

## BRIEF REPORT

# Mutualism, Reciprocity, or Kin Selection? Cooperative Rescue of a Conspecific From a Boa in a Nocturnal Solitary Forager the Gray Mouse Lemur

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Predator mobbing is a widespread phenomenon in many taxa but the evolution of cooperative mobbing as an adaptive behavior is still subject to debate. Here, we report evidence for cooperative predator defense in a nocturnal solitary foraging primate, the gray mouse lemur (*Microcebus murinus*). Several mouse lemurs mobbed a snake that held a non-related male conspecific until he could escape. Evolutionary hypotheses to explain cooperative mobbing include (1) by-product mutualism, when individuals defend others in the process of defending themselves; (2) reciprocity, where animals achieve a higher fitness when helping each other than when they do not cooperate; and (3) kin selection where animals help each other only if they share genes by common descent. Owing to the solitary activity of this species, reciprocity seems to be least likely to explain our observations. By-product mutualism cannot be ruled out entirely but, if costs of snake mobbing are relatively low, the available detailed socio-genetic information indicates that kin selection, rather than any of the other proposed mechanisms, is the primary evolutionary force behind the observed cooperative rescue. *Am. J. Primatol.* 70:410–414, 2008. © 2007 Wiley-Liss, Inc.

**Key words:** *Microcebus murinus*; cooperation; predation; anti-predator behavior; mobbing

## INTRODUCTION

Anti-predator behavior can be generally divided into two categories. First, prey animals avoid being targeted by a predator or, second, once a predator has been detected, prey can move away or they may exhibit mobbing behavior, defined as an approach toward a potential predator sometimes involving alarm calls or attacks with physical contact by the mobber [Curio, 1975, 1978; Hartley, 1950]. It has been assumed that the general function of predator mobbing is to decrease the predator's hunting efficiency [Caro, 2005; Curio, 1978; Ishihara, 1987; Lima, 1990], but the evolution of cooperative mobbing as an adaptive behavior is still subject to debate. Conspicuous mobbing comprises the additional risk of revealing oneself to other predators, and attacking predators may be even more costly. Evolutionary hypotheses to explain cooperative mobbing include (1) by-product mutualism, when individuals defend others in the process of defending themselves; (2) reciprocity, where animals achieve a higher fitness when helping each other than when they do not cooperate; and (3) kin selection where animals help each other only if they share genes by common descent, allowing them to spread those genes in their population. By-product mutualism, reciprocal altruism, and kin selection are not mutually exclusive

alternatives, and mechanisms stabilizing cooperation may vary even among populations of the same species [Olendorf et al., 2003; Ostreicher, 2003].

Cooperative mobbing has been reported from fish, birds, primates, and other mammals, but mainly from species that forage in groups [e.g., Dominey, 1983; Janzen, 1970; Olendorf et al., 2003; Tello et al., 2002]. Information about cooperative mobbing in solitary foraging species, which comprise the majority of mammals and more than a quarter of all primates, is rare [e.g., Gursky, 2005; Schülke, 2001]. Here, we report evidence for cooperative mobbing of a snake in the nocturnal solitary foraging gray mouse lemur (*Microcebus murinus*). Gray mouse lemurs are regularly preyed on by various predators, including owls and snakes, carnivores [Goodman et al., 1993], and a lemur, Coquerel's

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dwarf lemur [*Mirza coquereli*; Eberle & Kappeler, unpublished observation]. Their social organization is characterized by extensive home range overlap between and within sexes, and by female philopatry and male dispersal [Eberle & Kappeler, 2004b]. During the day, mouse lemurs rest in hollow trees. Males usually rest alone, whereas female kin form sleeping groups and raise their young cooperatively [Eberle & Kappeler, 2006; Kappeler, 2000]. Mobbing and cooperative predator attacks have been observed on a few occasions. The new observations that we report here were made during a long-term study on reproductive strategies, social organization, and dispersal that provides us with detailed socio-genetic information. Our new observations make it therefore possible to discuss the potential evolutionary causes of cooperative mobbing.

## METHODS

We have been studying a population of gray mouse lemurs (*M. murinus*) in Kirindy Forest, located about 60 km north-east of Morondava in Western Madagascar [Sorg et al., 2003] since 1994, where we captured 826 mouse lemurs inhabiting a 30-ha study area. We conducted captures in a 9-ha study area each month between March and December, and additionally within a surrounding 21 ha area in April and November. The study area is equipped with a rectangular system of foot trails at 25-m intervals. To trap mouse lemurs, we baited Sherman live traps with small pieces of banana and set them near trail intersections in the late afternoon on three consecutive nights per month. Captured animals were collected in the early morning, individually marked with subdermal transponders (or reidentified in case of recaptures), subjected to standard morphometric measurements, and released at the site of capture in the following late afternoon. Tissue samples for genetic analyses were taken from all captured animals in the form of small (2–3 mm<sup>2</sup>) ear biopsies during brief anesthesia induced by applying 0.01 mL Ketanest 100 (Parke-Davis, Berlin, Germany) [Rensing, 1999] subdermally. All adult animals inhabiting the 9-ha study area were individually marked (some 75 at a time, 123 between 1999 and 2001), with exception of a few roamers that appeared in the study area only during the brief annual mating seasons [for details, see Eberle & Kappeler, 2004b]. Our records of animals present in this area are therefore as complete as possible for a small, nocturnal mammal.

