

# Function of Snake Mobbing in Spectral Tarsiers

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**ABSTRACT** Numerous species are known for their tendency to approach and confront their predators as a group. This behavior is known as mobbing. Snakes seem to be one of the more consistent recipients of this type of predator-directed behavior. This paper explores individual differences (sex and age) in the mobbing behavior of the spectral tarsier toward live and model snakes. This study was conducted at Tangkoko Nature Reserve (Sulawesi, Indonesia) during 2003–2004. During this research, 11 natural mobbing events and 31 artificially induced mobbing events were observed. The mean number of individuals at a mobbing was 5.7. The duration of mobbing events was strongly correlated with the number of assembled mobbers. Adults were more likely than other age classes

to participate in mobbings. Males were more likely than females to participate in mobbings. Mobbing groups often contained more than one adult male, despite the fact that no spectral tarsier group contains more than one adult male. No difference in body size between extragroup males and resident males was observed, refuting the “attract the mightier” hypothesis. The number of mobbers did not affect whether the tarsier or the snake retreated first, countering the “move-on” hypothesis. The “perception advertisement” hypothesis was tentatively supported, in that live snakes were rarely seen in the area following mobbing calls, in comparison to when tarsiers either ignored the snake or alarm call. *Am J Phys Anthropol* 129:601–608, 2006. © 2005 Wiley-Liss, Inc.

While most animals make considerable effort to avoid their predators, numerous species are known for their tendency to approach and confront their predators as a group. This behavior is known as mobbing, and was observed in fish, birds, mammals, and primates (Owings and Coss, 1977; Shields, 1984; Bartecki and Heymann, 1987; Kobayashi, 1987, 1994, 1996; Loughry, 1988; Tamura, 1989; Heymann, 1990; Srivastava, 1991). There are numerous costs to predator mobbing. To begin with, there is an increased risk of mortality to the individual approaching the predator (Sordahl, 1990). Individuals who approach predators make themselves more conspicuous during their approach. There are many accounts in the literature of predators attacking and killing individual prey that approached too closely. This is because the attack success rate for many predators is known to be greater when prey are closer to the predator. For example, when guppies with predator-inspection tendencies were placed in a tank with a fish predator, there was a negative correlation between how closely an individual approached a predator and its probability of survival (Brosnan et al., 2003). Milinski et al. (1997) found a 50% risk of predation association with close-range inspection for the lead fish. There are also lost opportunity costs, i.e., individuals who spend their time approaching the predator could be spending their time getting away from the predator, and searching for food or mates. Among black-tailed prairie dogs and Formosan squirrels, there is a negative correlation between time spent foraging and time spent inspecting predators (Tamura, 1989; Dugatkin and Godin, 1992; Brown and Godin, 1999). Reduced food intake, especially in species with short life spans, may compromise a parent's future reproductive success through lowered fecundity and survivorship (Dill, 1987; Dugatkin and Godin, 1992). Just as importantly, individuals who approach predators risk being exploited by others who benefit from another individual's willingness to approach the predator without paying the cost of close approach (Magurran and Nowak, 1991). In

a mobbing group, the individual closest to the predator is more likely to die from a predator retaliatory attack than are others in the mob. Thus, there are asymmetries in risk-taking among members of the mobbing group (Dugatkin and Godin, 1992).

Despite the putative costs that result from mobbing behavior, numerous primate species were observed exhibiting this behavior. They include hanuman langurs (*Presbytis entellus*), saddle-back tamarins (*Saguinus fuscicollis*), Geoffroy's marmosets (*Saguinus geoffroyi*), white-faced capuchins (*Cebus capucinus*), spectral tarsiers (*Tarsius spectrum*), and *Galago* sp. (Chapman, 1986; Bartecki and Heymann, 1987; Heymann, 1990; Srivastava, 1991; Ross, 1993; Passamani, 1995; Bearder et al., 2002; Gursky, 2002a). To account for the function of mobbing behavior by primates and other mammals, numerous hypotheses were proposed (Curio, 1978; Dugatkin and Godin, 1992; Ross, 1993; Flasskamp, 1994; Schradin, 2000). These include 1) the selfish herd hypothesis: animals tend to use others as “living shields,” which causes clumping of individuals; 2) the confusion effect: predators find it difficult to focus their concentration and pursuit on a specific individual prey animal when a large number of prey are escaping from them at the same time, going in different directions, and making a lot of

