual selection.

In callitrichines, females compete for the usually single reproductive position in each group. The ultimate factors leading to reproductive monopolisation in callitrichine groups are not yet well understood, but competition for male helpers may be a key factor. Garber et al. (1984) and Koenig (1995) have shown that female reproductive success (measured in terms of infant survival) correlates with the number of adult males present in a group. While this does not necessarily imply that females also copulate with all males, polyandrous matings have been observed in several studies (Goldizen 1987, 1989; Soini 1987; Ferrari 1992; Baker et al. 1993; Garber et al. 1993; Heymann 1996). Competition between males for females is probably less pronounced than in other primates. There is generally very little agonistic behaviour between males, but mate guarding during presumed oestrus periods of the reproductive female may occur (Soini 1987; Goldizen 1989; Baker et al. 1993; Heymann 1996). Male-male competition may take place at the level of sperm, as indicated by the relatively large testes in some callitrichine species (Harcourt et al. 1995). Competition between males might be relaxed through the habitual twinning, with twins being dizygotic and therefore potentially fathered by different males. Furthermore, co-operation between males may be essential for successful rearing of infants. The lower level of scent marking in males would be consistent with the



**Fig. 2** Comparison of scent-marking frequencies of adult and subadult males and females before and after the death of the reproducing adult female of group PI

presumed lower level of intrasexual competition. This hypothesised relation between intrasexual competition and scent marking would predict variation in the degree of sexual dimorphism in scent marking in relation to the degree of intrasexual competition in different callitrichine species. At present, too few data are available from field studies to conduct relevant analyses.

Competition for mates in one sex and mate choice by the other sex are important components of sexual selection and may act simultaneously (Johnson 1988a,b; Andersson 1994). In this case, the same trait or signal may be employed in intrasexual contest interactions as well as in courtship (Kodric-Brown and Brown 1984; Krebs and Davies 1993). For example, Jannett (1986) suggested that scent marking in male voles, *Microtus* sp., aids in territorial maintenance (intrasexual component) and in the facilitation of mate choice by females (intersexual component). Similarly, Gosling and Wright (1994) showed that scent marking by male coypus, *Myocastor coypus*, is linked to intrasexual competition, but also suggested that females should base their choice of a mate on information provided by scent marks. In ring-tailed lemurs, *Lemur catta*, male scent marking functions primarily in intrasexual competition, but for females a role in both mate attraction and intrasexual competition has been suggested (Kappeler 1998).

The patterns of scent marking and responses to scent marks observed in this study suggest that a primary function of female olfactory signals is the attraction of males. First, females scent mark frequently even if no other female lives in the group. Second, sniffing of scent marks was significantly more frequent in males. Results of studies in captivity also suggest that female olfactory signals function in intrasexual competition: scent marks produced by reproducing females may temporarily inhibit ovarian cycles or delay the time to first ovulation in other females (Epple and Katz 1984; Savage et al. 1988; Barrett et al. 1990). However, such an "inhibitory" function of female scent marks is not easily understood given that olfactory signals have poor directionality and that the sender has little control over who will receive the signal (Endler 1993). It is also difficult to explain why a female should sniff the scent marks produced by another female if this results in physiological manipulation, i.e. being reproductively inhibited. While in captivity, scent marking may result in a high concentration of "pheromones" in a limited space, which might be sufficient for a physiological effect without the receiver sniffing at the marks, this is unlikely to be the case under natural conditions.

The increase in scent marking by the two females remaining in group PI after the death of the reproducing female is consistent with both an intrasexual and an intersexual model of selection. The death of the reproducing female may have released the two females from some "inhibitory" effect, and may have caused increased competition between the two remaining females for the vacant reproductive position in the group. The increase

in scent marking could, however, also be seen as an increased effort to display towards the males. The role of males in determining which females reproduce is not understood, but there is some evidence that their contribution can be essential (Anzenberger et al. 1996). Subsequent to this study, group PI had split up into two groups by October 1986 (B. Ruth, personal communication) but the exact pattern of group splitting could not be reconstructed. In captive cotton-top tamarins, *S. oedipus*, changes in the social environment stimulate the growth of scent glands and lead to increased rates of scent marking in females (French et al. 1984). The observations reported here are consistent with these findings.

