

## Group size and aggression: 'recruitment incentives' in a cooperatively breeding primate

COLLEEN M. SCHAFFNER & JEFFREY A. FRENCH

*Department of Psychology, University of Nebraska at Omaha*

*and*

*Nebraska Behavioral Biology Group*

*(Received 22 February 1996; initial acceptance 20 May 1996;  
final acceptance 9 October 1996; MS. number: A7531R)*

**Abstract.** In many cooperatively breeding birds and mammals, group size is positively correlated with reproductive success. In marmoset and tamarin monkeys, species that display cooperative breeding, the presence of helpers appears to be critical for offspring survival, and breeders might be expected to display social strategies that would regulate group size. This study investigated the association between group size and aggression towards strangers in Wied's black tufted-ear marmosets, *Callithrix kuhli*, from small groups (with no helpers present) and large groups (with helpers present). Residents were exposed to multiple presentations of male and female strangers. Breeding females from large groups spent more time in close proximity to strangers, showed higher levels of agonistic displays and engaged in higher levels of aggressive behaviour towards intruders than did breeding females from small groups. Breeding male behaviour did not dramatically differ as a function of group size. After the removal of the intruder, female breeders from large groups showed higher levels of scent-marking relative to baseline observations, and time spent in close proximity to the partner increased after exposure to female intruders in large, but not small, groups. The results reveal that breeders from small groups are tolerant of strangers, which may facilitate the recruitment of additional group members, whereas breeders from large groups, particularly females, are intolerant of strangers, which may inhibit immigration. These findings have implications for understanding mechanisms that regulate immigration in cooperatively breeding animals, and suggest of how breeders from small groups might reconcile the serious limitation of having few or no helpers.

© 1997 The Association for the Study of Animal Behaviour

Among cooperatively breeding vertebrates, group size is a critical variable associated with the reproductive output of breeders within the group. In numerous avian and mammalian taxa, the presence of helpers (and hence, larger group size) is positively correlated with increased reproductive success (reviewed in Stacey & Koenig 1990; Solomon & French 1996). The mechanisms whereby enhanced reproductive output is linked with group size vary from between species and include (1) increased feeding rates of dependent young by helpers (Moehlman 1983; Emlen 1990), (2) increased ability to detect and deter potential predators (Rabenold 1990; Mumme 1992; Caine 1993), (3) reduced parental effort and increased

reproductive life span of breeders (Reyer 1984; Russell & Rowley 1988; Rood 1990) and (4) group size effects that appear to be independent of the delivery of alloparental care (e.g. ability of larger groups to defend better territories; Koenig & Mumme 1990). Regardless of the mechanism, non-breeding group members (helpers) are an important social resource in species characterized by cooperative breeding. It seems likely, therefore, that species that engage in cooperative breeding should be expected to express behavioural and social strategies to maintain or increase group size.

Recent work suggests that for species in which helpers are critical resources for reproductive success, breeders may provide 'incentives' to subordinate helpers to maintain large group size (Reeve & Ratnieks 1993; Keller & Reeve 1994; Emlen 1995; Sherman et al. 1995). These incentives for

Correspondence and present address: C. M. Schaffner, Department of Psychology, St. John's University, Collegeville, MN 56321, U.S.A. (email: cschaffner@tiny.computing.csbsju.edu).

subordinates may be expressed most prominently as 'peace incentives' (opportunities for subordinates to breed to reduce aggression and intra-group conflict initiated by subordinates) and 'staying incentives' (the opportunity for reproduction by the subordinates in order to encourage subordinates to remain in the group). In cases where group size is critical for reproductive success, but initial group size is below the minimum required for efficient reproduction, breeders in small groups might offer 'recruitment incentives' to increase group size. One possible manifestation of recruitment incentives would be conditional aggression targeted at potential immigrants into established groups: low aggression towards potential immigrants when group size is small and additional group members would enhance breeding performance, and enhanced aggression when group size is larger and additional helpers would have less effect on reproductive success. The conditional links between aggression and group size should hold only for cooperatively breeding species in which the relationship between group size and reproductive success is non-linear and asymptotic; that is, species or populations in which the presence of one or a few helpers enhances offspring production, but additional helpers do not (e.g. golden jackal, *Canis aureus*, Moehlman 1986; red-cockaded woodpecker, *Picoides borealis*, Walters 1990; arabian babbler, *Turtoides squamiceps*, Zahavi 1990). In contrast, cooperatively breeding species in which the relationship between group size and reproductive success is essentially linear throughout the range of group size (e.g. silverbacked jackals, *C. mesomelas*, Moehlman 1986; white-fronted bee eaters, *Merops bullockoides*, Emlen 1990) should not be expected to show group-size-dependent aggression towards potential immigrants, since increases in group size will always yield enhanced reproductive success.