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noise; 3) alerting kin: kin are preferentially alerted to mobbing, not strangers; 4) attracting the mightier: mobbing attracts stronger allies; 5) silencing offspring: mobbing distracts predators from the offspring who are silent during the exchanges; 6) site avoidance: individuals will avoid the site where a predator was previously observed and mobbed; 7) the move-on hypothesis: predators should leave an area sooner, the more intensely it is mobbed when they enter an area; 8) perception advertisement: animals identify themselves to the predator, informing it that the surprise element has been removed; and 9) cultural transmission: individuals learn to fear a predator and avoid it. These hypotheses are not mutually exclusive, and mobbing can be performed for more than one reason.

The spectral tarsier, *Tarsius spectrum*, is a small (110 g) nocturnal primate. It lives in groups of 2–10 individuals, which defend their territories through scent-marking and vocal duets (Gursky, 2003b). Approximately one territorial dispute occurs every other night. Spectral tarsiers primarily utilize strangling *Ficus* trees for sleeping sites (MacKinnon and MacKinnon, 1980; Gursky, 1997). Home ranges vary between 1.6–4.1 hectares (ha), with an average size of 2.3 ha for females and 3.1 ha for males (Gursky, 1998a). Although most groups exhibit a monogamous mating system, a few exhibit a polygynous mating system (Nietsch and Niemitz, 1992; Gursky, 1995). They are highly insectivorous, consuming a wide variety of insects, with a preference for Orthopterans and Lepidopterans (Gursky, 2000). Births are seasonal, with most occurring in April–May, and a few in November–December. Infants are transported in the mother's mouth and then parked on branches while the mother forages nearby, often within the same tree (Gursky, 1997). When a tarsier sees a predator nearby, it reacts by ignoring the predator, emitting an alarm call, or jointly mobbing the predator with other group members (Gursky, 2005). Mobbing involves uttering alarm calls, while alternately approaching and retreating from the predator. This pattern continues for approximately 15 min to as long as 1 hr.

Of the nine hypotheses mentioned above, three have already been partially refuted in attempts to understand the mobbing behavior of spectral tarsiers. Contradicting the site avoidance hypothesis (no. 6), Gursky (2003a) found that on nights following a mobbing event, mothers continued to park their infants in the same tree or in a tree near where the mobbing occurred. Infants were parked, on average, less than 5 m from the location where the mobbing had previously taken place, thus refuting the site avoidance hypothesis.

No evidence was found to support the silencing offspring (no. 5) or cultural transmission (no. 9) hypotheses (Gursky, 2003a, 2005). Gursky (2005) found that females regularly attended mobbing events with their infants. That is, they consistently transported their infants toward the dangerous predator, instead of away from the predator. If parents want to protect their offspring from predators by having them remain silent, it does not make sense that they should actively bring their offspring to a mobbing event. They would be safer parked at a distance from the mobbing event. Gursky (2005) also found no significant difference in the number of vocalizations infants emitted on nights with predator mobbings and nights without predator mobbings, thereby refuting the silencing offspring hypothesis.

Similarly, while studying the response of infants to model snakes, Gursky (2003a) found that nursing in-

fant (even infants less than 1 week old) alarm-called when exposed to a potential snake predator, despite having never seen a snake. The mother then responded to the infant by calling, which sometimes led to a mobbing event. The observation that very young infants alarm-called in the presence of snakes suggests that infants recognize that snakes are dangerous and do not need to learn to avoid snakes, thereby refuting the cultural transmission hypothesis for spectral tarsiers (Gursky, 2003a, 2005).

