

## Female-female aggression and male indifference in response to unfamiliar intruders in lion tamarins

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**Abstract.** The role of intolerance toward unfamiliar conspecifics in promoting exclusivity of mating and preferential association among breeding pairs was examined in captive golden lion tamarins, *Leontopithecus rosalia*. In their home cage, resident breeding pairs were presented with an intruder that varied in sex and age (adult or subadult). Resident female tamarins directed high levels of attack, agonistic displays, and approaches toward subadult and adult female intruders. Male residents, in contrast, showed virtually no attack responses to intruders of any sex-age class, and showed only moderate levels of agonistic displays in the presence of adult male intruders. Attacks and threats by resident females were associated with the number of subadult helpers present in the social group: females in groups with more helpers present exhibited higher levels of aggression to intruders. The results suggest that female intolerance of conspecifics may be important in the regulation of sociosexual relationships in breeding pairs, and that female-female reproductive competition is particularly extreme in this species.

Most definitions of monogamous mating systems that do not limit the definition to the ways in which gametes combine (e.g. Gowaty 1981) contain at least a passing statement about the social relationship between the breeding adult male and female (e.g. Kleiman 1977b; Dewsbury 1988). While it is generally recognized that a special social relationship between a male and female need not be present for a mating relationship to be considered monogamous (Wickler & Seibt 1983), such relationships do in fact occur with regularity in mated pairs for a variety of vertebrate species. Dewsbury (1988) has identified three important dimensions of monogamy, two of which, exclusivity of mating and preferential association, involve some assessment of the social and reproductive relationship between breeding partners in a monogamous setting. There are many behavioural manifestations of these two dimensions, including the restriction of copulation to the breeding male and female, joint nesting, shared home ranges, coordinated travel, and close spatial and temporal proximity. These patterns have been documented in monogamous social systems for a number of diverse taxonomic forms (Kleiman 1977b).

Although patterns of exclusive mating and preferential association have been widely reported in monogamous species, the behavioural processes that produce these outcomes have not received as much attention. There are, potentially, two mechanisms that can promote and maintain mating and

social stability between monogamous partners. First, each partner can preferentially direct affiliative and sexual responses exclusively toward the long-standing pair-mate. In effect, the characteristic social relationship between mated pairs is an emergent property resulting from selectivity in the behavioural responses of both individuals involved in a relationship (Anzenberger 1985). An alternative mechanism that would promote mating exclusivity between partners and would enforce preferential association patterns is the situation in which either or both partners exhibit an extreme intolerance for conspecifics of their own sex. This would produce an aggressive exclusion of potential reproductive competitors from the social group or home range.

Long-term captive studies and recent field reports suggest that the social system of callitrichids is characterized by communal rearing (extended residence of offspring and possibly unrelated adult individuals of both sexes in breeding groups) with a monogamous (and, in some species, possibly polyandrous) mating relationship among the two breeding adults in a social group (Epple 1975; Kleiman 1977a; Terborgh & Goldizen 1985; Sussman & Garber 1987). Only one female in each social group is sexually active (e.g. Abbott 1984; French et al. 1984), and sexual behaviour is limited almost exclusively to one adult male and this female (Rothe 1975; French et al. 1984; but see Epple 1975; Goldizen 1987). This is true even in

cases where more than one adult of a sex is present in a social group (Kleiman 1978). For these reasons, callitrichid primates represent good species in which to evaluate mechanisms for promoting exclusivity and fidelity in social and mating relationships.

Both processes for maintaining the social and sexual integrity of breeding pairs in several species of marmosets and tamarins have been reported. In captive settings, callitrichid primates show an extreme intolerance for unfamiliar conspecifics (e.g. Epplé 1977; Sutcliffe & Poole 1978; French & Snowdon 1981). In most cases, agonistic displays and attacks by members of the resident pair are directed toward adult, same-sex intruders. Reports of encounters between neighbouring groups or solitary individuals and established social groups in free-ranging callitrichids (Neyman 1977; Izawa 1978; Dawson 1979) suggest that the patterns observed in captivity are characteristic of encounters in the field. Thus, mating exclusivity and preferential association in the breeding pair could be maintained through intolerance for same-sex conspecifics by one or both members of the breeding pair.