The tamarins and marmosets from the primate family Callitrichidae are cooperative breeders that live in extended family groups; in all species studied to date, young delay dispersal and serve as helpers for subsequent litters of offspring (Goldizen 1987; Rylands 1993; French 1997). Although the notion that helpers promote infant survivorship and breeding performance in callitrichids has been widely cited in the callitrichid literature (reviewed in Tardif 1996), only recently has there been sufficient information on wild

populations to assess the relationship between the presence of helpers and reproductive success. Goldizen et al. (1996) presented breeding records derived from a long-term field study of saddleback tamarins, *Saguinus fuscicollis*, and Koenig (1995) reviewed the relationship between group size and reproductive success from 18 published studies on the common marmoset, *Callithrix jacchus*. A re-analysis of these data suggests that the addition of two or three helpers in a group size of four to five yields large increases in reproductive performance over smaller groups, but that additional helpers produce diminishing reproductive returns for the breeding pair (J. A. French, unpublished data). Thus, helpers appear to promote reproductive success of breeders in groups, but the relationship is non-linear and may approach an asymptote at moderate group sizes.

Although the mechanism responsible for enhanced productivity of breeders in larger groups has yet to be described for callitrichid primates, helpers are likely to reduce the cost of infant care for breeders, particularly the female. Female marmosets produce neonates that cumulatively weigh as much as 50% of maternal body weight per year (Ford & Davis 1992; French 1997), and females typically undergo a postpartum ovulation within 2 weeks of parturition (French et al. 1996b). In addition, callitrichids incur the highest relative energetic cost, in terms of lactation and carrying young, among neotropical primates (Tardif 1994). Infant care is also associated with other, less easily quantifiable costs, such as reduced foraging behaviour and less frequent social interaction with other group members (Price 1992). Non-breeding helpers are therefore extremely important to reproductive attempts by breeders, and some have suggested that single male-female pairs in the wild would be incapable of successfully rearing offspring (Goldizen & Terborgh 1989; Goldizen et al. 1996). Since helpers constitute such critical resources for callitrichids, and given the non-linear and asymptotic relationship between group size and reproductive success in at least some species, the callitrichid primates therefore constitute a useful taxon in which to address the possibility of behaviourally mediated 'recruitment incentives' in small breeding groups.

Marmosets and tamarins use aggression to regulate inter-group movement, including the immigration of new individuals into existing

**Table I.** Characteristics of family and pair groups that served as subjects

Group size	Breeding pair	Months paired prior to study	Juvenile offspring <6 months	Subadult offspring <12 months	Adult offspring >12 month
Large	Reb/Geo	29	2	1	3
Large	Cor/Coi	15			2
Large	Ang/Raj	31	1	2	2
Small	Bai/Att	9			
Small	Reb/Geo	7	1 (<3 months)		
Small	Bev/Hum	9			
Small	Cor/Joe	9			
Small	Mar/Pis	15			

groups (Peres 1989; Garber et al. 1993). In captivity, agonistic responses towards strangers can easily be elicited by presenting 'intruders' to resident animals in their home environment (French & Inglett 1991; Anzenberger 1992). The intruder paradigm has proven useful in assessing variations in the intensity of aggression as a function of the gonadal status of the residents (Epple 1982; Epple et al. 1987), the social and endocrine status of the intruder (French & Inglett 1989), the social context in which the intruder is presented (Evans 1983; Anzenberger 1985), and the familiarity of the intruder and residents (French et al. 1995). In this study, we tested whether the presence or absence of non-breeding helpers affects aggression towards intruders in Wied's black tufted-ear marmoset, *C. kuhli*. Group size in free-ranging populations of this species ranges from five to nine, and encounters with neighbouring groups or individuals are common (Stevenson & Rylands 1988; Rylands 1989). Since helpers constitute important resources for parental care in this, as in all callitrichid species (Santos et al. 1992; Tardif 1996), we predicted that responses towards intruders by breeding adults from small groups without helpers should be less aggressive than the responses of breeders from large groups with many helpers.

## METHODS

### Subjects

Three family groups (breeding adults plus helpers) and five pairs (breeding adults only) of Wied's black tufted-ear marmosets, served as subjects. The data for pair groups was collected between May and August 1992, and the results presented here are part of a larger data set examining the role of familiarity in mediating

aggression towards intruders (French et al. 1995). One pair group contained a dependent infant less than three months of age. The observations on family groups were conducted in May 1994. Each family group contained from two to six juvenile, subadult and/or adult helpers (Table I). The animals were housed at the Callitrichid Research Facility at the University of Nebraska at Omaha. The groups were maintained within large enclosures that ranged in size from 2.6 to 3.4 m<sup>3</sup>. The animals were fed a varied diet two times per day, and water was available ad libitum to all groups. Lighting was controlled automatically and set for a 12:12 h light:dark cycle, with the light phase beginning at either 0700 or 0800 hours (see also French et al. 1995; Schaffner et al. 1995).

### Design and Procedure

#### Intruder trials

We were interested in the differential responses of the breeding pairs from small groups (no helpers present) and large groups (with helpers present) to intruders of different sexes. Intruders were adult animals that were not housed in the same colony room as residents and that occupied a breeding position in their group. Each resident group was exposed to four intruder trials: two replicate trials with unfamiliar females and two replicate trials with unfamiliar males. The series of trials was counterbalanced for sex of intruder. To minimize idiosyncratic patterns of responses, different intruders were used in the two replicate trials. Animals that served as residents did not serve as intruders.

