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BRIEF REPORT

Intragroup Lethal Aggression in Wild Spider Monkeys

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We report the first evidence of intragroup coalitionary aggression leading to the death of a wild young adult male spider monkey. During a long-term study of a well-habituated community at the Otoch Ma'ax Yetel Kooh reserve in Yucatan, Mexico, a young adult male sustained severe injuries repeatedly between January and March 2002. On 1 April 2002 the same male was the victim of an intragroup attack by at least one adult male that resulted in his death. We highlight several causes of intragroup aggression that may account for the killing. Am. J. Primatol. 68:732–737, 2006.

Key words: aggression; coalitions; intragroup killing; male–male competition; spider monkeys

INTRODUCTION

Lethal aggression in the form of infanticide occurs with some regularity in certain primate social groups [Melo et al., 2003; Newton-Fisher, 1999; Swedell & Tesfaye, 2003; van Schaik & Janson, 2000]. Intragroup aggression leading to the death of weaned individuals occurs much less frequently and has been observed predominantly in wild chimpanzees (*Pan troglodytes*) at Mahale [Nishida et al., 1995], Budongo [Fawcett & Muhumuza, 2000], and Ngogo [Watts, 2004], and in capuchin monkeys (*Cebus capuchinus*) [Gros-Louis et al., 2003]. Here we report a series of observations of intragroup coalitionary aggression directed by adult males toward a young adult male spider monkey (*Ateles geoffroyi yucatanensis*), which led to his death.

The observations are among the first of their kind for a group of wild spider monkeys, a species that lives in multi-male/multi-female groups with a high

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degree of fission-fusion dynamics, male philopatry, and female dispersal [McFarland Symington, 1987]. Three more instances of coalitionary aggression have been observed at Barro Colorado Island, Panama, in which adult male spider monkeys (*A. g. ornatus*) directed severe aggression toward subadult males that probably resulted in the death of two of the young males [Campbell, in press]. Our observations and those of Campbell [in press] are intriguing given that older males are likely the fathers or brothers of younger males, adult males affiliate with each other at higher rates than any other sex/age-class combination [Fedigan & Baxter, 1984; McFarland Symington, 1990; van Roosemalen & Klein, 1988], males have heretofore rarely been observed being aggressive toward each other [Fedigan & Baxter, 1984], and adult males rely on each other for intergroup territorial displays and boundary patrols [McFarland Symington, 1990; Wallace, 2001].

MATERIALS AND METHODS

The observations reported here were part of a long-term study of the behavior and ecology of spider monkeys (*A. g. yucatanensis*) in two communities (Eastern and Western) carried out at the Otoch Ma'ax Yetel Kooh reserve (20°38′ N, 87°38′ W, 14 m above sea level), in the Yucatan peninsula of Mexico [Ramos-Fernandez et al., 2003]. In January 2002 the Eastern community consisted of five adult males, one subadult male, five adult females, four juvenile females, and five infants. Three of the adult males (PA, BE, and DA) were $\geq$8 years of age, whereas the other two males (AR and JO) were only 6–7 years of age and were slightly smaller than the older adult males (see McFarland Symington [1988] for similar classification). The monkeys inhabited an area of approximately 2.2 km^2 that was covered by medium semi-evergreen forest interspersed within a matrix of 30–50-year-old successional forest growing on a plateau of calcareous rock [Valero, 2004]. The members of the Eastern community, which was the focus of the observations reported here, have been habituated, individually recognized, and followed at least two half days per week since 1997. During 2002, independently moving individuals were the subjects of whole-day follows by the first author with continuous recording of behavior of a focal animal [Altmann, 1974]. In addition, two half-day subgroup follows were also carried out each week in which all occurrences of aggressive behavior and 20-min scans of social behavior and group composition were scored by well-trained field assistants. The monkeys were typically observed from a distance of 10–20 m, and were easy to see given the forest structure and the use of binoculars. The vocalizations identified below follow descriptions given by van Roosmalen and Klein [1988].

RESULTS

History Before the Lethal Attack

On 2 January 2002 JO was seen bleeding from his rump near the base of his tail and moving slowly. Females in the subgroup were observed inspecting the wound. It is not known how the injury occurred.

On 7 January 2002 JO was attacked by PA and BE while he was being groomed by his mother. He immediately ran toward the ground and fled the subgroup.

On 14 January 2002 screaming was heard just before JO was observed moving away from a subgroup on the ground. BE was the only male in that subgroup at the time.

On 24 January 2002 BE chased JO and AR briefly, and JO left the subgroup 30 min later.

On 3 February 2002 three to four adult males were observed attacking JO in the morning. At midday he was observed resting alone at the top of a tree. He was bleeding from a large wound on his right shoulder and had a new puncture on his left flank close to the tail.

During the next 2 weeks JO was seen sporadically sleeping and traveling alone. His shoulder appeared to be healing; however, his locomotion was impaired, since he was observed moving very slowly from one tree to another and was seen on 18 February walking on the ground along the road outside the village.

The first time we observed JO entering a subgroup of other monkeys after the injury to his shoulder occurred was on 22 March 2002. He may have been in other subgroups in the meantime but was not seen by us. He avoided using the injured arm while moving. When JO first joined the subgroup he maintained distance from the other monkeys, staying on the periphery of the subgroup. After 20 min, JO slowly started moving toward the other adult males. When he approached within 15 m, all four adult males and the subadult male chased him while making aggressive vocalizations. PA led the chase and JO was defended by his mother, who blocked the path of PA by positioning herself in front of him. This also appeared to deflect the attack, as PA then threatened the mother by shaking branches at her. JO fled the subgroup by moving quickly on the ground.