We equipped 56 females and 14 males with radio-tag collars (Biotrack TR-4, Biotrack, Wareham Dorset, UK) and observed them for a total of 905 hr by means of focal-animal sampling [Altmann, 1974] between 1999 and 2001 during the three annual mating seasons between mid-October and mid-

November and during lactation between January and March 2000 [for details, see Eberle & Kappeler, 2004b]. We determined genetic relationships among 313 individuals trapped in the 30-ha study area between 1999 and 2001, and 63 of 192 individuals trapped in the same area between 1994 and 1998. We isolated DNA from the collected ear biopsies and conducted precise parentage analyses as described in Eberle and Kappeler [2004b]. Additionally, we calculated the pair-wise Queller and Goodnight's [1989] relatedness  $R$  among all animals, using the software Relatedness 5.08. We calculated  $R$  only among animals that were simultaneously present in the area. We calculated  $R$  year-wise because gray mouse lemurs in Kirindy give birth only during a period of 3 to 4 weeks in late December/early January. Finally, we considered only dyads of individuals with overlapping home ranges for calculations of  $R$ . To determine location, size, and overlap of home ranges, we combined coordinates of the intersections where animals were captured, together with coordinates of sleeping trees, and radio tracking data. On the basis of radio-tracking data, we estimated the size of home ranges at 1.3 ha for females ( $N = 22$ ) and 1.9 ha for males ( $N = 12$ ). We calculated the center of activity for each individual and fitted a circular home range of these mean sizes around it.

All research reported in this manuscript adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates. All research protocols reported in this manuscript were reviewed and approved by the appropriate Malagasy and German institutional and governmental agencies that regulates research with animals. All research reported in this manuscript adhered to the legal requirements of Germany and Madagascar and complied with the protocols approved by the appropriate institutional Animal Care and Use Committee. Our research received clearance from, and complied with, the protocols approved by the equivalent institutional animal care committees of Germany and Madagascar (Bundesministerium für Naturschutz (BfN), Germany; Ministère de l'Environnement et des Eaux et Forêts (MINEEF), Madagascar).

## RESULTS

### Observations

During focal observations of a radio-tagged adult female in March 2000, M.E. heard characteristic gray mouse lemur threat-vocalization [vocal repertoire, see Zimmermann, 1995] from a distance. Eighty meters away, a Malagasy tree boa (*Sanzinia madagascariensis*) held an adult male gray mouse lemur in a tight grip at 6 m of height. The boa curled itself around both the mouse lemur and the branch on which it sat. Another radio-tagged adult female and

an unidentified adult male attacked the boa while emitting characteristic mobbing vocalization. The two jumped repeatedly on the branch near the hind end of the boa or on a close parallel branch, bit the snake, and jumped away. A single attack lasted no longer than a few seconds. After 2 min, the attacking male fell to the ground, climbed up again but disappeared. The female that was subject to focal observation before the snake's attack, and that spent an hour foraging 50–100 m apart from the place of the attack, arrived 3 min after M.E. at the scene. She also emitted mobbing vocalization and joined in attacking the snake. The boa uncurled slowly its front end and threatened the two attacking mouse lemurs by stretching out toward them while they continued leaping around the snake. The male caught by the boa escaped from the uncurled snake a few minutes later and fell to the ground, where he could be identified with the help of a transponder-reading device before he disappeared. The two females remained sitting another 10 min at a distance of 4–5 m to the snake, still emitting mobbing-vocalization, before they left the scene. The focal female that M.E. observed before the boa's attack went back within 15 min to the area where she foraged before.

We observed two further encounters between gray mouse lemurs and a tree boa during our study. In both cases, only a single female encountered a snake without prey. The two females sat at a distance of 2 m from the boa for 18 and 20 min, respectively. In the first case, the female remained silent and in the other case she gave alarm calls throughout the period that she was with the snake.

### Genetic data

We could perform precise pedigree analysis for each year and each parent separately by means of exact mismatch analyses [for details, see Eberle & Kappeler, 2004a,b,]. Relatedness analysis between all animals with overlapping home ranges revealed an positive average relatedness  $R$ , mainly because of the female–female dyads, but also male–male dyads were above average related (Table I). Only female–male dyads were related below average in 2 out of 3 years. The two defending females were aunt

and niece. Both females were slightly below average related with the victim (Queller & Goodnight's  $R$  was  $-0.02$  between the older female and the victim, and  $-0.09$  between her niece and the victim).

