

BRIEF REPORT

Rescue Behavior in White-Faced Capuchin Monkeys During an Intergroup Attack: Support for the Infanticide Avoidance Hypothesis

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In this work we report the first published observational evidence of rescue behavior during an intergroup interaction in white-faced capuchin monkeys (*Cebus capucinus*). The study groups (groups AA and RR) inhabit the forest of Lomas Barbudal Biological Reserve in Guanacaste, Costa Rica, and have been under investigation since 1990 and 1997, respectively. Here we report a single interaction in which a victim mother–infant pair was rescued from potential injury or death by the intervention of an adult male from their social group during an intergroup encounter. We discuss several hypotheses that may be relevant in explaining this unique observation. *Am. J. Primatol.* 68:1012–1016, 2006. © 2006 Wiley-Liss, Inc.

Key words: cooperation; infanticide; intergroup aggression; altruism; *Cebus capucinus*

INTRODUCTION

In an attempt to explain the common pattern of year-round male–female associations in nonhuman primates, van Schaik and Kappeler [1997] proposed the hypothesis that the risk of infanticide is responsible for the evolution of such associations. They suggested that females with their infants are at greater potential risk for infanticide from unfamiliar male attacks when they are solitary than when they are accompanied by males with whom they share an association. Here we describe an observation of rescue behavior during an intergroup conflict in white-faced capuchins (*Cebus capucinus*), a species characterized by frequent coalitions and long-term associations among adult males and females [Perry, 1997; Vogel, 2005a]. The description is followed

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by a discussion of how this observation provides support for the infanticide avoidance hypothesis.

MATERIALS AND METHODS

White-faced capuchin monkeys were studied in Lomas Barbudal Biological Reserve, the surrounding Instituto Para Desarrollo Agricultura (IDA) property, and Finca El Pelón de la Bajura. Lomas Barbudal is a 2,279 ha reserve located in the Guanacaste Province, northwest Costa Rica (10°30' N and 85°22' W). The forest is classified as a tropical deciduous forest [Frankie et al., 1988]. All data reported here were collected from two study groups of white-faced capuchins (groups AA and RR) containing 34 and 35 individuals, respectively. During this study each group was composed of four adult males, eight to 10 adult females, one to four subadults, seven to nine juveniles, and three to six infants [Vogel, 2004]. The home ranges of the study groups during the study period varied from 2.76 to 4.40 km² and overlapped with those of other white-faced capuchin groups by approximately 10%.

Data collection on the study groups started in January 2000 and ended in August 2001, and observation time was split equally between the two groups, for a total of 2,184 contact hours. Groups AA and RR were habituated in 1990 and 1997, respectively [Gros-Louis et al., 2003]. Most of the data were collected during the longer dry season, although some of the data were collected a few months into the rainy season. Data collection began after all observers agreed on the identification and behaviors of all group members, and the monkeys showed no signs of fear or avoidance toward the observers [Vogel, 2005b].

RESULTS

Adult female MM of group AA gave birth to MN on 10 April 2001. On 20 April 2001, group AA was positioned alongside the Cabuyo River, in the study group's home range, when group RR approached group AA from downstream. Since 18 February 2001, group RR has won all observed intergroup encounters between the two study groups (n = 9). In general, although adult and subadult males are the primary participants in such encounters, the alpha and beta females have also been observed to participate in such interactions [Perry, 1996] (Vogel, personal observation).

On 20 April 2001 at 1228 hr, group AA fled rapidly upstream from their resting area, without vocalizing. As usual during intergroup encounters, the females and juveniles fled first, followed by the subadult and adult males. We pursued group AA, with A.F.J. accompanying the females, infants, and juveniles, and E.R.V. accompanying the adult and subadult males. A total of six males (two adults, three subadults, and one large juvenile) from group RR pursued group AA on the ground. At 1231 hr, E.R.V. observed that female MM with infant MN on her back was partially submerged in a still pool connected to the Cabuyo River. The six males from group RR stopped chasing the males of group AA as they fled and surrounded the partially submerged MM and her infant MN. The males made threatening vocalizations to MM while they attempted to grab at infant MN. MM responded by making loud alarm calls and submerging herself deeper into the river until just the heads of the mother and infant remained above the water. At 1233 hr the beta male of group AA, TL, responded to the alarm calls and returned traveling downstream along the trail in the direction of MM and the males from group RR. When TL came within 15 m of the interaction, he stood up bipedally