A small intruder cage, measuring 60 × 40 × 40 cm and constructed of wire mesh, was used to house intruders during the trials. The

cage was designed to permit extensive visual, acoustic and olfactory contact between intruders and residents, while minimizing the opportunity for physical injury. Prior to beginning trials, resident animals were exposed to the empty intruder cage for a minimum of 8 h to habituate them to the presence of the cage itself. Before each intruder trial, the intruder was lured from its home cage into a small portable transport cage and then transferred into the intruder cage. The animal was allowed to acclimate to the cage for approximately 15 min, then placed in the middle of the floor of the residents cage for a 10-min intruder trial (small groups) or a 20-min intruder trial (large groups).

The intruder trial was divided into 15-s intervals by an audible tone. Two observers, each monitoring the behaviour of one of the breeding adult residents, recorded all occurrences of agonistic and aggressive displays directed towards the intruder on standardized check sheets. Aggression and agonistic displays were categorized as described in French et al. (1995) and following Stevenson & Poole (1976). Agonistic displays included scent-marking, twitter vocalizations and genital displays. Aggressive interactions included attempted attacks, chases at and around the intruder cage and 'erh-erh' vocalizations. We also recorded the number of approaches by each resident to the intruder cage during the trial, as well as the number of intervals that the resident was in physical contact with the intruder cage or in close proximity (<10 cm). Inter-observer reliability was high throughout the study (89%).

#### *Pre- and post-intruder observations*

One observer conducted observations of intra-pair behaviour of the residents in the absence of intruders to assess the possibility that exposure to strange conspecifics would produce modifications in these patterns. Immediately preceding the intruder trials and immediately following the presentation of intruders, we conducted 5-min observations on small groups and 10-min observations on large groups of marmosets to record the social behaviour between the breeding adult residents. Instantaneous sampling was used to score the activity of the female every 30 s. We also scored all occurrences of social and territorial behaviour for both males and females (see Schaffner et al. 1995).

#### **Analyses**

Although the duration of intruder trials with large and small groups of marmosets differed, all data were normalized to rate of occurrence (or number of intervals) per 10-min observation. When we tested a subset of the scores from the 20-min large group observations for differences in behavioural patterns during the first versus second 10 min of the trials, no differences were detected. Therefore, rates of behavioural interactions from the observations on large groups were normalized to rates per 10 min to allow comparison with the observations derived from the 10-min intruder encounters with small groups. Likewise, behavioural interactions recorded during pre- and post-observations for large groups were normalized to 5-min periods to correspond with the data from small groups. Analyses contrasting the effects of group size were performed using a three-factor mixed design analysis of variance (group size  $\times$  intruder sex  $\times$  resident sex). Changes in the behaviour of the residents prior to and following presentation of the intruder was also evaluated using ANOVAs, with resident sex and intruder sex as factors in the analysis. Tukey's honestly significant differences test was used to test cell means following significant main effects and interactions when necessary (Keppel 1991). An alpha level of 0.05 was adopted for all analyses.

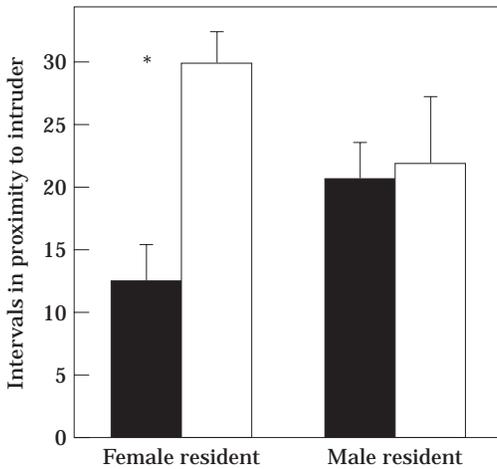
## **RESULTS**

#### **Proximity to Intruders**

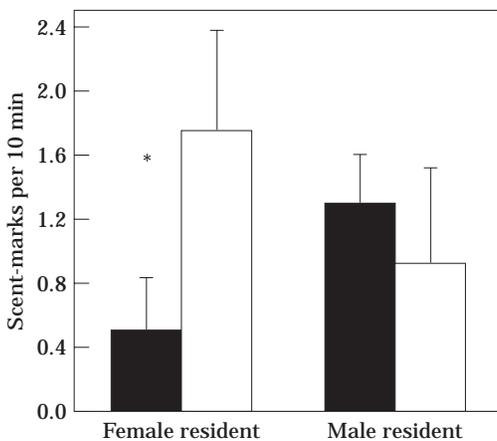
Group size influenced the number of observational intervals in which female residents, but not male residents, spent in close proximity and contact with intruders. Female residents from large groups spent significantly more intervals in contact with intruders than did female residents from small groups ( $F_{1,24}=5.37$ ,  $P<0.05$ ; Fig. 1). Females from large groups were in close proximity or in contact with the intruder cage more than twice as much as females from small groups.