A tendency toward intersexual social aversion for unfamiliar conspecifics may also contribute to exclusivity in some species. When exposed to unfamiliar conspecifics of the opposite sex, the behaviour of mated common marmosets, *Callithrix j. jacchus*, is distinct from that of non-mated individuals. Mated individuals, particularly females, respond assertively and often aggressively to conspecifics of the opposite sex, and sexual encounters are rare. The opposite is true of non-mated marmosets in the same situation; submissive, affiliative, and sexual behaviour is frequent (Evans 1983; Anzenberger 1985). Based upon these data, then, mated individuals are less likely than non-mated individuals to be receptive to unfamiliar conspecifics.

Detailed studies of sociosexual interactions in captive callitrichids have found high levels of affiliative behaviour, including preferential grooming, huddling and spatial proximity between the breeding adult male and female in a social group (Kleiman 1977a; Ruiz 1982; Evans & Poole 1983, 1984; Stribley et al., in press). In captive studies where more than one adult of either or both sexes have been established in a single social group, a clear sociosexual relationship exists between only one male and female (Kleiman 1978; Abbott 1984;

French et al. 1984). These patterns between pairs of animals persist even in cases where the male or female is gonadectomized (Kendrick & Dixon 1984; Epplé et al. 1987). There is evidence, therefore, that social relationships may be maintained in callitrichid primates through a strong social attraction between partners.

In this series of observations, we evaluated the potential role of intolerance toward unfamiliar conspecifics as a potential mechanism for maintaining exclusivity of mating and preferential association in captive pairs of lion tamarins, *Leontopithecus rosalia*. We monitored the responses of paired adult male and female lion tamarins to the presentation of an unfamiliar conspecific in their resident cage. Three questions were addressed: (1) Do male and female residents respond differently to conspecific intruders? (2) Do the responses of residents differ as a function of the sex of the intruder? (3) Does resident responsiveness to conspecific intruders differ as a function of the age of the intruder?

## METHOD

### Animals and Housing

Thirteen golden lion tamarins were used as either focal resident subjects or intruders, or served in both roles in this study. The tamarins were members of a colony housed in the University of Nebraska at Omaha callitrichid vivarium. Table I presents the demographic characteristics of the social groups from which the subjects and intruders were drawn. Tamarins were housed in social groups consisting either of a breeding pair ( $N=1$ ) or a breeding pair and their offspring ( $N=3$ ). The number of subadult offspring in each family group ranged from zero to four (Table I).

Cages were large and designed to encourage activity and social interactions. The cages were constructed of wood frames and wire-mesh walls, and contained nest boxes, branches and a variety of suspended and attached objects to enhance exploration and activity. Breeding pairs with offspring were housed in family cages measuring  $2.0 \times 2.0 \times 1.8$  m, while the breeding pair without offspring was housed in a  $2.0 \times 1.0 \times 1.8$ -m cage. One adult male who served as an intruder was housed alone throughout the first replication of the study. Separate social groups were housed in auditory and olfactory, but not visual, contact. The

Table 1. Characteristics of resident pairs used as focal animals

Breeding female ISIS* (ID)	Breeding male ISIS (ID)	Subadult residents	
		N	Age/sex (male; female)
104187 (Ch)	104753 (Sa)	0	
104659 (Em)	105594 (Ru)	2	6-month-old twins (1:1)
101187 (Al)	100068 (Be)	3	18-month-old twins (1:1) 9-month-old singleton (1:0)
10233 (Sh)	100319 (Br)	4	24-month-old twins (2:0) 12-month-old twins (2:0)

\*ISIS: International Species Inventory System animal code.

tamarins were provided with fresh fruits, vegetables, dairy products, canned Zu-Preem marmoset diet, and fresh water once daily between 0730 and 0930 hours.

#### Experimental Design and Procedure

Our main research questions dealt with differential responsiveness of residents to sex and social status characteristics of intruding animals. Therefore, each resident pair received exposure to both male and female intruders who varied in social status within their own social group. Two categories of social status were defined. (1) adult: intruders who occupied the breeding role in their own social group; and (2) subadult: intruders who were offspring of breeding pairs and resided in their natal family group, and hence did not occupy a breeding role in their own social group. Subadult intruders ranged in age from 1.5 to 3.5 years, and were postpubertal (French 1987; French & Stribley 1987).

In all cases, the tamarins selected to serve as intruders for each resident pair were visually unfamiliar to the residents. Because all cages were contained in a common colony suite, residents were familiar with the odours and vocalizations of intruders. This situation is probably very similar to the experience of free-ranging lion tamarins, where neighbouring groups encounter each other frequently (A. Baker, personal communication). With two exceptions, intruders were also unrelated to either member of the resident pair. In the two exceptions, a subadult female intruder was a younger sibling of the resident adult female. However, the resident female and the intruder female had never co-resided in the family group, and hence were not visually familiar with each other.

