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AGGRESSIVE RESPONSE TOWARD INTRUDERS BY CAPTIVE MALE *LEONTOPITHECUS CHRYSOMELAS*

Introduction

Among callitrichid primates, aggression between residents and intruders of the same sex has been documented in several studies in captive settings. Usually, the pattern of responses is interpreted in terms of the maintenance of the pair bond and monogamy, territorial defense, and the exclusion of competitors (Anzenberger, 1985; Araújo and Yamamoto, 1994; Epple, 1978; French and Inglett, 1989; French and Snowdon, 1981). In these earlier studies, there was considerable variation in the responses against intruders of the same sex. For example, in *Callithrix jacchus* both males and females attacked an intruder; in *Saguinus oedipus* the male exhibited attack behavior while the female increased rates of marking behavior; and in *Leontopithecus rosalia* the females demonstrated high levels of agonistic behavior and the males exhibited lower levels of aggression in the presence of intruders. These response differences among species may be attributable to differences in the mechanisms of reproductive suppression among subordinates, and, possibly, to differences in the systems of pair-bond maintenance (Araújo and Yamamoto, 1994; French and Inglett, 1991; Snowdon, 1990). Other factors may also regulate the responses to intruders, including kin discrimination (Harrison and Tardif, 1988), familiarity with intruders (Koenig and Rothe, 1994; French *et al.*, 1995), and the size of the group (French and Inglett, 1989; Schaffner and French, 1997). Overall, the factors that are associated with variation in responses to intruders have not been extensively studied.

The work presented in this report describes: (1) cases of strong aggression toward males in golden-headed lion tamarins (*Leontopithecus chrysomelas*), which differ from observations in *L. rosalia*; and (2) differences in the responses of the resident breeding male, and an apparent relationship with the size of the group.

Methods

The data reported in this paper come from observations of the reactions of members of a captive family group to encounters with unfamiliar, reproductively-aged males that had escaped from neighboring groups in *L. chrysomelas*

(Table 1). Two encounters were noted on separate occasions. We used an observation protocol based on *ad libitum* sampling, which continued until the escaped animals were captured. The animals that participated in these events were housed at the Laboratório Tropical de Primatologia (LTP) of the Universidade Federal da Paraíba. The family group was maintained in a large wire enclosure (2.7 x 2.7 x 5.45 m), with natural branches, platforms, and nest boxes. Visual contact with other social groups in neighboring enclosures was minimal since there was dense foliage blocking visual access. The LTP is situated in the interior of an "island remnant" of the Atlantic coastal forest and the enclosures were subject to normal environmental and climatic conditions.

Table 1. Composition of the family group during the two aggressive incidents. A = Adult, Sa = Subadult, J = Juvenile.

Date	Animals	Sex	Age
19 Oct 1995	Clotilde (Clo)	F	A
	Gorbi (Go)	M	A
	David (Da)	M	A
	Thais (Th)	F	Sa
	Marina (Ma)	F	J
	Mariana (Mr)	F	J
12 Oct 1996	Clotilde	F	A
	Gorbi	M	A
	David	M	A
	Thais	F	A

Results and Discussion

At 09:10 h on 19 October 1995, the adult male *Mi* escaped from his enclosure and approached that containing the focal family group. He hung on to the wire of the enclosure and displayed agonistically toward the animals in the group. The adult-aged son *Da* then attacked *Mi*, and attempted to bite and grab the intruder male through the wire of the enclosure. *Da* continued to attack the intruder even after the daily food rations had been provided. At 09:40 h, the reproductive adult male resident *Go* initiated his participation in the attacks on the intruder, while *Da* continued to attack, displaying vocalizations and arch-displays (see Rathbun, 1979). The breeding *Go* and *Da* attacked the intruder simultaneously, jumping at the wire mesh and attempting to grab him. However, aggression by the son *Da* was more frequent and more intense than that of the adult male. The other animals in the group did not display aggressive interactions towards the intruder. In an attempt to capture the escaped male, we placed his female mate in a small cage near the enclosure of the focal family group. The resident reproductive female *Clo* vocalized and displayed agonistically toward the unfamiliar female, with the apparent intention of attacking her. At 09:55 h, the observations were terminated.

In the second instance of aggression we observed, another adult male (*Aureo*) escaped from a different enclosure at approximately 09:30 h. For 5-10 minutes he remained close to his home cage, and then approached the enclosure containing the focal family group and began to interact aggressively with the resident animals. The reproductive male *Go* and his son *Da* became actively involved in

attacks directed toward the intruder, similar to the behavior we described above. However, in this case the father and son initiated their attacks together. The intruder male ran back and forth on top of the enclosure, attempting to bite both resident males. In this interaction, the females also participated in the aggressive attacks on three occasions, although it was not possible to determine whether the mother, daughter, or both were involved in the attacks. The intruder attempted to chase and fight with both males (*Go* and *Da*) for a total of 10 minutes. In this second agonistic event the adult male *Go* was more active than his son *Da*, and he received serious injuries to his hands during the fight. At 10:00 h the observations were terminated.

In these two opportunities to study a confrontation between intruding males and the residents of a single social group, the resident males responded aggressively, but the responses of the males differed. In the first case, the subordinate male initiated the attack and exhibited higher rates of aggressiveness. In the second case it was the dominant breeding male that exhibited higher aggression, when both males attacked simultaneously. In the two situations, the responses of the individuals may have been influenced by the size of the group, with 6 and 4 animals in the first and second case, respectively. This point will be explored later.