#### **Agonistic Displays and Aggressive Responses Towards Intruders**

Males and females from small groups and large groups differed in their rates of low-intensity agonistic displays directed towards intruders. When we contrasted rates of scent-marking, there

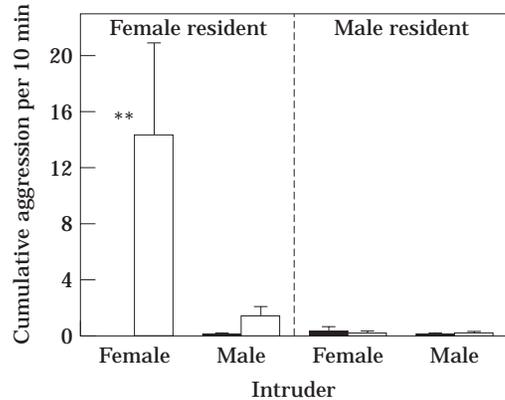


**Figure 1.** Mean + SE intervals that residents spent in proximity to intruders by residents from large groups (□) and pair groups (■). \*Indicates significant post hoc comparison ( $P < 0.05$ ).



**Figure 2.** Mean + SE frequencies of scent-marking in response to the presentation of intruders by residents from large groups (□) and residents from small groups (■). \*Indicates significant post hoc comparison ( $P < 0.05$ ).

was a significant interaction between group size and resident sex ( $F_{1,24} = 7.24$ ,  $P < 0.025$ ; Fig. 2). Post hoc comparisons revealed that females from large groups scent-marked three times more often in the presence of an intruder (of either sex) than females from small groups. Scent-marking rates by males in the presence of intruders was more variable and did not significantly differ as a function of group size. There were no differences in the



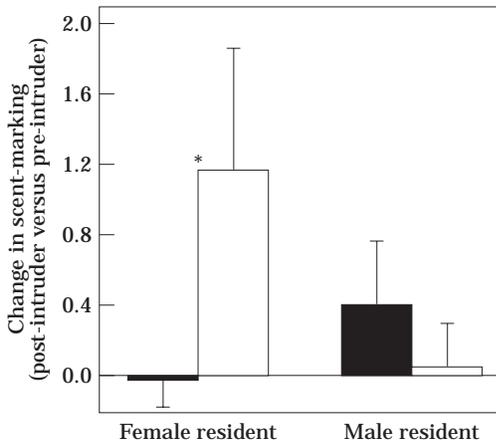
**Figure 3.** Mean + SE frequencies of aggressive behaviour directed towards intruders by residents from large (□) and small groups (■). \*\*Indicates significant post hoc comparison ( $P < 0.01$ ).

rates of genital displays or twitters in response to intruders as a function of either group size or resident sex.

Aggressive responses of resident females, but not males, changed as a function of group size and intruder sex ( $F_{1,24} = 7.39$ ,  $P < 0.025$ ; Fig. 3). Rates of aggressive behaviour towards female intruders were significantly higher in females that resided in large groups than in those residing in small groups. In fact, all resident females in large groups chased, vocalized and attacked female intruders on every trial, but none of the resident females in small groups did so on any trial. Resident females displayed considerably lower rates of aggressive behaviour towards male intruders, and aggression did not vary significantly as a function of group size. Aggressive behaviour was displayed by male residents at extremely low rates, and these rates did not differ as a function of either group size or the sex of the intruder.

### Changes in Resident Intra-pair Behaviour Following Intruder Encounter

Exposing marmosets to intruders produced modifications in patterns of intra-pair behaviour and agonistic displays that persisted after the intruders were removed, but the nature of the changes was highly dependent upon group size. Changes in rate of huddling behaviour between pair-mates occurred following the presentation of intruders, and these changes varied as a function



**Figure 4.** Mean  $\pm$  SE change in the frequency scent-marking behaviour from pre-intruder baseline observations to post-intruder observations by residents from large groups (□) and residents from small groups (■). \*Indicates significant post hoc comparison ( $P < 0.05$ ).

of group size and intruder sex ( $F_{1,12} = 6.75$ ,  $P < 0.025$ ). Relative to pre-intruder baselines, residents from large groups increased their rate of huddling significantly more after exposure to a female intruder ( $\bar{X} \pm SE = 2.1 \pm 1.2$ ) than did residents from small groups ( $-2.1 \pm 1.2$ ). After exposure to male intruders, residents from both large and small groups displayed a slight but non-significant decrease in huddling with the partner. Modification in rates of scent-marking were also affected by group size ( $F_{1,24} = 5.40$ ,  $P < 0.05$ ). Immediately following the presentation of either a male or female intruder, female residents from large groups increased their rates of scent-marking significantly (relative to pre-intruder baseline), but female residents in small groups showed no changes in rates of marking. Male residents in both large and small groups showed slight but non-significant increases in scent-marking after the intruder was removed (Fig. 4).