Due to small sample sizes, Gursky (2003a, 2005) was unable to evaluate the other six hypotheses for the function of mobbing. Using new data, the goal of this paper was to evaluate three additional hypotheses for the evolutionary function of mobbing behavior in spectral tarsiers. In particular, this paper will evaluate: 1) the move-on hypothesis, 2) the attracting the mightier hypothesis, and 3) the perception advertisement hypothesis. If the move-on hypothesis is supported, then as the number of individuals mobbing increases, the number of minutes the predator remains in the area will decrease. If the attract the mightier hypothesis is supported, then extra-group males will exhibit a larger body mass than group males. If the perception advertisement hypothesis is supported, then snakes should spend less time in the area after tarsiers begin mobbing than if tarsiers only emitted alarm calls or ignored the snake.

## METHODS

### Field site

Sulawesi is located to the east of Borneo and northwest of Australia-New Guinea (longitude, 125° 14' East; latitude, 1° 34' North). Sulawesi is the eleventh largest island in the world. It is also the largest and most central island of the biogeographical region of Wallacea, where the Australian and Asian zoogeographical regions meet. Sulawesi exhibits a blend of Asian and Australian elements in its fauna and flora, in addition to exhibiting very high numbers of endemic taxa (Whitten et al., 1987).

This study was conducted at Tangkoko Nature Reserve, on the easternmost tip of the northern arm of the island. The reserve is approximately 3,000 ha and exhibits a full range of forest types, including beach-formation forests, lowland forests, submontane forests, and mossy cloud forests on the summit of Mt. Tangkoko (MacKinnon and MacKinnon, 1980; Whitten et al., 1987; Gursky, 1997). The reserve is far from pristine, due to heavy selective logging and encroaching gardens along its borders. The forest canopy is very discontinuous and contains a high proportion of *Ficus* trees (Gursky, 1997, 1998a). Rainfall averages approximately 2,300 mm annually (World Wildlife Fund, 1980; Gursky, 1997). Additional details concerning the habitat types at Tangkoko Nature Reserve can be found in Gursky (1997).

The main predators of spectral tarsiers within Tangkoko Nature Reserve include monitor lizards (*Varanus indicus*), snakes (e.g., *Python reticulatus*), the Malaysian civet (*Viverra zibethica*), and various birds of prey, including falcons (*Falco* sp.) (Gursky, 1997). No quantitative survey of the abundance of predators was conducted, but *ad libitum* observations of encounters with possible predators were noted while conducting focal follows. For example, over the course of this research, more than 40 encounters with snakes occurred while conducting focal follows of spectral tarsiers. Most of the time, the snake was observed in a tree near the focal animal. Over the course of observations, only one predation event was ob-

TABLE 1. Group size and composition of spectral tarsier groups studied at Tangkoko Nature Reserve during 2003–2004

Group	Group size	Adult females	Adult males	Subadult females	Subadult males	Juveniles	Infants
K50	4	1	1	0	1	0	1
I50	3	1	1	0	0	1	0
I450	5	1	1	1	0	1	1
I550	3	1	0	0	0	1	0
G350	4	1	1	0	1	1	0
M300	4	1	1	1	1	0	0
M600	4	2	1	0	1	0	0
L300	5	1	1	1	0	1	1
J750	7	2	1	1	1	1	1

served, and another predation event was inferred. The observation involved predation by a python (Gursky, 2002b). The inference involved possible predation by a falcon: a radio collar and part of a skeleton were found in a tree hole approximately 1 km away from the individual's territory and sleeping tree. The hole was visited regularly by a large bird of prey (*Falco* sp.), but it is difficult to say with certainty what animal killed the tarsier and brought it to the tree hole. These observations confirm that spectral tarsiers are at risk of predation.

### Data collection

In 2003–2004, nine groups were intensely observed for a 12-month study period. The size and composition of these groups, prior to actual data collection (i.e., excluding births, dispersals, and disappearances), are presented in Table 1.