In our observations, the patterns of aggressiveness of the adult male differ from the results reported by French and Inglett (1989) for *L. rosalia*, in which resident males remained tolerant in the presence of intruding males. In our experience with other escapes in our colony, we have also noted male-male aggression. It is possible that in *L. chrysomelas*, male-male competition for reproductive dominance is more intense than it is in *L. rosalia*, a species which is known to reside in stable polyandrous groups in the wild (Baker *et al.*, 1993). Recently, Baker and Dietz (1996) described cases of aggression by resident males against intruders in wild groups of *L. rosalia*, but in some cases the intruder male was tolerated by the resident male. Familiarity of males with the intruder reduces aggressiveness toward the intruder (Koenig and Rothe, 1994; French *et al.*, 1995), a possibility that Baker and Dietz (1996) considered as a reasonable explanation for the low levels of aggression toward intruding males in *L. rosalia* reported by French and Inglett (1989).

It is interesting that the response of the adult breeding male was different in the two occasions that he was confronted with an unfamiliar male. When the size of the group was large, the participation of the adult male was low and the majority of the aggression was carried out by the older son. With a smaller group size, the male was the primary participant in aggressive interactions: Koenig and Rothe (1991, p.192) reported similar observations in *C. jacchus*, and proposed that there is a division of labor among the members of the group with increasing family size. Non-reproductive males in large groups, then, may selectively engage in aggressive interactions that could maintain or increase territory size. However, alternative

interpretations could explain the differences in aggression in the two resident males during the two events reported here.

The reproductive state of the female is an important factor that might regulate the responses of males to intruders, but none of the published studies on captive animals have analyzed the influence of this variable. The reproductive state of the female apparently elevates the level of intrasexual competition in males. In wild groups that are demographically polyandrous (contain at least 2 adult males) in *Cebuella pygmaea* (v. Soini, 1987) *L. rosalia* (v. Baker *et al.*, 1993) and *Saguinus mystax* (v. Heymann, 1996), levels of aggression among males within the group are higher throughout the period of female receptivity. It is possible in the second case we report here that the female was in estrus, which may explain the fact that the reproductive male exhibited higher aggression toward the intruder. This aggression would minimize the opportunity for a sexual encounter between the resident female and the intruding male.

Another aspect worthy of discussion is the behavior of the intruder relative to the residents. In the second case, for example, the intruder appeared to behave more aggressively. This might be the reason that the resident adult male showed higher aggression in this case. It is important to keep in mind that the majority of other studies with the intruder paradigm (e.g., Araújo and Yamamoto, 1994; Epple, 1978) were conducted under different conditions than those reported here. For example, the intruder is typically kept in a small cage, which is not his normal "territory". If, under these conditions, the intruder exhibited exclusively submissive behavior, this would reduce the aggressive behavior of the adult male resident. It is interesting to note, in this light, that in wild groups of *L. rosalia* intruder males can be accepted permanently into groups as subordinates (Baker *et al.*, 1993), which would produce benefits for both residents and intruders.

Dominant females in *L. chrysomelas* only show heightened aggression against other females, as revealed by observations during other escapes at our facility, and judging by the reactions of *Clo* toward male intruders. One interesting observation is the low level of participation of the daughter *Th* in the defense of the group. If a strange male is successful in establishing his territory, then it is possible that the daughter will usurp the reproductive position. Thus, the low levels of aggression toward intruding males by subordinate daughters may be advantageous for them. On the other hand, the intense participation of the son in the defense of the group is more difficult to explain. In accordance with Baker and Dietz (1996) males that disperse together have a higher probability of successfully entering a new territory (but see McGrew and McLuckie, 1986). Thus, why should sons defend family territories? It is possible that in helping their fathers defend the territory, sons are gaining indirect fitness benefits. The size of our sample is small, and does not permit broad generalizations, but it is worthwhile to pose three

questions: 1) What is the nature of the daughter's reaction if the intruder is a female? Since it is possible that the daughter might inherit the reproductive position (Baker and Dietz, 1996) then daughters should show high levels of aggression toward potential female competitors: 2) What is the nature of the son's reaction if the intruder is a female? 3) Does the son also react aggressively in this context?

The majority of research on aggression has dealt principally with aspects of the relationships that deal with mating systems and pair-bond formation (e.g., Anzenberger, 1985; Araújo and Yamamoto, 1994; Epple, 1978; French and Snowdon, 1981). However, the behavioral responses described here indicate the need for further research in this area, especially as regards the influence of group size and composition, reproductive state of the female, and the participation of the sons and daughters in agonistic encounters with intruders.

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Antônio Christian de A. Moura, Simone Porfírio, and Carmen Alonso, Departamento de Sistemática e Ecologia - CCEN, Universidade Federal da Paraíba, 58059-900 João Pessoa, Paraíba, Brazil.

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A STUDY OF THE BLACK UAKARI, *CACAJAO MELANOCEPHALUS MELANOCEPHALUS*, IN THE PICO DA NEBLINA NATIONAL PARK, BRAZIL

Following preliminary surveys in 1991 (Boubli, 1994), from June 1994 to October 1995, I conducted the first long-term field study of the ecology of the black uakari monkey, *Cacajao melanocephalus melanocephalus*, in the Pico da Neblina National Park (PNNP), Brazil (01°10'N to 00°26'S, 65°03'W to 66°52'W) (Boubli, 1997). Pico da Neblina is the second largest National Park in Brazil, with an area of 2,200,000 ha, and is located on the left bank of the Rio Negro, in the extreme north-western part