Two trials were conducted for each of the four

intruder conditions (male and female, adult and subadult) in all cages. In all cases except one, the two replications used a different tamarin for a given sex-status combination. In one case, the female adult intruder was the same tamarin which had been used in the first replication, because the resident female was related to and familiar with all but one other adult female in the colony.

An intruder cage was used to introduce tamarins into the cage of resident pairs. Five of the six walls of the intruder cage (45 × 60 × 45 cm) were made of wire mesh and were held together by galvanized steel corner junctions. A wood perch was fitted in the centre of the cage. Intruder tamarins were placed within the intruder cage and remained there, in visual contact with their home cage, for approximately 5 min to allow them to habituate to the cage. Immediately after the 5-min habituation phase, the intruder was placed within the mated pair's cage and the trial began.

Trials were 20 min in duration and were divided into 80 15-s intervals by a soft click from a timer. In some cases an intruder was presented to more than one cage in a single day. However, resident pairs each received only one trial in any given day, and often several days intervened between successive trials. The intruder cage was washed with disinfectant soap and hot water after each day's trials, and was allowed to air dry prior to subsequent trials.

#### Behavioural Methodology

Behavioural responses of the adult male and female were recorded on standardized check sheets by two trained human observers. The observers were each assigned a focal adult resident to observe; the assignments rotated between trials. Inter-observer reliability between the observers in

this experiment (BJI and JAF) was monitored as part of a previous study on social and sexual behaviour of lion tamarins (Stribley et al., in press), and was found to be consistently high ( $r > 0.90$ ). The behavioural responses of intruder tamarins and offspring housed with the resident pair were not recorded systematically; however, significant events involving intruders or offspring were noted after the trial. We assessed three major categories of behaviour in response to the presentation of intruders: (1) spatial relationship between residents and the intruder and investigatory behaviour; (2) non-contact, agonistic displays; (3) attempts at potentially injurious aggression. All behaviour sampling methods are after Altmann (1974).

#### *Spatial behaviour and investigation*

Proximity of focal resident tamarins to both the intruder cage and their mate was recorded at each signal from the timer (i.e. every 15 s; instantaneous sampling). Resident tamarins were recorded as either being in close proximity (in contact or within 8 cm) of the resident mate and the intruder, or as being more than 8 cm from the mate and intruder. Approaches of resident tamarins from greater than arm's length (approximately 8 cm) to less than arm's length to the intruder cage were recorded each time they occurred. All occurrences of sniffing the intruder cage or the intruder through the wire mesh were recorded.

#### *Agonistic displays*

Three forms of agonistic displays (visual, olfactory and vocal), and four manifestations of aggression were recorded. Each was recorded every time they occurred, with the exception of chatters and long calls (see below). It was rare for agonistic or aggressive displays to occur in isolation; usually there was a long, escalating sequence of several agonistic display patterns leading to aggressive interactions.

**Look away:** the tamarin was typically positioned with its back to the intruder cage and would repeatedly roll its head backward.

**Frontal stare:** the intruder tamarin and one of the resident adults were separated by 3–10 cm and looked directly into each others' eyes. Both look away and frontal stares have been noted during periods of colony disruption and immediately prior to intra-family aggressive altercations (Inglett et al., in press).

**Arch walk:** the tamarin arches the back and

stiffens the legs and arms and walks in a tottering, stiff manner. During this process the animal is usually piloerected. Rathbun (1979) has provided a more detailed description of this behaviour pattern and the conflict contexts in which it occurs.

**Scent mark:** both circumgenital and ventral marking were recorded. Both males and females exhibit these patterns (Kleiman & Mack 1980), and in other callitrichids scent marking is often associated with social communication, agonistic displays and aggression (e.g. French & Snowdon 1981; Eppe, et al. 1982).

**Vocalizations:** long calls and chatters were recorded. Long calls have been described by McLanahan & Green (1977). Our chatters are similar to the C trill also described by McLanahan & Green (1977). We recorded the number of 15-s intervals in which either long calls or chatters occurred.

#### *Attempts at contact aggression*

**Chase:** a resident adult rapidly followed the intruder tamarin as it moved about the intruder cage. The resident appeared to be trying to catch the intruder.