One month prior to data collection was spent locating, trapping, radio-collaring, and habituating groups. Groups were located from the vocalizations each individual tarsier emits upon returning to its sleeping site each morning (MacKinnon and MacKinnon, 1980; Niemitz, 1984; Nietsch and Niemitz, 1992; Gursky, 1997). These vocalizations were given for 3–5 min, and were heard from 300–400 m. The age and sex of all group members sharing a sleeping site were recorded. Sex was determined based on the sex-specific vocal calls given by all group members (MacKinnon and MacKinnon, 1980; Niemitz, 1984; Gursky, 1997). Age was estimated based on relative body size (Gursky, 1997). Mist nets were then set up at the sleeping site(s) of study groups approximately 1 hr before dusk, and were continually monitored (Bibby et al., 1992). Upon capture, individuals were placed in a cloth bag and weighed with a portable scale, providing an accuracy of  $\pm 1$  g. An SM1 radio collar (AVM Instrument Co., Livermore, CA), weighing 4.0 g, was attached to the neck of all group members except infants, by covering the folded-back thermoplastic band with heat-shrink tubing (Gursky, 1998b). Previous studies of the effect of radio collars on the activity patterns, mobility, foraging, body mass, and survival of spectral tarsiers suggest that wearing low-weight radio collars does not significantly affect this species (Gursky, 1998b). Groups were each identified according to the location of their sleeping tree within the trail system. Upon completion of each research project, the radio collars were removed from all but three study animals. Three individuals proved elusive to recapture by either hand or net.

A radio receiver using a 151-MHz frequency and three-element collapsible Yagi antenna was used to determine the location of each individual radio frequency. An Indonesian assistant and the author conducted behavioral focal follows. Initially, focal follows were con-

ducted together on a single individual until approximately 99% of the data recorded by both of us was identical. Subsequently, the Indonesian assistant collected data on one member of the male-female pair, while the author collected data on the other member of the male-female pair. Once each month thereafter, an interobserver reliability test was conducted to determine if we were still consistent in our data recording. The data recording was determined to be at least 98% consistent during each interobserver reliability test.

Over the course of research, over 2,000 hr of focal follows were conducted. Three primary methods of data collection were used (Altmann, 1974): 1) focal follows, 2) locational positions, and 3) predator experiments. While conducting nightly focal follows, all occurrences of mobbing and alarm-calling were collected *ad libitum*. Additional details of the behavioral methods utilized are presented in Gursky (1997, 2002, 2003a, and 2005).

On 216 nights, four types of predator experiments were conducted: 1) rubber snakes, 2) a wooden painted model of a monitor lizard, 3) a wooden painted model of a civet, and 4) plastic birds of prey. This paper will only explore the results of the 73 experiments using rubber snakes. The rubber snakes (*Python reticulatus*) were life-like in both size and color. When conducting these experiments, the author remained behind a blind of large *Livistonia* leaves. Two conditions were necessary prior to beginning the experiment. First, the focal animal had to be below 5 m in height. Second, the focal animal could not be near any group member. This was determined through general observation as well as scanning for other group members' radio signals with the radio attenuator on high. The predator experiment was conducted on each adult individual with a radio collar. Thus, focal individuals were restricted to individuals with radio collars. The predator model was attached to a bamboo stick and was exposed to the focal individual from either the top or the side of the blind. Focal animals were exposed to the predator models for 20 min, after which the predator model was removed and replaced behind the blind. While the predator was present, the behavior of the focal animal was observed, using both instantaneous sampling and *ad libitum* sampling (Altmann, 1974). During this set of experiments, the snake was not moved after it was placed outside the blind. *Ad libitum* data were collected to record all occurrences of alarm calls, as well as whether or not the predator was mobbed. Mobbing was defined as uttering alarm calls while alternately approaching and retreating from the predator. Occasionally, mobbing involves physically biting the predator. Data were collected for the 20 min the predator was present and the 20 min directly following removal of the predator. In addition, while the predator was present, at 30-sec intervals, the approxi-

mate distance of adult individuals from the predator was recorded.

Data were analyzed using Statistica 6.0 (Statsoft, Inc.). To explore the relationship between the duration snakes were present and the number of mobbers, a Pearson correlation was conducted (Sokal and Rohlf, 1981). A median test was conducted to explore whether the predator or the prey retreated first. Student's *t*-tests were utilized to evaluate whether there were differences in body weight or distance from the predator (during mobbing events) between focal males vs. extragroup males, as well as the distance of male and females from the predator.