Lethal Attack

At 0655 hr on 1 April 2002 the first author and a field assistant heard a spider monkey squawking loudly (i.e., screaming) about 40 m away from their current position. Within seconds they heard several additional loud squawks coming from the same location. The field assistant rushed to the location and observed JO lying on the ground surrounded by PA, BE, and DA. BE was seen lifting JO off the ground and biting his shoulder repeatedly. AR observed the attack from a few meters away and squealed during the incident. When PA, BE, and DA saw the field assistant they climbed into the trees. At about the same time JO's mother arrived and started to alarm-call by emitting ook-barks when she spotted JO on the ground. When the first author arrived, JO was barely alive, lying on the ground. PA, BE, and DA vocalized and showed signs of arousal (i.e., continuous self-touching and baring of teeth). A few minutes later JO died. His death was confirmed by the lack of a pulse when the researchers palpated his chest and neck area. When the researchers lifted JO's corpse to take it to the base camp for further examination, the adult males dispersed into the canopy. JO's mother continued to ook-bark in the nearby trees, but she did not attempt to follow the researchers.

During the examination the following wounds were identified: 1) lacerations covered with blood on both shoulders, 2) fresh cuts on the left temporal area of the head and the face, 3) a puncture in the skin in the area between the anus and the base of the tail surrounded by fresh blood, and 4) one laceration on the inside of the left thigh. Some of the injuries were corroborated by a postmortem oteological analysis performed by the third author on JO's skeleton 3 months later. JO's left and right scapulae showed large unhealed bite wounds that had punctured the bone, confirming the shoulder injuries seen at the time of the attack. On the pelvis, unhealed bite wounds had punctured the left and right iliae. Most of the ribs were broken perimortem. JO's most serious bony injury was

located on the anterior and medial sides of the left humerus, just below the humeral head. The extent of the periosteal infection suggests that JO was wounded prior to the fatal attack–perhaps as much as several weeks earlier, based on the severity of the lesion. Other bite wounds, received prior to death, were located more distally on the left humerus.

DISCUSSION

The available evidence suggests that the injuries sustained by JO between January and March 2002 were the result of intragroup aggression from at least the three oldest adult males of the community. The fact that other adult males were present at the lethal attack, that we observed one of the males repeatedly biting the victim, and that the males were observed inflicting wounds on the victim in the previous months provides strong evidence for intragroup male coalitionary killing.

Several explanations have been proffered for the presence of intragroup coalitionary aggression toward adult males in other primate species. A case of such aggression in capuchin monkeys (*Cebus capuchinus*) was observed in the context of a group expulsion of an alpha male, which was largely carried out by adult females and immature males [Gros-Louis et al., 2003]. In chimpanzees, which have a social organization very similar to that of spider monkeys [Chapman et al., 1995; McFarland Symington, 1990], three separate incidents of intragroup coalitionary aggression in which older adult males attacked or killed younger adult males have been observed [Fawcett & Muhumuza, 2000; Nishida et al., 1995; Watts, 2004]. Two of these incidents were interpreted as stemming from the failure of young adult males to behave appropriately toward other adult males [Nishida et al., 1995; Watts, 2004]. However, Fawcett and Muhumuza [2000] attributed their observed killing jointly to the failure of the young male to act in accordance with his position in the hierarchy, and to heightened reproductive competition.

One possible explanation for the intragroup attacks we witnessed may be the degree of male reproductive competition, which depends somewhat on the availability of females. In other spider monkey populations the adult female-to-male sex ratio is on average 2.6:1 [Chapman et al., 1989]. Historically, the Eastern group had an extremely skewed adult female-to-male sex ratio (e.g., 7:1 in December 1997). From January 2000 until January 2002, the sex ratio in the Eastern community was still female biased (1.7:1). At the time of the intragroup killing the adult sex ratio in the Eastern community crested at 1:1, thus there was the potential for stronger male–male competition. Furthermore, the female-to-male operational sex ratio (i.e., the ratio of ready-to-mate females to the number of ready-to-mate males) at the time of the attacks was 0:5, since all of the females were either pregnant or had been lactating since April 2001. Thus, tension due to the low availability of mating opportunities may be a proximate trigger for male coalitionary killing in spider monkeys.

If JO had behaved in an abnormal manner toward the older adult males, that might have explained the intragroup killing. However, our long-term observations indicate that his behavior did not depart from that shown by other young males (unpublished data). A third plausible explanation for the intragroup killing we observed is competition over food. The series of attacks we observed all occurred during the dry season, when food was more difficult to find in the core area. Although feeding competition in spider monkeys is more intense among females than among males [Chapman et al., 1989], our data are not sufficiently

detailed to rule out food competition as an explanation. A fourth explanation that could account for intragroup coalitionary killing is competition for the top-ranking position in the dominance hierarchy. Two reported incidents in chimpanzees fit this explanation [de Waal, 1986; Nishida, 1996]; however, it seems unlikely that JO was killed for this reason, given his young age and the absence of any behavioral indication that he was attempting to challenge the older more dominant males (unpublished data).

Our observations pertaining to JO's death constitute the first report of the death of a weaned male spider monkey related to intragroup male–male coalitionary aggression. As such, comprehensive relevant data to test the proposed explanations as to why the killing occurred are lacking. Long-term studies of primate behavior, however, are bound to provide insights into the causes of intragroup lethal aggression against weaned individuals.

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