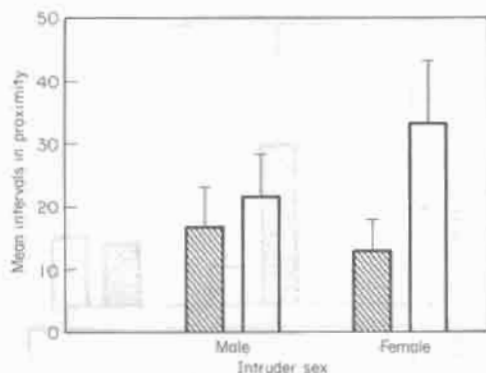
**Charge:** a resident adult would run approximately 10–30 cm at a rapid speed toward the intruder cage. The tamarin would stop just before contacting the cage screen, and often a chase would ensue.

**Grab:** a tamarin probed or attempted to reach through the screen toward the intruder. This was typically a rapid almost frantic action and was interpreted as an aggressive attempt at contact.

**Attack:** the resident tamarin would leap onto the mesh of the intruder cage and try to grab or bite the intruder through the mesh. Jumping and pulling on the screen were noted as part of the attack. This pattern was observed in both resident adults and intruders but we were only able consistently to record attacks by resident adults directed toward the intruder. One trial was stopped after approximately 13 min because of extreme levels of aggression between the resident female and an adult female intruder. The data for all behavioural categories for this trial were normalized to the frequency of occurrence per 20 min prior to analysis.

#### **Analyses**

A mixed-design analysis of variance, with resident sex, intruder sex, intruder social status, and replication as factors, was used to assess treatment effects. Preliminary analyses revealed no significant



**Figure 1.** Mean (+1 SE) number of intervals (out of a total possible of 80) that resident males and females were in close proximity to each other (in contact or within 8 cm) as a function of sex and social status of the intruder. ▨: resident responses to adult intruders; □: resident responses to subadult intruders.

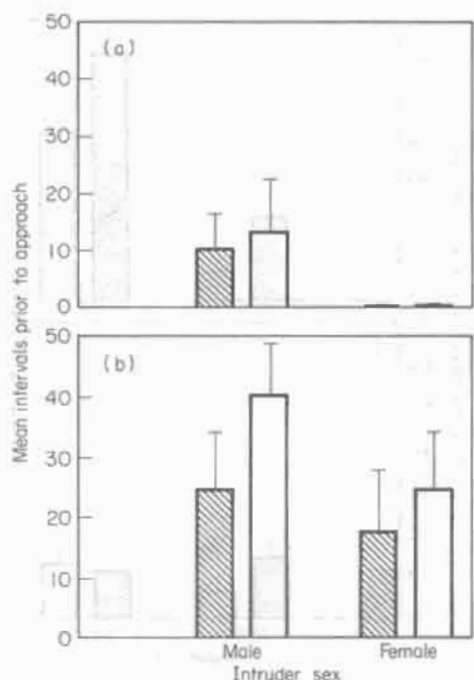
main effects or interactions involving the replication factor. Therefore, means for each behavioural category were collapsed across the first and second replication, and three-way analyses performed. Post-hoc analyses involved the use of least significant difference tests (Keppel 1982) on all interaction effects in which  $P < 0.05$ . Pearson correlation coefficients were calculated between levels of male and female resident agonistic displays and aggression toward intruders and the number of subadult offspring present in the cage during the time of testing.

## RESULTS

### Spatial Behaviour and Investigation of Intruder

The proximity between male and female residents was affected by the status, but not the sex, of the intruder tamarin. The residents were in close proximity to each other during more intervals when the intruders were subadults than when the intruders were adults ( $F = 6.15$ ,  $df = 1, 6$ ,  $P < 0.05$ ; Fig. 1). During the time that resident tamarins were in close proximity to each other, they were typically sitting quietly together or grooming on a branch or the nestbox. Differences in proximity between the residents did not differ significantly as a function of the sex of the intruder.