## DISCUSSION

We examined the effects of group size on the nature of the responses of adult male and female marmosets when confronted with strangers. Marmosets responded differently towards intruders as a function of group composition. Females from large groups responded to intruders with elevated

levels of agonistic displays. Females from large groups also showed the highest levels of aggressive behaviour, which was primarily directed towards female intruders. The differences between large and small groups were consistent during each intruder encounter (six trials for large groups and 10 trials for small groups) and were highly significant. The sex-specific pattern of agonistic responding parallels the typical callitrichid pattern of intra-sexual aggression prevalent in other intruder studies (Anzenberger 1992). Furthermore, the effects of presenting an intruder persisted even after the intruder was removed in large groups, in contrast to small groups. Females from large groups increased rates of scent-marking following the presentation of unfamiliar intruders, and breeding pairs from large groups increased their rates of huddling following exposure to unfamiliar females.

In other callitrichid species, sex-specific patterns of aggression towards unfamiliar intruders tends to be expressed at about equal rates by male and female residents. In saddle-back tamarins and common marmosets males and females are both intolerant of same-sex unfamiliar conspecifics (Evans 1983; Sutcliffe & Poole 1984; Epple & Alveario 1985). Sexually dimorphic response patterns, however, have been identified in lion tamarins, and in cotton-top tamarins, *S. oedipus*. Lion tamarin females show high-intensity aggression towards unfamiliar females, but male lion tamarins are passive and indifferent towards both unfamiliar males and females (French & Inglett 1989). Cotton-top tamarin males are the active aggressors towards intruding males, but resident females increase their rates of scent-marking in the presence of female intruders (French & Snowdon 1981). In the present study, resident females from family groups showed both high-intensity aggression and agonism towards intruders, and males showed less intense aggression. In groups composed of pairs only, however, male marmosets showed low-intensity aggression towards male intruders and at a rate lower than reported for other species of tamarins and marmosets (French et al. 1995).

The pattern of large-group aggression versus small-group tolerance towards conspecifics has been reported in other cooperatively breeding species as well. French & Inglett (1989) monitored the responses of lion tamarins to intruders in groups that ranged in size from two (breeding

male and female only) to six (adult pair and four helpers). Aggression by the resident female towards adult intruders was highly correlated ( $r=0.86$ ) with group size. In the stripe-backed wren, *Campylorhynchus nuchalis*, juvenile male immigration into groups without helpers is much more frequent than immigration into groups with helpers (Piper et al. 1995). Although the details of the social interactions that account for juvenile males immigrating more readily into groups without helpers have not been documented, it could be via a mechanism similar to the one we report here; namely, that juvenile males experience less aggression while attempting to immigrate into small groups than into large groups. This interpretation is supported by the results of a removal experiment in the stripe-backed wren. When adult females were removed to create a breeding vacancy, significantly higher levels of aggression between potential replacements was noted when the groups contained two or more helpers than when the groups contained one or zero helpers (Zack & Rabenold 1989).

Several explanations could account for the increased levels of aggression and agonism by marmosets as a function of group size. For example, breeders from large groups may behave more aggressively to defend dependent offspring from intruders; thus, the increased aggression could be parentally motivated. Our results argue against this interpretation for two reasons. First, one of the large groups contained no dependent infants under 6 months of age, yet high levels of aggression were noted in this group. Furthermore, one of the small groups contained a young infant during the time of testing, and the agonistic responses of this group were not different from those in other small groups. Second, if breeders are defending dependent offspring from intruders, we would expect male breeders to engage in rates of aggressive behaviour similar to that of females, and they did not. The rate of male aggression did not differ as a function of group size. A second explanation of the group size-aggression relationship is that enhanced intolerance towards intruders in large groups is produced by a socially facilitated aggressive response from the entire group (cf. Eppler & Alveario 1985). This explanation also seems unlikely, because helpers were rarely involved in agonistic encounters, tending to remain at some distance from the intruder present in their cage. Breeding males also did not show

increased aggression towards intruders as a function of group size. Breeding pairs from large groups had been together an average of 24.5 months, but breeding pairs from small groups had been together an average of only 9.8 months. Therefore, a third possible explanation for the link between group size and aggression is that intolerance towards strangers increases as a function of the duration of the relationship between the breeding adults. The opposite effect is seen in male common marmosets, however, where long-term pairing leads to reduced aggression towards intruders relative to newly-paired males (Araujo & Yamamoto 1992). Both the social and sexual aspects of pair relationships in marmosets are well established by 80 days after pairing, and the nature of the pair bond appears to change little after this time (Schaffner et al. 1995). A fourth possible explanation for the differences between pair and family group responses is that the data were collected at different times, and females could have been in different stages of the reproductive cycle. Females in both large and small groups were sampled in varying stages of the reproductive cycle, and intolerance towards intruders appears to be relatively independent of adult gonadal condition (Eppler 1982). Therefore, the differential patterning of aggression and agonistic behaviour in large versus small groups is consistent with the hypothesis that breeders in groups with few or no helpers should behave in such a way so as to increase group size.