## RESULTS

Over the course of this study, the spectral tarsiers encountered a total of 43 live snakes. During 35% of the encounters ( $n = 15$ ), they did not modify their behavior, i.e., there was no obvious vocal or behavioral response to the presence of the snake. However, during 40% of the encounters with live snakes, the tarsiers responded by alarm-calling ( $n = 17$ ). During the remainder of the encounters ( $n = 11$ , 25%), the tarsiers responded to the presence of the live snake by alarm-calling and mobbing it. By chance, each mobbing event occurred in a different group.

The number of tarsiers assembled at a mobbing site for a live snake varied from 3–10, the average being  $5.7$  ( $SD \pm 1.7$ ,  $n = 11$ ). The duration of mobbing bouts (i.e., the time from the first mobbing call to the last) ranged from 18–54 min, with a mean of 37.3 min ( $SD = 13.2$ ,  $n = 11$ ). The duration of mobbing bouts toward live snakes increased with an increase in the number of assembled mobbers ( $r = 0.78$ ,  $n = 11$ ,  $P = 0.0000$ ). There was also a correlation between the number of mobbers and the number of minutes that live snakes were present ( $r = -0.81$ ,  $n = 11$ ,  $P = 0.0000$ ). As the number of mobbers increased, the number of minutes the snake predator was present decreased.

During the predator experiments, the response of spectral tarsiers to the rubber snakes was quite variable. During 26% of the presentations ( $n = 73$ ), the tarsiers were not observed modifying their behavior, i.e., there was no response to the presence of the rubber snake. However, during 32% of the rubber snake presentations, the tarsiers responded by alarm-calling. During the remainder of the presentations ( $n = 31$ , 42%), the tarsiers responded to the presence of the rubber snake by alarm-calling and mobbing it.

The average number of tarsiers assembled at a mobbing site for the rubber snake was 5.8 ( $SD \pm 1.8$ ,  $n = 31$ ), and ranged from 3–9. The duration of mobbing bouts using the rubber snakes was 35.3 min ( $SD = 10.4$ ,  $n = 31$ ), and ranged from 14–51 min. The duration of mobbing bouts toward rubber snakes also increased with the increase in number of assembled mobbers ( $r = 0.8739$ ,  $n = 31$ ,  $P = 0.0000$ ).

In 8 of 11 natural mobbings, the mobbed snake retreated into a tree hole or bush. In five of these cases, the mobbers left after the snake, one by one, but in three (of the eight) mobbing events, the spectral tarsiers continued to attack (lunge and retreat) even after the snake retreated. In 3 out of 11 natural mobbings, the spectral tarsiers left the mobbing site before the snake retreated. These results are comparable to the observations of the tarsiers during the artificially induced mobbings. During 74% of the artificially elicited mobbing events, the tarsiers left before the rubber snake was removed (after 20 min).

In 14 of these cases, the mobbers left the site one by one, but in nine additional cases, the tarsiers continued to lunge and retreat even after the snake was removed (9/23). Comparing who retreated (or was removed) first (snake or tarsier) with the number of mobbers indicates that the tarsiers were more likely to retreat before the snake when there were few mobbers. In contrast, the snake was more likely to have been removed before the tarsiers when large numbers of mobbers were present. Although this difference was not statistically significant (median test  $\chi^2 = 42.857$ ,  $df = 30$ ,  $P = 0.0577$ ), the trend was strong enough to suggest that the result may reach significance with larger sample sizes.

Based on the adult sex ratio in the study population (Gursky, 1998a), adult males initiated mobbing events more than expected by chance ( $\chi^2 = 17.61$ ,  $df = 3$ ,  $P = 0.0001$ ). Adult females and subadult males were responsible for initiating 25% and 15% of mobbing events, respectively. Table 2 shows the members of 42 mobbing groups that occurred naturally or were obtained experimentally. Approximately 64% of natural mobbing groups and 68% of experimentally induced mobbing groups contained only one adult female. Two adult females were observed in 36% of the natural mobbing groups and in 32% of experimentally induced mobbing groups. However, in only four groups (one natural and three experimental) was a female from another group present. That is, when there was more than one adult female present, both females usually resided in the same territory and were members of the same group.