and gave an intense threat vocalization [Perry, 1997]. The six males of group RR immediately responded to the vocalization by leaving MM and her infant, and chased TL. TL turned and fled upstream and MM fled from the river, carrying her infant, without any apparent injuries. At 1240 hr, MM and MN joined the rest of group AA approximately 85 m away. At 1326 hr, TL returned to group AA without any signs of physical injury.

DISCUSSION

This observation provides support for the infanticide avoidance hypothesis [van Schaik & Kappeler, 1997]. According to this hypothesis, the benefit obtained by females from associations with males is protection from harassment from unfamiliar males. One of the most costly forms of harassment is infanticide [Harcourt & Greenberg, 2001]. This hypothesis predicts that females with infants should avoid new males and encounters with other groups [van Schaik & Kappeler, 1997], a behavior that is consistent with white-faced capuchins (Vogel, personal observation). Although adult females have been observed to participate in intergroup encounters [Perry, 1996] (Vogel, personal observation), females carrying infants have not been reported to take part in such interactions.

There are several reasons why males from group RR would attack a lone female and/or her infant (since it was not clear whether they were reaching for her or the infant on her back) from a neighboring group. Male infanticide is often associated with intergroup encounters during which protective males of fleeing groups disband [Hrdy et al., 1995]. Infanticide has been observed in this species during group takeovers by coalitions of unfamiliar males [Fedigan, 2003; Fedigan & Jack, 2004; Manson et al., 2003]. Male white-faced capuchins often take over groups in coalitions of two or more individuals [Fedigan & Jack, 2004], and the fact that three of the six males in group RR were subadults (i.e., close to dispersal age) may explain why they would attempt to injure the infant [Jack & Fedigan, 2004]. Alternatively, the males may have targeted MM because adult females have been reported to participate in intergroup encounters [Perry, 1996] (Vogel, personal observation) and thus may be considered as both competitors and threats during between-group competition over resources within their territories. In a simulation model based on real data, Harcourt and Greenberg [2001] found that lone female gorillas were three times more likely to experience infanticide compared to the actual observed rate in the wild for adult females that associate with at least a single male. Thus, it is very likely that when MM was separated from her social group, MN was at greater risk for both injury and infanticide.

Given the documented high costs associated with intergroup aggression, why would a lone individual male respond to the alarm call of a female group member and draw the attention of the attacking males away from the female and infant under attack toward himself? Two other hypotheses that may help shed light on this observation are reciprocal altruism and kin selection [Axelrod & Hamilton, 1981; Hamilton, 1964; Rubenstein & Wrangham, 1980; Trivers, 1971]. Researchers often attribute primate altruism to kin selection or reciprocal altruism [Cheney & Seyfarth, 1990; Chapais et al., 2001; de Waal, 2000; Hauser et al., 2003; Packer, 1977; Silk, 1982]. TL joined group AA in 1999 as an adult male. Although the exact gestation period for *Cebus capucinus* is unknown, it is thought to be similar to that for captive *Cebus apella* (155–160 days) [Fragaszy, 1990; Fragaszy et al., 2004]. Because MN was born on 10 April 2001, TL is a potential father of

MN. Thus, TL may have drawn attention away from MN and toward himself to prevent harm to a potential offspring. An alternative but not mutually exclusive explanation is that by assisting MM, TL ensured her cooperation with him in the future. Given that approximately 37% of within-group coalitionary aggression over food resources in this species is between female–male coalition partners that target adult males, future aid from a high-ranking female during within-group aggressive bouts would be beneficial [Vogel, 2004].

Although it is difficult to postulate on the basis of one observation why an adult male would aid a female under attack by unfamiliar males, this observation does provide support for the hypothesis that one of the benefits gained by females from long-term associations with males is prevention of harassment from unfamiliar males.