Scent marking was continuously observed throughout all study periods and there was no indication of seasonal peaks. The data collection schedule did not permit analyses of the presence of cyclical variation in scent marking frequencies. In studies of captive *Saguinus oedipus*, no cyclical variation or differences in scent marking rates between periovulatory or non-periovulatory periods have been detected (Heistermann et al. 1989; Ziegler et al. 1993). However, the latter study and a study by Converse et al. (1995) suggested that qualitative changes in scent marks indicate the oestrus cycle. Taking into consideration that mate choice in primates is probably not based on single stimuli or events but rather on repeated interactions between known individuals (Keddy-Hector 1992), continuous scent marking may be a form of permanent display that allows repeated control and evaluation by the receivers.

The production and maintenance of sexually selected traits should be costly for the individual if the trait is an honest advertisement of quality (Kodric-Brown and Brown 1984). It has been suggested that chemical signals are good indicators of individual quality (Endler 1993). However, it is not yet known how costly scent-marking behaviour is to callitrichines. Potential costs include the energy required for the development and maintenance of scent gland tissue and for the production of scent gland secretions, and perhaps the increased risk of being detected by predators guided by olfaction like cats and mustelids (see Jannett 1986).

Models of sexual selection propose that sexually selected traits are indicative of the quality of the bearer (Kodric-Brown and Brown 1984; Johnstone 1995). Evidence for this hypothesis has been provided mostly for visual and vocal traits and signals, but more evidence for olfactory signals is becoming available. Female mice can discriminate scents of parasitised and non-parasitised males which suggests that scent (in this case from urine) is a reliable indicator of the signaller's quality (Kavaliers and Colwell 1995a,b). In voles, the attractiveness of scents (of both males and females) has been found to vary with the protein content of the diet, which may be indicative of the signaller's quality (Ferkin et al. 1997). Gosling and Wright (1994) demonstrated for *M. coypus* that anal gland mass in males is limited by body condition. Experimental work on callitrichines in captivity

has demonstrated the ability of adult animals to discriminate between scents of intact and castrated males (Epple 1979) and between unfamiliar dominant and subordinate males (Epple 1973). No experiments have been designed so far to investigate the response to scents from females with different reproductive histories (good breeders vs bad breeders) or different reproductive condition (oestrus vs non-oestrus) to see whether consistent choices are made by males based on female scent.

Support for the proposed role of sexual selection in shaping patterns of tamarin olfactory communication and the suggestion that selection acts more strongly on females is provided by morphological data. Scent glands are sexually dimorphic in tamarins, with larger anogenital and suprapubic glands in females (Dawson and Dukelow 1976; French and Cleveland 1984; Zeller et al. 1988; Soini 1990; P. Soini, personal communication).

To unequivocally demonstrate the action of sexual selection it must be shown that variation in the trait, i.e. scent-marking behaviour, results in variation in reproductive success. This will only be possible through long-term field studies. Patterns of olfactory communication could then be analysed in relation to individual life histories and reproductive strategies and success. Comparative data from other wild callitrichines are clearly also needed. Finally, as suggested recently by Kappeler 1998, it will be necessary to examine the entire communicative process in more detail and more comprehensively, i.e. patterns of signal transmission from the sender to the receiver.