The number of males assembled per mobbing varied from 1–3 in the natural and experimental mobbings. Two or more males were present in 63.6% of natural and 41.9% of experimental mobbing groups. Because spectral tarsier groups contain only one male, the additional males must have been from other groups. The additional males are referred to as extragroup males. When the identity of the extragroup male was known, the body masses of the extragroup male and resident male were compared. There was no significant difference in body mass (live snake mobbing:  $t = -0.0861$ ,  $P = 0.9320$ ,  $df = 12$ ; rubber snake mobbing:  $t = 0.1906$ ,  $P = -0.8515$ ,  $df = 14$ ). That is, extragroup males were not significantly larger or smaller than resident males. The home-range sizes of extragroup males and resident males were also compared. Once again, there was no significant difference in home-range size (ha) (live snake mobbing:  $t = 0.934$ ,  $P = 0.3541$ ,  $df = 12$ ; rubber snake mobbing:  $t = 0.1906$ ,  $P = -0.2659$ ,  $df = 14$ ).

Comparing the mean distance of each adult individual to the potential predator, adult males were typically located closer to the predator than were adult females. On average, males were located approximately 2.1 m ( $SD$ , 0.9) from the predator, while females were located approximately 2.9 m ( $SD$ , 1.4) from the predator ( $t = 2.604$ ,  $df = 40$ ,  $P = 0.0116$ ). Comparing all adult males, there was no difference in mean distance that resident males (2.0 m;  $SD$ , 0.8 m) vs. extragroup males (2.2 m;  $SD$ , 0.9 m) were located from the predator. That is, they were both equally close to the predator ( $t = 0.7835$ ,  $df = 20$ ,  $P = 0.4361$ ).

Extragroup males were not present at all mobbing events. In fact, they seemed to preferentially join mobbing events based on the composition of the group performing the mobbing. During the seven occasions when an extragroup male was present at a natural mobbing event, only once did the male join a mobbing group that did not con-

TABLE 2. Number, sex, and relative age of mobbers observed in 42 mobbing episodes, including naturally occurring and experimentally induced events<sup>1</sup>

Experiment type	Number of individuals at mobbing site	Adult females	Adult males	Subadult females	Subadult males	Juveniles	Infants
Natural	7	2	2	1	0	1	1
	6	1	1	0	1	2	1
	5	1	2	1	0	1	0
	8	2	3	1	0	1	1
	9	1	3	1	0	1	2
	4	1	1	0	1	1	0
	5	1	2	1	1	0	0
	5	2	2	0	1	0	0
	5	1	1	1	0	1	1
	4	1	1	0	1	0	1
10	2	2	1	2	2	1	
Experimental	5	2	1	0	1	0	1
	5	1	1	1	1	1	0
	7	2	3	1	0	1	1
	4	1	1	1	0	0	1
	5	1	1	1	0	1	1
	9	2	3	1	1	1	1
	3	1	1	0	0	0	1
	5	1	1	0	1	1	1
	9	2	3	1	1	1	1
	8	1	2	1	1	2	1
	7	2	1	1	1	1	1
	6	1	1	0	1	1	2
	5	1	1	1	0	1	1
	4	1	1	1	0	1	0
	5	1	1	1	1	1	0
	9	2	2	1	1	2	1
	5	2	1	0	1	0	1
	6	2	1	1	0	1	1
	6	1	1	1	1	1	1
	3	1	1	0	0	1	0
	5	1	2	0	1	0	1
	4	1	2	1	0	0	0
	6	1	2	1	1	1	0
	8	2	2	1	1	1	1
	7	2	2	0	1	1	1
	3	1	1	0	0	0	1
	4	1	1	0	0	1	1
8	1	2	1	1	1	2	
6	2	2	0	1	0	1	
8	2	3	1	1	1	1	
4	1	1	1	0	0	1	

<sup>1</sup> Individuals present at mobbings include territorial groups in addition to extragroup individuals.

tain a subadult female. On the other six occasions, the male joined mobbing groups containing a subadult female. Of the 13 occasions when an extragroup male joined an experimentally induced mobbing event, they joined groups with subadult females on 10 occasions. In 3 of 13 mobbings involving extragroup males, the males joined a group that did not have a subadult female.