Marmosets are a cooperatively breeding species in which breeding is restricted to one or a few individuals (French 1997). In spite of delaying individual reproduction, subordinate helpers related to the breeders presumably gain indirect fitness benefits by helping parents rear related infants, and both unrelated and related subordinate helpers may acquire both immediate and delayed direct fitness benefits by residing in the group (Tardif et al. 1984; Snowdon et al. 1985; Caine 1993; French et al. 1996a). Since the presence of helpers, and hence group size, is so critical for reproductive success, though, there may be conditions under which breeders must provide 'staying incentives' (Keller & Reeve 1994), such as shared breeding, to keep helpers in the group. Reports of marmoset and tamarin groups with multiple breeding females (reviewed in French 1997) may be a manifestation of this strategy by breeders.

For cooperatively breeding species like marmosets, in which offspring survival depends upon helping behaviour, breeders may use strategies that recruit individuals into their group if group size is at or below the minimum required for successful reproduction. One strategy to accomplish this is the recruitment of close kin as helpers. In white fronted bee-eaters, resident male breeders harass male offspring that attempt to breed independently. Harassment of sons often results in abandonment of the son's breeding attempt and his subsequent return to the natal nest to help the father rear his offspring (Emlen & Wrege 1992). In a second scenario, breeders may attempt to recruit unrelated helpers from outside the natal group. The behavioural manifestation of this strategy would be reduced aggression towards potential immigrants, as we report here. For the immigrant, immediate incentives would be offered in the form of access to an established territory, in which residents would share their feeding and sleeping sites. Recruitment incentives could also include the possibility of mating opportunities with breeders, and recruitment incentives may be expressed more directly by group members through actual solicitation in the form of sexual enticements or contact calls. For example, after experimental removal of breeders from existing groups of striped-back wrens, the remaining breeding partner directs sexual solicitation patterns toward potential immigrants (Zack & Rabenold 1989).

To conclude, responses to intruders by resident marmosets differed as a function of group size: animals from large groups were more aggressive than animals from small groups. This result was particularly prominent for resident females. That more pronounced differences were observed in females than in males indicates that breeding females, who rely most heavily upon the resources provided by helpers, may be particularly important in regulating the number of helpers recruited from outside the natal family group, and hence group size, in callitrichid primates.

#### ACKNOWLEDGMENTS

This study was supported in part by grants from the National Science Foundation (IBN 92-09528 and OSR-92-55225) to J.A.F. and by a Presidential Fellowship, University of Nebraska at Omaha to C.M.S. We thank Denise Hightower-Merritt

and Dan Reevers for their outstanding dedication to the care and maintenance of the marmoset colony, and Dr Corrine Brown and Omaha's Henry Doorly Zoo for veterinary support. We thank C. J. Manning, T. E. Smith and W. DeGraw for consultation and commentary on earlier forms of the manuscript, as well as two anonymous referees who provided extremely helpful and pertinent comments. The Callitrichid Research Facility of the University of Nebraska at Omaha is a U.S.D.A.-licensed and A.A.A.L.A.C.-accredited facility. The research described in this protocol was reviewed and approved by the UNO/UNMC IACUC (#91-110-03).

#### REFERENCES

- Anzenberger, G. 1985. How stranger encounters of common marmosets (*Callithrix jacchus jacchus*) are influenced by family members: the quality of behavior. *Folia primatol.*, **45**, 204-224.
- Anzenberger, G. 1992. Monogamous social systems and paternity in primates. In: *Paternity in Primates Genetic Tests and Theories* (Ed. by R. D. Martin, A. F. Dixson & E. M. Wickings), pp. 203-224. Basel: S. Karger.
- Araujo, A. & Yamamoto, M. E. 1992. Reaction to conspecific intruders in *Callithrix jacchus*: the influence of social status. *14th Congress of the International Primatological Society*, p. 292. Strasbourg, France: International Primatological Society.
- Caine, N. G. 1993. Flexibility and co-operation as unifying themes in *Saguinus* social organization and behavior: the role of predation pressures. In: *Marmosets and Tamarins: Systematics, Behaviour and Ecology* (Ed. by A. B. Rylands), pp. 200-219. Oxford: Oxford University Press.
- Emlen, S. T. 1990. White-fronted bee-eaters: helping in a colonially nesting species. In: *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (Ed. by P. B. Stacey & W. D. Koenig), pp. 489-526. Cambridge: Cambridge University Press.
- Emlen, S. T. 1995. An evolutionary theory of the family. *Proc. natn. Acad. Sci.*, **92**, 8092-8099.
- Emlen, S. T. & Wrege, P. H. 1992. Parent-offspring conflict and the recruitment of helpers among bee-eaters. *Nature, Lond.*, **356**, 331-333.
- Epple, G. 1982. Effects of prepubertal ovariectomy on the development of scent glands, scent marking, and aggressive behaviors of female tamarin monkeys (*Saguinus fuscicollis*). *Horm. Behav.*, **16**, 330-342.
- Epple, G. & Alveario, M. 1985. Social facilitation of agonistic responses to strangers in pairs of saddle back tamarins (*Saguinus fuscicollis*). *Am. J. Primatol.*, **9**, 207-218.
- Epple, G., Alveario, M. C. & St. Andre, E. 1987. Sexual and social behavior of adult saddle-back tamarins (*Saguinus fuscicollis*), castrated as neonates. *Am. J. Primatol.*, **13**, 37-49.