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## References

- Andersson M (1994) Sexual selection. Princeton University Press, Princeton, NJ
- Anzenberger G, Hotz A, Keller M (1996) Behavioral endocrinology of inbreeding avoidance in female common marmosets (*Callithrix jacchus*). Abstracts of the XVIth Congress of the International Primatological Society, 11–16 August 1996, Madison, Wis., p 26
- Arnold SJ, Houck LD (1982) Courtship pheromones: evolution by natural and sexual selection. In: Nitecki MH (ed) Biochemical aspects of evolutionary biology. Chicago University Press, Chicago, pp 173–211
- Baker AJ (1991) Cuidado com filhotes pelos pais e outros indivíduos em grupos selvagens de micos leões-dourados (*Leontopithecus rosalia*). In: Rylands AB, Bernardes AT (eds) A primatologia no Brasil 3. Fundação Biodiversitas, Belo Horizonte, pp 209–212
- Baker AJ, Dietz JM, Kleiman DG (1993) Behavioural evidence for monopolization of paternity in multi-male groups of golden lion tamarins. *Anim Behav* 46:1091–1103
- Barrett J, Abbott, DH, George LM (1990) Extension of reproductive suppression by pheromonal cues in subordinate female marmoset monkeys, *Callithrix jacchus*. *J Reprod Fertil* 90:411–418
- Blaustein AR (1981) Sexual selection and mammalian olfaction. *Am Nat* 117:1006–1010
- Box HO, Morris JM (1980) Behavioural observations on captive pairs of wild caught tamarins (*Saguinus mystax*). *Primates* 21:53–65
- Brown RE (1979) Mammalian social odors: a critical review. *Adv Stud Anim Behav* 10:103–162
- Brown RE, Macdonald DW (1985) Social odours in mammals. Clarendon, Oxford
- Buchanan-Smith HM, Jordan T (1992) An experimental investigation of the pair bond in the callitrichid monkey, *Saguinus labiatus*. *Int J Primatol* 13:51–72
- Castro R (1990) Interacciones sociales en parejas reproductivas de *Saguinus mystax* en cautiverio. In: Dirección General Forestal y de Fauna, Instituto Veterinario de Investigaciones Tropicales y de Altura, Organización Panamericana de Salud (eds) La primatología en el Perú. Investigaciones primatólogicas (1973–1985). Imprenta Propacep, Lima, pp 547–554
- Castro R (1991) Behavioral ecology of two coexisting tamarin species (*Saguinus fuscicollis nigrifrons* and *Saguinus mystax mystax*, Callitrichidae, Primates) in Amazonian Peru. PhD dissertation, Washington University
- Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton, NJ
- Clutton-Brock TH, Albon SD (1979) The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69:145–170
- Clutton-Brock TH, Parker GA (1992) Potential reproductive rates and the operation of sexual selection. *Q Rev Biol* 67:437–456
- Clutton-Brock TH, Vincent ACJ (1991) Sexual selection and the potential reproductive rates of males and females. *Nature* 351:58–60
- Coates A, Poole TB (1983) The behavior of the callitrichid monkey, *Saguinus labiatus labiatus*, in the laboratory. *Int J Primatol* 4:339–371
- Converse L, Carson A, Ziegler T, Snowdon CT (1995) Communication of ovulatory state to mates by female pygmy marmosets, *Cebuella pygmaea*. *Anim Behav* 49:615–621
- Darwin C (1871) The descent of man and selection in relation to sex. Murray, London
- Dawson GA, Dukelow RW (1976) Reproductive characteristics of free-ranging Panamanian tamarins, *Saguinus oedipus geoffroyi*. *J Med Primatol* 5:266–275
- Digby LJ (1995) Infant care, infanticide, and female reproductive strategies in polygynous groups of common marmosets (*Callithrix jacchus*). *Behav Ecol Sociobiol* 37:51–61
- Digby LJ, Ferrari SF (1994) Multiple breeding females in free-ranging groups of *Callithrix jacchus*. *Int J Primatol* 15:389–397
- Eisenberg JF, Kleiman DG (1972) Olfactory communication in mammals. *Annu Rev Ecol Syst* 3:1–32
- Encarnación F, Aquino R, Moro J (1990) Flora y vegetación de la Isla Iquitos y Padre Isla (Loreto, Perú): su relación con el