Table 3 gives a comparison of mobbing intensity among adults and immatures of both sexes observed in the 11 natural and 31 experimental mobbings. At the 11 natural mobbings, 20 adult males were present, 60% of which mobbed intensively (i.e., close approach, touch, sniff, and pouncing on the snake, as well as alarm-calling), and 40% mobbed passively (i.e., merely attending a mobbing event at a distant point from the snake, and alarm-calling). While a similar number of adult females were present at these natural mobbing events, only 46% of adult females intensively mobbed, and 54% mobbed passively. During exposure to rubber snakes, a similar

pattern was discerned. At the 31 experimental mobbings, 80% of adult males mobbed intensively, while 20% of adult males mobbed passively. Fifty-eight percent of adult females at the experimental mobbings mobbed intensively, while 42% mobbed passively. A similar pattern of sex differences was observed between subadult males and subadult females. Subadult males also tended to actively mob (100% natural vs. 63% artificial), while subadult females did not (29% natural vs. 40% artificial). Although juveniles and infants were regularly present at mobbings, they were never observed participating in either natural or artificial mobbings.

## DISCUSSION

The results of this study indicate that tarsiers respond to snakes either by ignoring them, alarm-calling, or mobbing. Previous research (Gursky, 2002a, 2003a, 2005) indicated that the variation in response of the tarsier to the

TABLE 3. Mobbing intensity in adults and immatures of both sexes observed in natural and experimental mobbings<sup>1</sup>

	Number of intense mobbings	Number of passive mobbings
<b>Natural</b>		
Adult male	12	8
Adult female	7	8
Subadult male	7	0
Subadult female	2	5
Juvenile	0	10
Infant	0	8
<b>Experimental</b>		
Adult male	40	10
Adult female	25	18
Subadult male	12	7
Subadult female	8	12
Juvenile	0	24
Infant	0	27

<sup>1</sup> Mobbing intensity was characterized as intense or passive (see text). Number of adult males and adult females includes individuals from neighboring groups who joined in to mob the snake.

snake primarily reflected the type of snake as well as size of the snake. That is, spectral tarsiers are more likely to mob pythons relative to other types of snakes. This may have to do with the large size of the snake as well as its hunting strategy. However, the presence of this variation in the tarsier's response to the rubber snakes (where only one type of snake and one size of snake were used) suggests that other factors are also responsible for this variation. In particular, variation in prior exposure to pythons may play a role. Future research needs to clarify how prior exposure to snakes affects the tarsier's reaction to future snakes.

The results of this study also clearly indicate that mobbing behavior in spectral tarsiers varied according to an individual's age and sex. Adult spectral tarsiers were more likely to mob snakes than were subadults or juveniles. Similarly, adult males and subadult males were more likely to mob intensively than were adult females or subadult females. This result is consistent with results of several other studies which highlighted the special role of the adult male in predator avoidance (Koenig, 1998; van Schaik and van Noordwijk, 1989).

The total time spent mobbing increased with the increase in number of mobbers. In addition, mobbing groups were generally larger than group size, as measured at their sleeping site. This result suggests that individuals external to the main group are joining the mobbing event. In particular, it is noteworthy that the majority of mobbing groups contained multiple adult males. Given that spectral tarsier groups contain only one adult male, this implies that adult males from other groups also participated in mobbing events. In a few mobbing events, some of the additional males were radio-collared and/or bird-banded, allowing their individual and group identification. They were usually from neighboring groups, although once a male from several territories (4 ha away) over was observed at a mobbing event. Unfortunately, a lack of genetic data prevents a more complete understanding of the relationship between individuals at these mobbing events. The fact that spectral tarsiers allow access to individuals from outside the group during mobbing is somewhat surprising, given that they also actively defend their territories from other

groups. One possibility is that they selectively allow certain individuals, perhaps related individuals (uncles, cousins, and nephews), in their territory during dangerous situations. Once again, additional research on the genetic relationship between individuals is necessary to test this hypothesis.

In contrast, the majority of females only attended mobbings that occurred within their home range, and rarely trespassed onto a neighbor's home range to mob. This pattern of sex differences in mobbing is not unique to spectral tarsiers, but was also observed in numerous other animals. For example, in the great tit, males mobbed more intensely than females (Regelmann and Curio, 1986). Similarly, in black-tailed prairie dogs living in coterries containing several female kin defended by one dominant male, males spent more time driving away snakes than did females (Loughry, 1988).