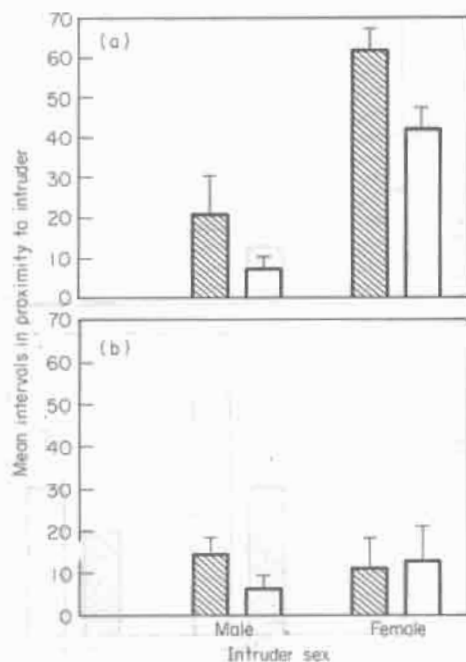
Dramatic differences were found in the latency for residents to approach the intruder as a function of the intruder's sex ( $F = 6.44$ ,  $df = 1, 6$ ,  $P < 0.05$ ;



**Figure 2.** Mean (+1 SE) latency to approach the intruder after the onset of the trial. Latency was calculated by recording the number of 15-s intervals until the resident tamarin first approached within 8 cm of the intruder cage. (a) Female resident latency to approach; (b) male resident latency to approach. ▨: resident responses to adult intruders; □: resident responses to subadult intruders.

Fig. 2). Female intruders were approached more quickly than male intruders (within 10.78 versus 18.28 intervals, respectively). Adult intruders were approached significantly more quickly than subadult intruders (adults: within 9.41 intervals; subadults: within 19.65 intervals;  $F = 7.66$ ,  $df = 1, 6$ ,  $P < 0.04$ ). Female residents quickly discriminated the sex of the intruder tamarin, and invariably approached a female intruder of either adult or subadult status within the first 15-s interval. Males approached the intruder more slowly than females, taking more than 10 min (40 15-s intervals) to approach the intruder cage if it contained a subadult male. The absolute frequency of approaching the intruder cage was not affected by resident sex, intruder sex, or intruder status. Female intruders tended to be approached more frequently than male intruders (7.81 versus 5.25 approaches, respectively), and adult intruders were approached



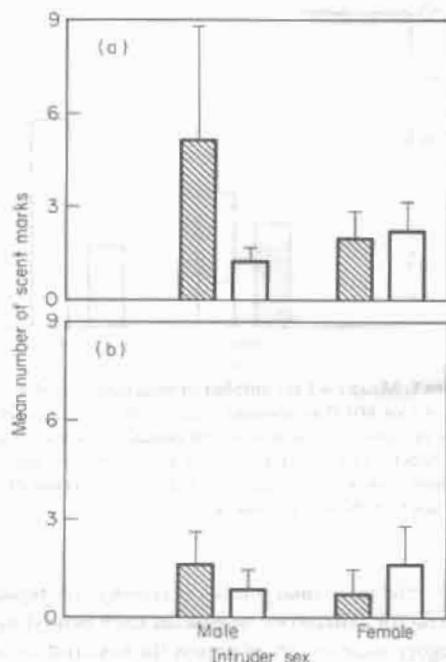


**Figure 3.** Mean ( $\pm 1$  SE) number of intervals in which resident female (a) and male (b) tamarins were observed in close proximity (within 8 cm) to the intruder. See legend to Fig. 2 for details.

an average of 7.94 times and subadults 4.87 times per trial.

The regulation of social distance between residents and the intruder differed markedly across the intruder conditions (Fig. 3). A significant three-way interaction revealed that proximity to the intruder by male and female residents was differentially influenced by intruder sex and status ( $F=10.94$ ,  $df=1,6$ ,  $P=0.016$ ). Post-hoc tests showed that female residents were in close proximity to adult female intruders for significantly more intervals than any other intruder status/sex classification. Female residents also tended to spend more time near adult intruders of both sexes ( $P<0.01$ ). Male residents, in contrast, showed no differential tendency to stay near intruders of either sex or status.

Olfactory investigation of the intruder was measured by the frequency of sniffing the intruder or the intruder cage. An interaction between the sex and status of the intruder was found ( $F=12.57$ ,  $df=1,6$ ,  $P=0.01$ ), and post-hoc analyses indicated that adult female intruders received significantly



**Figure 4.** Mean ( $\pm 1$  SE) number of scent marks (both circumgenital and ventral) directed toward intruders by resident females (a) and males (b). See legend to Fig. 2 for details.

more sniffs from both male and female residents than any other intruder sex/age category ( $P<0.05$ ).