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REFERENCES

- Axelrod R, Hamilton WD. 1981. The evolution of cooperation. *Science* 211:1390–1396.
- Chapais B, Savard L, Gauthier C. 2001. Kin selection and the distribution of altruism in relation to degree of kinship in Japanese macaques (*Macaca fuscata*). *Behav Ecol Sociobiol* 49:493–502.
- Cheney DL, Seyfarth RM. 1990. How monkeys see the world. Chicago: Chicago University Press. p 1–361.
- de Waal FBM. 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Anim Behav* 60:253–261.
- Fedigan LM. 2003. Impact of male takeovers on infant deaths, births and conceptions in *Cebus capucinus* at Santa Rosa, Costa Rica. *Int J Primatol* 24:723–741.
- Fedigan LM, Jack KM. 2004. The demographic and reproductive context of male replacements in *Cebus capucinus*. *Behaviour* 141: 755–775.
- Fragaszy DM. 1990. Early behavioral development in capuchins (*Cebus*). *Folia Primatol* 54:119–128.
- Fragaszy D, Visalberghi E, Fedigan L. 2004. The complete capuchin. Cambridge: Cambridge University Press. p 1–339.
- Frankie GW, Vinson SB, Newstrom LE, Barthell JF. 1988. Nest site and habitat preferences of *Centris* bees in the Costa Rican dry forest. *Biotropica* 20:301–310.
- Gros-Louis J, Perry S, Manson JH. 2003. Violent coalitionary attacks and intraspecific killing in wild white-faced capuchin monkeys (*Cebus capucinus*). *Primates* 44: 341–346.
- Hamilton WD. 1964. The genetic evolution of social behavior. *J Theor Biol* 7:1–52.
- Harcourt AH, Greenberg J. 2001. Do gorilla females join males to avoid infanticide? A quantitative model. *Anim Behav* 62: 905–915.
- Hauser MD, Chen MK, Chen F, Chuang E. 2003. Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proc R Soc Lond B Biol* 270: 2363–2370.

- Hrdy SB, Janson CH, van Schaik CP. 1995. Infanticide: let's not throw out the baby with the bath water. *Evol Anthropol* 3: 151–154.
- Jack KM, Fedigan L. 2004. Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 1: patterns and causes of natal emigration. *Anim Behav* 67:761–769.
- Manson JH, Gros-Louis J, Perry S. 2003. Three apparent cases of infanticide by males in wild white-faced capuchins (*Cebus capucinus*). *Folia Primatol* 75:104–106.
- Packer C. 1977. Reciprocal altruism in *Papio anubis*. *Nature* 265:441–443.
- Perry S. 1996. Intergroup encounters in wild white-faced capuchins (*Cebus capucinus*). *Int J Primatol* 17:309–330.
- Perry S. 1997. Male-female social relationships in wild white-faced capuchins (*Cebus capucinus*). *Behaviour* 134:477–510.
- Rubenstein DI, Wrangham RW. 1980. Why is altruism towards kin so rare? *Z Tierpsychol* 54:81–387.
- Silk JB. 1982. Altruism among female *Macaca radiata*: explanations and analysis of patterns of grooming and coalition formation. *Behaviour* 79:162–188.
- Trivers RL. 1971. The evolution of reciprocal altruism. *Q Rev Biol* 46:35–57.
- van Schaik CP, Kappeler PM. 1997. Infanticide risk and the evolution of male-female association in primates. *Proc R Soc Lond B* 264:1687–1694.
- Vogel ER. 2004. The ecological basis of aggression in white-faced capuchin monkeys, *Cebus capucinus*, in a Costa Rican dry forest. Ph.D. dissertation, Stony Brook University, Stony Brook, NY.
- Vogel ER. 2005a. Ecological and social correlates of coalition formation in white-faced capuchin monkeys, *Cebus capucinus*: why escalate? *Am J Phys Anthropol* 40:215–215.
- Vogel ER. 2005b. Rank differences in energy intake rates in white-faced capuchin monkeys, *Cebus capucinus*: the effects of contest competition. *Behav Ecol Sociobiol* 58:333–344.