- Evans, S. 1983. The pair-bond of the common marmoset, *Callithrix jacchus jacchus*: an experimental investigation. *Anim. Behav.*, **31**, 651–658.
- Ford, S. & Davis, L. C. 1992. Systematics and body size: Implications for feeding adaptations in New World monkeys. *Am. J. Phys. Anthropol.*, **88**, 415–468.
- French, J. A. 1997. Proximate regulation of singular breeding in callitrichid primates. In: *Cooperative Breeding in Mammals*. (Ed. by N. G. Solomon & J. A. French), pp. 34–75. Cambridge: Cambridge University Press.
- French, J. A. & Inglett, B. J. 1989. Female–female aggression and male indifference in response to unfamiliar intruders in lion tamarins. *Anim. Behav.*, **37**, 487–497.
- French, J. A. & Inglett, B. J. 1991. Responses to novel social stimuli in tamarins: a comparative perspective. In: *Primate Responses to Environmental Change* (Ed. by H. Box), pp. 275–294. London: Chapman & Hall.
- French, J. A. & Snowdon, C. T. 1981. Sexual dimorphism in responses to unfamiliar intruders in the tamarin, *Saguinus oedipus*. *Anim. Behav.*, **29**, 822–829.
- French, J. A., Schaffner, C. M., Shepherd, R. E. & Miller, M. E. 1995. Familiarity with intruders modulates agonism toward outgroup conspecifics in Wied's black tufted-ear marmoset (*Callithrix kuhli*). *Ethology*, **99**, 24–38.
- French, J. A., Pissinatti, A., Coimbra-Filho, A. F. 1996a. Reproduction in captive lion tamarins (*Leontopithecus*): seasonality, infant survival, and sex ratios. *Am. J. Primatol.*, **39**, 17–34.
- French, J. A., Brewer, K. J., Schaffner, C. M., Schalley, J., Hightower-Merritt, D., Smith, T. E. & Bell, S. M. 1996b. Urinary steroid and gonadotropin excretion across the reproductive cycle in female Wied's black tufted-ear marmosets (*Callithrix kuhli*). *Am. J. Primatol.*, **40**, 231–245.
- Garber, P. A., Pruetz, J. D. & Issacson, J. 1993. Patterns of range use, range defense, and intergroup spacing in moustached tamarin monkeys (*Saguinus mystax*). *Primates*, **34**, 11–25.
- Goldizen, A. W. 1987. Tamarins and marmosets: communal care of offspring. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker), pp. 34–43. Chicago: The University of Chicago Press.
- Goldizen, A. W. & Terborgh, J. 1989. Demography and dispersal patterns of a tamarin population: possible causes of delayed breeding. *Am. Nat.*, **134**, 208–224.
- Goldizen, A. W., Mendelson, J. & Terborgh, J. 1996. Saddle-back tamarins (*Saguinus fuscicollis*) reproductive strategies: evidence from a thirteen-year study of a marked population. *Am. J. Primatol.*, **38**, 57–84.
- Keller, L. & Reeve, H. K. 1994. Partitioning of reproduction in animal societies. *Trends Ecol. Evol.*, **9**, 98–102.
- Keppel, G. 1991. *Design and Analysis: A Researchers Handbook*. Upper Saddle River, New Jersey: Prentice Hall.
- Koenig, A. 1995. Group size, composition, and reproductive success in wild common marmosets (*Callithrix jacchus*). *Am. J. Primatol.*, **35**, 311–318.
- Koenig, W. D. & Mumme, R. L. 1990. Levels of analysis, functional explanations, and the significance of helping behavior. In: *Interpretation and Explanation in the Study of Animal Behavior* (Ed. by M. Bekoff & D. Jamieson), pp. 268–303. Boulder, Colorado: Westview Press.
- Moehlman, P. D. 1983. Socioecology of silverbacked and golden jackals (*Canis mesomelas*) and (*Canis aureus*). In: *Advances in the Study of Mammalian Behavior* (Ed. by J. F. Eisenberg & D. G. Kleiman), pp. 423–453. American Society of Mammalogists Special Publication No. 7. Lawrence, Kansas: American Society of Mammalogists.
- Moehlman, P. D. 1986. Ecology of cooperation in canids. In: *Ecological Aspects of Social Evolution* (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 64–86. Princeton, New Jersey: Princeton University Press.
- Mumme, R. L. 1992. Do helpers increase reproductive success? An experimental analysis in the Florida scrub jay. *Behav. Ecol. Sociobiol.*, **31**, 319–328.
- Peres, C. A. 1989. Costs and benefits of territorial defense in wild golden lion tamarins, *Leontopithecus rosalia*. *Behav. Ecol. Sociobiol.*, **25**, 227–233.
- Piper, W. H., Parker, P. G. & Rabenold, K. N. 1995. Facultative dispersal by juvenile males in the cooperative stripe-backed wren. *Behav. Ecol.*, **6**, 337–342.
- Price, E. C. 1992. The costs of infant carrying in captive cotton-top tamarins. *Am. J. Primatol.*, **26**, 23–33.
- Rabenold, K. N. 1990. *Campylorhynchus* wrens: the ecology of delayed dispersal and cooperation in the Venezuelan savanna. In: *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (Ed. by P. B. Stacey & W. D. Koenig), pp. 159–196. Cambridge: Cambridge University Press.
- Reeve, H. K. & Ratnieks, F. L. W. 1993. Queen–queen conflicts in polygynous societies: mutual tolerance and reproductive skew. In: *Queen Number and Sociality in Insects* (Ed. by L. Keller), pp. 45–85. Oxford: Oxford University Press.
- Reyer, H. U. 1984. Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher, *Ceryle rudis*. *Anim. Behav.*, **32**, 1163–1178.
- Rood, J. P. 1990. Group size, reproduction and routes to breeding in dwarf mongooses. *Anim. Behav.*, **39**, 566–572.
- Russell, E. M. & Rowley, I. C. R. 1988. Helper contributions to reproductive success in the splendid fairy-wren. *Behav. Ecol. Sociobiol.*, **22**, 131–140.
- Rylands, A. B. 1989. Sympatric Brazilian callitrichids: the black tufted-ear marmoset, *Callithrix kuhli*, and the golden-headed lion tamarin, *Leontopithecus chrysomel*. *J. Human Evol.*, **18**, 679–695.
- Rylands, A. B. (Ed.). 1993. *Marmosets and Tamarins: Systematics, Behaviour and Ecology*. Oxford: Oxford University Press.
- Santos, C. V., French, J. A. & Otta, E. 1992. A comparative study of infant carrying behavior in Callitrichid primates: *Callithrix* and *Leontopithecus*. *Am. J. Primatol.*, **27**, 56.
- Schaffner, C. M., Shepherd, R. E., Santos, C. V. & French, J. A. 1995. Development of heterosexual relationships in Wied's black tufted-ear marmosets (*Callithrix kuhli*). *Am. J. Primatol.*, **36**, 185–200.