#### Agonistic Displays

The distribution of scent marking across trials was not affected by the nature of the intruder. No significant differences were detected in levels of scent marking as a function of intruder sociosexual status, although resident females may tend to scent mark more in the presence of adult male intruders (Fig. 4). Detailed examination of the individual trial transcripts revealed that the high score in this condition was primarily due to an extreme scent marking bout by one resident female during the second replication (35 scent marks during a 20-min trial). When the data were plotted with this extreme score removed, levels of scent marking by male and female residents were constant across intruder sex and status conditions.

A cumulative score for non-contact threat behaviour patterns was calculated by summing the scores for visual (look away, frontal stare and arch

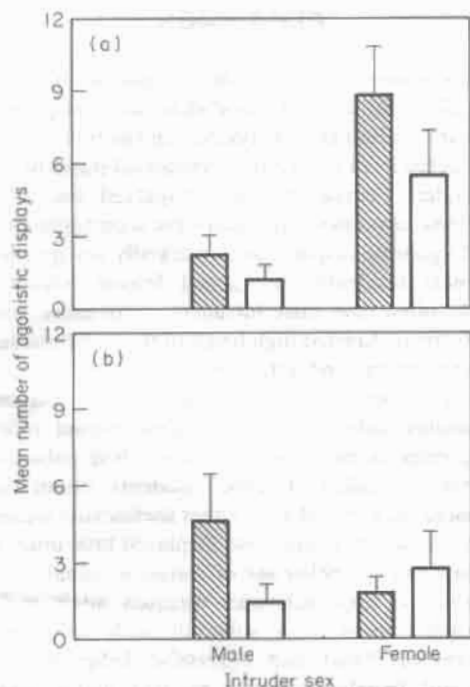


Figure 5. Mean (+1 SE) combined agonistic displays (visual, vocal and olfactory) by resident females (a) and males (b). See legend to Fig. 2 for details.

walk), auditory (long call and chatter) and olfactory (circumgenital and ventral scent mark) threats (Fig. 5). A significant intruder sex by resident sex interaction was obtained, and post-hoc comparisons indicated that threats from resident females to female intruders were significantly greater than all other resident sex-intruder sex conditions ( $F=11.08$ ,  $df=1,6$ ,  $P<0.02$ ). Adult intruders also received significantly higher levels of total threats than subadult intruders ( $F=15.27$ ,  $df=1,6$ ,  $P<0.01$ ).

#### Aggressive Behaviour

The scores of each resident for aggressive behaviour patterns (chasing, charging, grabbing and attacking) were combined for analysis. The greatest degree of sex-specificity in resident responses toward intruding tamarins was observed for these behaviour patterns (Table II). A significant three-way interaction between resident sex, intruder sex and intruder status was obtained ( $F=7.64$ ,  $df=1,6$ ,  $P<0.03$ ). Female residents exhibited extremely high levels of aggression, but only to female

Table II. Mean number of cumulative attacks (chase, charge, grab and attack) by male and female residents

Sex of resident	Male intruders		Female intruders	
	Adult	Subadult	Adult	Subadult
Female	0	0	10.70 (4.60)	1.50 (1.50)
Male	0.25 (0.25)	0	0.36 (0.36)	0

Numbers in parentheses indicate +1 SE.

intruders. Aggression by female residents toward adult female intruders was significantly higher than toward subadult females ( $P<0.01$ ). Females were never observed to behave aggressively toward male intruders of either status. The reaction of resident females to adult female intruders was intense and severe, and one trial had to be stopped prior to its completion to prevent serious injury to both the resident and intruding adult female. The aggression during this trial was extreme but not uncharacteristic of aggression observed during previous trials with adult female intruders.

Only one male resident (Br) exhibited aggressive behaviour toward intruders (three instances). Two attacks were observed during a trial with an adult male intruder, and one attack during a trial with an adult female intruder. The single attack of the female adult intruder occurred when Br's mate was involved in an extremely intense aggressive bout with the female adult intruder. No other males were ever observed to exhibit any aggressive behaviour during trials in this study.

#### Agonistic Displays, Aggression and Number of Resident Subadult Offspring

Table I indicates that the number of subadult offspring present in the four family groups ranged from zero to four. To assess the influence of different numbers of non-breeding helpers on aggression by breeding adults toward intruders, we calculated Pearson correlation coefficients between the number of subadults in each pair's cage and levels of aggression (in adult female residents) and total agonistic displays (both male and female residents). The mean number of aggressive acts toward adult female intruders by female residents was highly correlated with the number of subadult

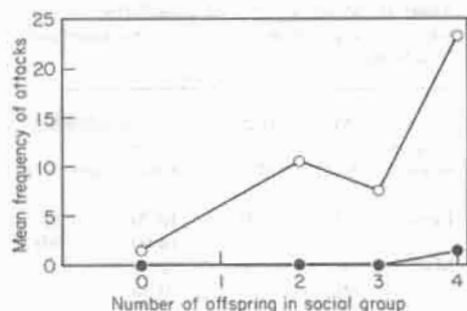


Figure 6. Mean number of attacks directed toward female intruders (adult:  $\circ$ ; subadult:  $\bullet$ ) by female residents as a function of the number of subadult offspring present in the female resident's social group.