- manejo semiextensivo de *Saguinus mystax*, *Saimiri sciureus* y *Aotus*. In: Dirección General Forestal y de Fauna, Instituto Veterinario de Investigaciones Tropicales y de Altura, Organización Panamericana de Salud (eds) La primatología en el Perú. Investigaciones primatólogicas (1973–1985). Imprenta Propacep, Lima, pp 475–488
- Endler JA (1993) Some general comments on the evolution and design of animal communication systems. *Phil Trans R Soc Lond B* 340:215–225
- Epple G (1973) The role of pheromones in the social communication of marmoset monkeys (Callitrichidae). *J Reprod Fertil [Suppl]* 19:447–454
- Epple G (1974) Olfactory communication in South American primates. *Ann NY Acad Sci* 237:261–278
- Epple G (1979) Gonadal control of male scent in the tamarin, *Saguinus fuscicollis* (Callitrichidae, Primates). *Chem Sens Flav* 4:15–20
- Epple G, Katz Y (1984) Social influences on estrogen excretion and ovarian cyclicity in saddle back tamarins (*Saguinus fuscicollis*). *Am J Primatol* 6:215–227
- Epple G, Belcher AM, Smith AB III (1986) Chemical signals in callitrichid monkeys – a comparative review. In: Duvall D, Müller-Schwarze D, Silverstein RM (eds) Chemical signals in vertebrates 4. Plenum, New York, pp 653–672
- Ewer R (1968) Ethology of mammals. Logos, London
- Ferkin MH, Sorokin ES, Johnston RE, Lee CJ (1997) Attractiveness of scents varies with protein content of the diet in meadow voles. *Anim Behav* 53:133–141
- Ferrari SF (1992) The care of infants in a wild marmoset (*Callithrix flaviceps*) group. *Am J Primatol* 26:109–118
- Ferrari SF, Corrêa HKM, Coutinho PEG (1996) Ecology of the “southern” marmosets (*Callithrix aurita* and *Callithrix flaviceps*) – how different, how similar? In: Norconk MA, Rosenberger AL, Garber PA (eds) Adaptive radiation of neotropical primates. Plenum, New York, pp 157–171
- French JA (1997) Proximate regulation of singular breeding in callitrichid primates. In: Solomon NG, French JA (eds) Cooperative breeding in mammals. Cambridge University Press, Cambridge, UK, pp 34–75
- French JA, Cleveland J (1984) Scent-marking in the tamarin, *Saguinus oedipus*: sex differences and ontogeny. *Anim Behav* 32:615–623
- French JA, Abbott DH, Snowdon CT (1984) The effect of social environment on estrogen excretion, scent marking and socio-sexual behavior in tamarins (*Saguinus oedipus oedipus*). *Am J Primatol* 6:155–167
- Garber PA, Moya L, Malaga C (1984) A preliminary field study of the moustached tamarin monkey (*Saguinus mystax*) in north-eastern Peru: questions concerned with the evolution of a communal breeding system. *Folia Primatol* 42:17–32
- Garber PA, Pruetz JD, Isaacson J (1993) Patterns of range use, range defense, and intergroup spacing in moustached tamarin monkeys (*Saguinus mystax*). *Primates* 34:11–25
- Goldizen AW (1986) Tamarins and marmosets: communal care of offspring. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. Chicago University Press, Chicago, pp 34–43
- Goldizen AW (1987) Facultative polyandry and the role of infant-carrying in wild saddle-back tamarin (*Saguinus fuscicollis*). *Behav Ecol Sociobiol* 20:99–109
- Goldizen AW (1988) Tamarin and marmoset mating systems: unusual flexibility. *Trends Ecol Evol* 3:36–40
- Goldizen AW (1989) Social relationships in a cooperatively polyandrous group of tamarins (*Saguinus fuscicollis*). *Behav Ecol Sociobiol* 24:79–89
- Goodrich BS, Mykytowycz R (1972) Individual and sex differences in the chemical composition of pheromone-like substances from the skin glands of the rabbit *Oryctolagus cuniculus*. *J Mammal* 53:540–548
- Gosling LM, Wright KHM (1994) Scent marking and resource defence by male coypus (*Myocastor coypus*). *J Zool (Lond)* 234:423–436