- Sherman, P. W., Lacey, E. A., Reeve, H. K. & Keller, L. 1995. The eusociality continuum. *Behav. Ecol.*, **6**, 102–108.
- Snowdon, C. T., Savage, A. & McConnell, P. B. 1985. A breeding colony of cotton-top tamarins (*Saguinus oedipus*). *Lab. Anim. Sci.*, **35**, 477–480.
- Solomon, N. & French, J. A. 1997. *Cooperative Breeding in Mammals*. Cambridge: Cambridge University Press.
- Stacey, P. B. & Koenig, W. D. 1990. *Cooperative Breeding in Birds*. Cambridge: Cambridge University Press.
- Stevenson, M. F. & Poole, T. B. 1976. An ethogram of the common marmoset, *Callithrix jacchus*: general behavioural repertoire. *Anim. Behav.*, **24**, 428–451.
- Stevenson, M. F. & Rylands, A. B. 1988. The marmosets, genus *Callithrix*. In: *Ecology and Behavior of Neotropical Primates, Vol. 2*. (Ed. by A. Mittermeier, A. B. Rylands, A. Coimbra-Filho & A. B. Fonseca). pp. 131–222. Washington, D.C.: World Wildlife Fund.
- Sutcliffe, A. F. & Poole, T. B. 1984. Intragroup agonistic behavior in captive groups of the common marmoset *Callithrix jacchus jacchus*. *Int. J. Primatol.*, **5**, 473–489.
- Tardif, S. D. 1994. Relative energetic cost of infant care in small-bodied neotropical primates and its relation to infant-care patterns. *Am. J. Primatol.*, **34**, 133–144.
- Tardif, S. D. 1996. The bioenergetics of parental behavior and the evolution of alloparental care in marmosets and tamarins. In: *Cooperative Breeding in Mammals* (Ed. By N. G. Solomon & J. A. French), pp. 11–33. New York: Cambridge University Press.
- Tardif, S. D., Richter, C. B. & Carson, R. L. 1984. Effects of sibling rearing experience on future reproductive success in two species of Callitrichidae. *Am. J. Primatol.*, **6**, 377–380.
- Walters, J. R. 1990. Red-cockaded woodpeckers: a 'primitive' cooperative breeder. In: *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (Ed. by P. B. Stacey & W. D. Koenig), pp. 67–102. Cambridge: Cambridge University Press.
- Zack, S. & Rabenold, K. N. 1989. Assessment, age and proximity in dispersal contests among cooperative wrens: field experiments. *Anim. Behav.*, **38**, 235–247.
- Zahavi, A. 1990. Arabian babblers: the quest for social status in a cooperative breeder. In: *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (Ed. by P. B. Stacey & W. D. Koenig), pp. 103–131. Cambridge: Cambridge University Press.