Table III. Pearson correlations between levels of agonistic displays by residents and the number of subadult offspring in the family group

Sex of resident	Intruder category			
	Adult female	Subadult female	Adult male	Subadult male
Female	0.798*	0.637	-0.618	-0.451
Male	0.356	0.118	-0.537	-0.227

\*  $P < 0.05$ .

offspring in the family group ( $r = 0.858$ ,  $P < 0.05$ ; Fig. 6). The only aggression toward subadult female intruders occurred in the family group with four subadult offspring present. Table III shows Pearson correlation coefficients between total agonistic displays and number of helpers for various intruder sex/status combinations. The only significant positive correlation between threats by residents and number of subadult helpers in a family group occurred for resident females in the presence of adult female intruders. As the number of subadults in the social group increased, resident females tended to show higher levels of threats. Threats by female residents and male residents to male intruders were negatively (but not significantly) correlated with the number of subadult offspring. Threats by male residents toward female intruders were only slightly positively correlated with the number of subadults present in the social group.

## DISCUSSION

These observations indicate that paired male and female lion tamarins modulate their responses toward unfamiliar conspecifics on the basis of the sex of the intruder and the sociosexual status of the intruder. Female residents displayed the most extreme responses to intruders, but their aggression and agonistic displays were markedly sex-specific. Female residents approached female intruders more often than male intruders, spent more time near them, directed high levels of threat behaviour toward them, and attempted to engage them in bouts of potentially injurious aggression. For most measures, adult female intruders elicited more responses from female residents than subadult female intruders. Female residents essentially ignored male intruders of either sociosexual status. Male residents, in contrast, displayed little interest in intruders of either sex or status, although they tended to approach and threaten adult male intruders more than subadult male intruders. Levels of threat and aggressive behaviour by resident females, but not resident males, were associated with the number of subadult offspring present in the social group: adult female residents with more subadult offspring displayed higher levels of threat and aggression. As indicated by these results, mating exclusivity and preferential association among breeding pairs in lion tamarins could be maintained at least in part by intolerance of unfamiliar conspecifics, especially by breeding females (see also Kleiman 1979).

Patterns of sex-specificity in threat and aggression directed toward unfamiliar conspecifics have been reported in several other callitrichid species. However, no study has reported such a skewed distribution of aggression and threat, strongly biased toward female-female aggression. In common marmosets and saddleback tamarins, *Saguinus fuscicollis*, aggression and threat are almost exclusively directed toward same-sex intruders, and quantitative comparisons of aggression suggest that males and females are equally intolerant of intruders (Epple 1977; Sutcliffe & Poole 1978, 1984; Epple et al. 1982; Epple & Alveario 1985). Encounters between unfamiliar cotton-top tamarins, *Saguinus o. oedipus*, result in potentially injurious aggression between adult males only, although female residents do display threat behaviour toward both male and female intruders (French & Snowdon 1981). The present study revealed that



agonistic displays and aggression by male lion tamarins are rare, even in the presence of an unfamiliar adult male. In contrast, encounters between unfamiliar females are characterized by high levels of both threat and aggression. Other potential hypotheses purporting to account for intolerance to intruders, such as territorial defence or protection of paternity (Gowaty 1981b) do not account for the patterns reported in this study. The fact that aggression to intruders is highly sex-specific and limited to females suggests that reproductive competition among female lion tamarins is particularly extreme.