- Gwynne DT (1991) Sexual competition among females: what causes courtship-role reversal? *Trends Ecol Evol* 6:118–121
- Harcourt AH, Purvis A, Liles L (1995) Sperm competition: mating system, not breeding season, affects testes size of primates. *Funct Ecol* 9:468–476
- Heistermann M, Kleis E, Pröve E, Wolters H-J (1989) Fertility status, dominance, and scent marking behavior of family-housed female cotton-top tamarins (*Saguinus oedipus*) in absence of their mothers. *Am J Primatol* 18:177–189
- Heymann EW (1985) Untersuchungen zur vokalen und olfaktorischen Kommunikation des Schnurrbarttamarins *Saguinus mystax mystax* (Spix, 1823) (Primates: Callitrichidae). PhD thesis, University of Giessen
- Heymann EW (1987) A field observation of predation on a moustached tamarin (*Saguinus mystax*) by an anaconda. *Int J Primatol* 8:193–195
- Heymann EW (1990a) Social behaviour and infant carrying in a group of moustached tamarins, *Saguinus mystax* (Primates: Platyrrhini: Callitrichidae), on Padre Isla, Peruvian Amazonia. *Primates* 31:183–196
- Heymann EW (1990b) Interspecific relations in a mixed-species troop of moustached tamarins, *Saguinus mystax*, and saddle-back tamarins, *Saguinus fuscicollis* (Primates: Callitrichidae), at the Rio Blanco, Peruvian Amazonia. *Am J Primatol* 21:115–127
- Heymann EW (1995a) Urine washing and related behaviour in wild moustached tamarins, *Saguinus mystax* (Callitrichidae). *Primates* 36:259–264
- Heymann EW (1995b) Sleeping habits of tamarins, *Saguinus mystax* and *Saguinus fuscicollis* (Mammalia; Primates; Callitrichidae), in north-eastern Peru. *J Zool (Lond)* 237:211–226
- Heymann EW (1996) Social behavior of wild moustached tamarins, *Saguinus mystax*, at the Estación Biológica Quebrada Blanco, Peruvian Amazonia. *Am J Primatol* 38:101–113
- Heymann EW (1997a) Aspekte der Verhaltensbiologie von Schnurrbarttamarinen, *Saguinus mystax* (Callitrichinae; Cebidae; Primates) in ökologischer, evolutionärer und phylogenetischer Perspektive. Habilitationsschrift, Justus-Liebig-Universität Giessen
- Heymann EW (1997b) The relationship between body size and mixed-species troops of tamarins (*Saguinus* spp.). *Folia Primatol* 68:287–295
- Heymann EW, Zeller U, Schwibbe MH (1989) Muzzle rubbing in the moustached tamarin, *Saguinus mystax* (Primates: Callitrichidae) – behavioural and histological aspects. *Z Säugetierkd* 54:265–275
- Jannett FJ Jr (1986) Morphometric patterns among microtine rodents. I. Sexual selection suggested by relative scent gland development in representative voles (*Microtus*). In: Duvall D, Müller-Schwarze D, Silverstein RM (eds) Chemical signals in vertebrates 4. Plenum, New York, pp 541–550
- Johnson K (1988a) Sexual selection in pinyon jays. I. Female choice and male-male competition. *Anim Behav* 36:1038–1047
- Johnson K (1988b) Sexual selection in pinyon jays. II. Male choice and female-female competition. *Anim Behav* 36:1048–1053
- Johnson RP (1973) Scent marking in mammals. *Anim Behav* 21:521–535
- Johnstone RA (1995) Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biol Rev* 70: 1–65
- Kappeler PM (1998) To whom it may concern: the transmission and function of chemical signals in *Lemur catta*. *Behav Ecol Sociobiol* 42:411–421
- Kavaliers M, Colwell DD (1995a) Discrimination by female mice between odours of parasitized and non-parasitized males. *Proc R Soc Lond B* 261:31–35
- Kavaliers M, Colwell DD (1995b) Odours of parasitized males induce aversive response in female mice. *Anim Behav* 50:1161–1169
- Keddy-Hector AC (1992) Mate choice in non-human primates. *Am Zool* 32:62–70