The function of these individual differences in mobbing behavior is harder to understand. A thorough perusal of the literature indicates that nine different hypotheses were proposed to explain snake mobbing (Curio, 1978; Dugatkin and Godin, 1992; Ross, 1993; Flasskamp, 1994; Brown and Godin, 1999; Schradin, 2000). Previous studies (Gursky, 2002a, 2003a, 2005) already refuted the site avoidance hypothesis, the silencing offspring hypothesis, and the cultural transmission hypothesis. Based on the observations made during this study, there are no data to even tentatively address hypothesis 2 (selfish herd), hypothesis 3 (confusion effect), or hypothesis 6 (alerting kin). That is, no data were presented that mobbing minimizes risk by dividing it among all mobbers, that animals behave so unpredictably that the predator cannot focus on a single prey, or that kin are alerted to mobbing (no genetic data). This leaves three additional hypotheses for discussion: the move-on hypothesis, perception advertisement hypothesis, and attract the mightier hypothesis.

The move-on hypothesis states that a predator should leave an area sooner, the more intensely it is mobbed. Preliminary observations provide some tentative support for this hypothesis. In particular, this study demonstrated that the snake was more likely to retreat before the tarsiers when there were many mobbers. The tarsiers were more likely to retreat before the snake when there were few mobbers. However, although this trend was quite strong, it was not statistically significant. Additional support for this hypothesis comes from the observation that as the number of mobbers increased, the number of minutes the live predator was present decreased. That is, predators moved on more quickly, the more intensely they were mobbed. However, once again, the sample size was quite small, and this trend was not statistically significant.

The perception advertisement hypothesis states that animals identify themselves to the predator, informing it that the surprise element of the attack has been removed. Given the importance of crypticity for snakes, the removal of the surprise element is clearly negative for the snake's hunting success. Thus, snakes should be more likely to move quickly to a new area after the surprise element has been lost. This hypothesis is supported by the observation that the snakes spent less time in the area following mobbing calls than when the tarsiers only emitted an alarm call or just ignored the snake.

The attract the mightier hypothesis states that mobbing attracts stronger allies to assist in dealing with the potential predator. However, no difference in body size

between extragroup males and resident males was observed. That is, extragroup males were not any larger, and thus mightier, than resident males, thereby refuting this hypothesis. Extragroup males were also no smaller than resident males. As body mass is not the only indicator of might, I also evaluated home-range size. Once again, there was no difference in home-range size of resident males and extragroup males.

An additional hypothesis that has not yet been proposed to account for mobbing behavior is the costly signaling hypothesis (Maynard Smith and Harper, 2003). The basic idea behind this hypothesis is that animals need a means to communicate, i.e., to signal to kin and strangers their abilities, intentions, and fears. In order for individuals to trust the veracity of the information that is presented, it is argued that the signal must be costly to produce. If it were not costly to communicate, then individuals would regularly lie and cheat. It is possible that mobbing behavior is an honest signal by which adult male tarsiers advertise their quality as potential mates. The idea of mobbing as a costly signal is intriguing, because by approaching a predator, an individual can advertise very specific information. While aggregating around a potentially lethal snake, tarsier males may demonstrate their current physical condition, agility, and speed. This information would be very useful for a subadult female who is making a decision about whether to stay longer in her parental group, or disperse and establish her own group. Mobbing may be a way for young females to evaluate the ability and willingness of males to protect them and their future offspring against potential predators. The observation that males are more likely to join mobbings outside their territory provides some potential indication that intense mobbing by spectral tarsiers males may represent costly signaling.

Clearly, additional research is needed to determine the function of mobbing behavior in this species. More detailed and mutually exclusive predictions need to be developed for each of the 10 hypotheses, and data must be further analyzed to address the predictions generated by each hypothesis. Future directions for research include exploring the relationship between mobbing and the costly signaling hypothesis, exploring the genetic relationship between mobbers, exploring whether prior interactions with specific predator types account for the variation in mobbing behavior, and exploring whether the pattern of mobbing toward civets, monitor lizards, and birds of prey is the same as that for snakes.

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