Resident tamarins were able to recognize the sociosexual status of intruders, as evidenced by distinctions in aggressive behaviour and agonistic displays directed toward subadult and adult intruders. Residents spent more time near adult intruders, threatened them more, and, in the case of female intruders, directed aggression toward them. In many callitrichid species, subadult females in social groups are reproductively suppressed, and exhibit low and non-cyclic levels of oestrogen and luteinizing hormone production (Abbott 1984; French et al. 1984; Ziegler et al. 1987b). It is possible that discrimination of sociosexual status in these species could be accomplished on the basis of some endocrine-dependent cue, such as odour (Epple 1979). However, in lion tamarins both subadult females (French & Stribley 1987) and males (French 1987) are indistinguishable from breeding adults in endocrine status. Thus, discrimination of sociosexual status must rely on behavioural differences between subadults and adults, or on non-endocrine differences in odours. Although the behaviour of intruder tamarins was not recorded systematically during intruder trials, an analysis of notes recorded after each trial indicated that subadult intruders tended to be less active within the intruder cage than adults, and rarely responded in kind to agonistic displays and attacks from residents, whereas adult intruders, especially females, did so often. Subadult intruders also did not initiate or attempt to engage in visual contact with residents.

Although the sample size in the study was small, a significant relationship was discovered between the number of subadults present in the social group and the levels of intolerance by the resident adult female toward female intruders. Females with potentially more helpers were more aggressive toward intruders. It is well established that repro-

duction is costly for female marmosets and tamarins. Females routinely produce twin offspring that can weigh up to 20–25% of maternal weight at birth (Leutenegger 1973) and often initiate subsequent reproductive efforts shortly after parturition (French & Stribley 1985; Ziegler et al. 1987a). Helpers, including breeding adult males, subadult offspring, and unrelated adults, are considered to be essential for the successful rearing of offspring (Epple 1975; Terborgh & Goldizen 1985). Some researchers have speculated that the presence of helpers contributes substantially to the reproductive success of breeding males and females (Goldizen 1987). Our results suggest a potential mechanism whereby smaller groups could recruit additional helpers; namely, through the regulation of behavioural intolerance to unfamiliar conspecifics. Small groups of callitrichids could recruit unrelated helpers, even immigrant adult females, by minimizing attacks and agonistic displays. Larger, established groups could rely on older offspring for assistance in carrying and provisioning immature offspring. Hence these groups would not require additional helpers and could exclude immigrating individuals (and potential reproductive competitors) through aggression and agonistic displays. These results contribute to the growing body of literature indicating that social behaviour and mating systems are remarkably flexible in the family Callitrichidae, and that both may be sensitive to social context (Evans 1983; Anzenberger 1985; Epple & Alveario 1985).

The results of this experiment suggest that the social relationship between an adult male and female lion tamarin is maintained by intolerance of same-sex conspecifics, especially in the case of females. Although pair-bonds may develop between adult males and females, they appear to be of lesser importance for maintaining social cohesion. Support for this interpretation can be found in studies demonstrating flexibility in the responses of callitrichids to unfamiliar conspecifics in differing social contexts. Several studies have revealed that male common marmosets respond differently to opposite-sex tamarins in the presence of their pair-mate than they do in their absence. Interactions between adult males and unfamiliar females tend to be characterized by affiliation and friendly contact-seeking behaviour in the absence of the mate, while male aggression is common when tested in the presence of the female pair-mate (Evans 1983; Sutcliffe & Poole 1984; Anzenberger

1985). The responses of females toward unfamiliar males consist of disinterest or slightly aggressive behaviour, regardless of social context (Anzenberger 1985). Preliminary evidence from our laboratory on the social preferences of adult lion tamarins also suggests that female-female aggression in lion tamarins is important for stability in the breeding pair. Paired females show little interest in unfamiliar males when given a choice between their mate and the unfamiliar male, but paired males approach unfamiliar females more often than their mate approaches unfamiliar males (Inglett 1988). High levels of female aggression could effectively prevent contact between males and unfamiliar females, and maintain reproductive exclusivity and preferential association.

Reproductive competition is certainly a critical pressure on callitrichid primates. However, the manifestation of this competition differs between species and across sexes. Intrasexual reproductive competition in cotton-top tamarins has been documented in both males and females, but the mechanism used by each sex differs from the other. Male cotton-top tamarins are overtly aggressive to potential reproductive competitors, while females are not (French & Snowdon 1981). Female cotton-top tamarins possess the capacity directly to inhibit reproductive function in all other females in the social group (French et al. 1984). In golden lion tamarins, females use the same competitive mechanism as male cotton-top tamarins: females are aggressively intolerant of other females. The lack of either overt aggression (present study) or physiological suppression (French 1987) in male lion tamarins is surprising, and the reasons for the absence of reproductive competition in males are not apparent. For female tamarins, however, the ultimate outcome of reproductive competition is the same regardless of its manifestation: both aggression and reproductive suppression lead to a reduction in competition for limited reproductive resources.

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