- Kirkpatrick-Tanner M, Aeschlimann C, Anzenberger G (1996) Occurrence of an infanticide within a captive polygynous group of common marmosets, *Callithrix jacchus*. *Folia Primatol* 67:52–58
- Knogge C (1998) Tier-Pflanze-Interaktionen im Amazonas-Regenwald: Samenausbreitung durch die sympatrischen Tamarinarten *Saguinus mystax* und *Saguinus fuscicollis* (Callitrichinae, Primates). PhD thesis, University of Bielefeld
- Kodric-Brown A, Brown JH (1984) Truth in advertising: the kinds of traits favored by sexual selection. *Am Nat* 124:309–323
- Koenig A (1995) Group size, composition, and reproductive success in wild common marmosets (*Callithrix jacchus*). *Am J Primatol* 35:311–317
- Koprowski JL (1993) Sex and species biases in scent-marking by fox squirrels and eastern grey squirrels. *J Zool (Lond)* 230:319–323
- Krebs JR, Davies NB (1993) An introduction to behavioural ecology, 3rd edn. Blackwell, Oxford
- Lincoln GA (1994) Teeth, horns and antlers: the weapons of sex. In: Short RV, Balaban E (eds) The differences between the sexes. Cambridge University Press, Cambridge, UK, pp 131–158
- Martin P, Bateson P (1993) Measuring behaviour. Cambridge University Press, Cambridge, UK
- Mittermeier RA, Rylands AB, Coimbra-Filho A, Fonseca GAB (1988) Ecology and behavior of neotropical primates, vol 2. World Wildlife Fund, Washington, DC
- Moya L, Ique C, Soini P (1990) Introducción experimental y desarrollo de una población de *Saguinus mystax* en Padre Isla, Iquitos, Perú. In: Dirección General Forestal y de Fauna, Instituto Veterinario de Investigaciones Tropicales y de Altura, Organización Panamericana de Salud (eds) La primatología en el Perú. Investigaciones primatólogicas (1973–1985). Imprenta Propacep, Lima, pp 526–536
- Mykytowycz R (1972) The behavioural role of the mammalian skin glands. *Naturwissenschaften* 59:133–139
- Payne AP, Swanson HH (1970) Agonistic behaviour between pairs of hamsters of the same and opposite sex in a neutral observation area. *Behaviour* 36:259–269
- Ralls K (1971) Mammalian scent marking. *Science* 171:443–449
- Reynolds JD, Harvey PH (1994) Sexual selection and the evolution of sex differences. In: Short RV, Balaban E (eds) The differences between the sexes. Cambridge University Press, Cambridge, UK, pp 53–70
- Rohrhuber B (1990) Qualitative und quantitative Unterschiede zwischen den Geschlechtern im Verhalten paarweise lebender Lisztaffen (*Saguinus oedipus oedipus*). PhD thesis, University of Kassel
- Ryan MJ (1985) The Tungara frog: a study in sexual selection and communication. University of Chicago Press, Chicago
- Rylands AB (1986) Infant-carrying in a wild marmoset group, *Callithrix humeralifer*: evidence for a polyandrous mating system. In: Thiago de Mello M (ed) A primatologia no Brasil 2. Sociedade Brasileira de Primatologia, Brasília, pp 131–144
- Savage A, Ziegler TE, Snowdon CT (1988) Sociosexual development, pair bond formation, and mechanisms of fertility suppression in female cotton-top tamarins (*Saguinus oedipus oedipus*). *Am J Primatol* 14:345–359
- Schultze-Westrum J (1965) Innerartliche Verständigung durch Düfte beim Gleitbeutler *Petaurus breviceps papuanus* Thomas (Marsupialia, Phalangeridae). *Z Vergl Physiol* 50:151–220
- Smith AC (1997) Comparative ecology of saddleback (*Saguinus fuscicollis*) and moustached (*Saguinus mystax*) tamarins. PhD thesis, University of Reading
- Snowdon CT, Soini P (1988) The tamarins, genus *Saguinus*. In: Mittermeier RA, Rylands AB, Coimbra-Filho A, Fonseca GAB (eds) Ecology and behavior of neotropical primates, vol 2. World Wildlife Fund, Washington, DC, pp 223–298
- Soini P (1987) Sociosexual behavior of a free-ranging *Cebuella pygmaea* (Callitrichidae, Platyrrhini) troop during postpartum estrus of its reproductive female. *Am J Primatol* 13:223–230
- Soini P (1990) Ecología y dinámica poblacional de pichico común *Saguinus fuscicollis* (Callitrichidae, Primates). In: Dirección General Forestal y de Fauna, Instituto Veterinario de Investigaciones Tropicales y de Altura, Organización Panamericana de Salud (eds) La primatología en el Perú. Investigaciones primatólogicas (1973–1985). Imprenta Propacep, Lima, pp 202–253
- Soini P, Soini M de (1990) Distribución geográfica y ecología poblacional de *Saguinus mystax*. In: Dirección General Forestal y de Fauna, Instituto Veterinario de Investigaciones Tropicales y de Altura, Organización Panamericana de Salud (eds) La primatología en el Perú. Investigaciones primatólogicas (1973–1985). Imprenta Propacep, Lima, pp 272–313
- Thompson VD, Fadem BH (1989) Scent marking in the koala (*Phascolarctos cinereus*): related behavior and sex differences. *Zool Garten NF* 59:157–165
- Zeller U, Epple G, Küderling I, Kuhn H-J (1988) The anatomy of the circumgenital scent gland of *Saguinus fuscicollis* (Callitrichidae, Primates). *J Zool (Lond)* 214:141–156
- Ziegler TE, Epple G, Snowdon CT, Porter TA, Belcher AM, Küderling I (1993). Detection of the chemical signals of ovulation in the cotton-top tamarin, *Saguinus oedipus*. *Anim Behav* 45:313–322

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