### DISCUSSION

The three hypotheses that may explain cooperative mobbing are not mutually exclusive. Below, we discuss which hypothesis may best explain this case of cooperation, based on theoretical considerations and socio-genetic information. First, participating in predator mobbing can be driven by by-product mutualism. It may be beneficial to all participants as a common effort further reduces the attractiveness of the own home range as hunting area. Such an explanation is most likely in the case of communal mobbing of predators without prey as observed in other solitarily foraging lemur species, where members of two species, *Phaner furcifer* and *M. coquereli*, communally mobbed a *S. madagascariensis* [Schülke, 2001]. In this study, however, the mouse lemurs took additional risk on behalf of an unrelated conspecific. Mobbing would have been mutually beneficial had the two females defended a potential mate. The male was indeed one out of three mating partners of the younger female during the preceding mating season, and one out of six mating partners of the older female during the following mating season, but he did not sire offspring with either female [Eberle & Kappeler, 2004b]. Purposely defending a particular potential mating partner (that was not vigilant) seems unlikely because the operational sex ratio in this population is highly male-biased and females mate with several males [Eberle & Kappeler, 2004b]. Additionally, not only the two females but also a male attacked the snake. Attacks of prey animals on snakes, on the other hand, are common in mammals [Caro, 2005], indicating that the costs of attacks are low once a snake has been detected. Mutualism may therefore still be involved if the costs of such an attack are relatively small compared with benefits owing to predator distraction within the own home range. Mobbing mouse lemurs attacked the boa only when the snake caught a conspecific. Without a victim the mouse lemurs mobbed the snake only vocally. If this pattern is the rule, mutualism is

**TABLE I. Average Queller and Goodnight's Relatedness  $R$  Among Adult Individuals With Overlapping Home Ranges in 1999, 2000, and 2001**

Year	All	ff	mm	fm
1999	0.028 (0.071, 112)	0.072 (0.112, 56)	0.013 (0.091, 51)	$-0.001$ (0.087, 49)
2000	0.023 (0.069, 105)	0.069 (0.096, 59)	0.003 (0.070, 42)	$-0.013$ (0.088, 47)
2001	0.031 (0.074, 100)	0.072 (0.087, 47)	0.019 (0.078, 47)	0.008 (0.086, 45)

Columns contain annual average relatedness  $R$  among all individuals (all), among females (ff), among males (mm), and between sexes (fm). Values in brackets are standard deviation (SD) and number of dyads ( $n$ ).

unlikely to be the main force behind the observed cooperative attack.

Second, reciprocal altruism is another possible explanation [Trivers, 1971]. As mobbing is costly, there may be a temptation to cheat, thereby avoiding the costs of mobbing. Reciprocity makes the payoff from cooperative behavior frequency-dependent, which can stabilize a cooperative population against invasion by cheaters. However, cooperation cannot arise by means of reciprocal altruism among anonymous non-relatives, but only if individuals can differentially distribute such behavior to others according to whether or not they have already been cooperative and altruistic toward the donor or, in other words, if cheaters can be punished [Dugatkin, 2002; Hamilton, 1984; Krams & Krama, 2002; Trivers, 1971]. In solitary species, usually only one animal is threatened at a time and a decision as to whether absent animals cheat cannot be made. Thus, reciprocal altruism is also unlikely to serve as mechanism for the evolution of cooperative mobbing on behalf of a conspecific in this species.

Third, kin selection can stabilize cooperation. Again, the costs of snake mobbing could be relatively small compared with indirect fitness benefits due to shared genes. The evolution of cooperation by means of kin selection requires the ability to recognize kin, or, if kin cannot be discriminated, a population structure where close relatives gain more from cooperation than more distantly related animals. Discrimination of unfamiliar animals as kin or non-kin by means of phenotypic matching is rare in vertebrates [see Pfennig, 2002]. Phenotypic matching by means of visual cues has been reported from chimpanzees [e.g., Parr & de Waal, 1999], phenotypic matching by non-visual cues has been demonstrated in several non-primates [e.g., Erhart et al., 1997; Pfennig, 2002]. It is not known whether gray mouse lemurs discriminate relatives other than their next kin with whom they shared a nest during breeding [Eberle & Kappeler, 2006]. Despite male migration in gray mouse lemurs [Eberle & Kappeler, 2004b; Radespiel et al., 2003], not all males migrate and many males are related above average among each other as well as with females (note the SD-values in Table I). It might therefore be on average likely enough that an animal encounters distant male relatives within its home range for this altruistic behavior to evolve. Indiscriminate defense of conspecifics can be beneficial as long as the average benefits supersede the costs, i.e., as long as Hamilton's rule is satisfied [Hamilton, 1964]. In conclusion, identifying the relative impact of possible proximate and ultimate causes for cooperative predator defense remains puzzling. The available information indicates that kin selection, rather than any of the other proposed mechanisms, is the primary evolutionary force behind the

observed cooperative rescue in gray mouse lemurs. Because predation can hardly be investigated systematically in the field experiments such as playback designs with individuals of varying relatedness and familiarity, are needed to further illuminate this issue.

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