Reviewed Article

Hawk Calls Elicit Alarm and Defensive Reactions in Captive Geoffroy's Marmosets *(Callithrix geoffroyi)*

Yvonne M. Searcy   Nancy G. Caine

California State University, San Marcos, Calif., USA

Abstract
Most descriptions of callitrichid antipredator behavior have come from observations of visual encounters with predators, but there is also anecdotal evidence suggesting that callitrichids may use auditory cues associated with raptors for the early detection of potential danger. In the present study, Geoffroy's marmosets consistently reacted to the tape-recorded calls of a red-tailed hawk *(Buteo jamaicensis)* with high-intensity antipredator behaviors. Compared to the taped calls of a raven *(Corvus corax)* and the taped sound of a power drill, the hawk calls elicited more startle reactions, more alarm calls, longer freeze times, increased use of safe areas of their enclosure and greater disruption in ongoing behavior. Once in a relatively safe location in the enclosure, the marmosets visually monitored the site of origin of the calls for 10 min and minimized locomotion for 30 min, but resumed baseline levels of other activities that had been disrupted by the hawk calls. Marmosets may use the auditory cues associated with predators for early detection, and subsequent avoidance, of a potential predator in the vicinity.

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Predation pressure has likely been an important force in the evolution of many aspects of callitrichid (family Callitrichidae) behavior. Because direct observation of actual predation of callitrichids is rare (but see Goldizen [1987] and Heymann [1990]), the belief that predation pressure has a strong influence on callitrichid behavior is based less upon documented rates of predation and more upon the obser-

vation that marmosets *(Callithrix)* and tamarins *(Saguinus* and *Leontopithecus)* display a wide array of behavioral adaptations for maximizing the detection of potential predators [Caine, 1993] and minimizing the risk of predation once such threats are detected [Heymann, 1990; Ferrari and Lopes Ferrari, 1990]. For example, a suddenly appearing or rapidly approaching raptor may cause one or more marmosets in a group to emit a brief alarm call, after which group members immediately cease current activity, rapidly take cover and remain motionless (freeze) until the perceived threat has passed. Ferrari and Lopes-Ferrari [1990] describe such behavior as high-intensity predator avoidance responses. Predator detection in callitrichids may be facilitated by high levels of visual vigilance [Goldizen, 1987; Caine, 1987] and the use of sentinels [Moynihan, 1970; Dawson, 1979; Goldizen, 1987; Zullo and Caine, 1988; Koenig, 1994] and by olfactory sensitivity [Caine and Weldon, 1989].

While studies provide evidence that visual and olfactory encounters with predatory threats elicit antipredator behaviors in callitrichids, anecdotal reports suggest that callitrichids may also use auditory cues for the early detection of potential danger. For example, callitrichids react to the alarm calls of congeners [Epple, 1968; Heymann, 1990] and to the sound of flapping wings of raptors [Izawa, 1978] with high-intensity antipredator behaviors. We have observed that captive Geoffroy's marmosets in outdoor enclosures react with high-intensity avoidance behaviors to a variety of sudden noises, including nearby squirrel alarm calls, the territorial calls of hawks and the vocalizations of a small bird mobbing a hawk that was not yet visible to the marmosets.

The loud, high-pitched cries that characterize many species of large hawks are used primarily in intraspecific territorial advertisement [Brown and Amadon, 1968]; however, recognition of these calls by primates could provide forewarning that a raptor is nearby [Macedonia and Yount, 1991]. Field studies have shown that free-ranging red-tail monkeys *(Cercopithecus ascanius),* blue monkeys *(C. mitis),* red colobus monkeys *(Colobus badius),* lemurs *(Lepilemur*, *Hapalemur*, *Eulemur*, *Varecia*, *Avahi* and *Propithecus* spp.) and semicaptive ring-tailed lemurs *(Lemur catta)* recognize and react defensively to the calls of aerial predators [Hauser and Wrangham, 1990; Macedonia and Yount, 1991; Karpanty and Grella, 2001]. However, there are no studies regarding bird calls as a basis for detection of potential predators by callitrichids. Neither has there been systematic study of how, and for how long, behavior is affected after the primates have been startled by the sounds of an aerial predator.

The present experiment tested whether marmosets respond differently to the calls of a raptorial and non-raptorial bird, and the extent to which these sounds affect subsequent behavior. The reactions of two family groups of captive marmosets *(Callithrix geoffroyi)* to the taped calls of a red-tailed hawk *(Buteo jamaicensis),* a common raven *(Corvus corax)* and a non-animal control sound are reported. Baseline rates of marmoset behavior (locomote, forage, play, stationary look, selfgroom, visual fixation, huddle/social groom) and enclosure use were measured and compared to post-exposure rates. We tested the predictions that the taped calls of a red-tailed hawk would cause more startle reactions, more alarm calls, longer freeze times, increased use of safe areas of the enclosure and greater disruption in ongoing behavior than would the calls of a raven or a non-animal sound.

Methods

Subjects

Thirteen Geoffroy's marmosets *(C. geoffroyi)* living in two family groups were observed. Five marmosets composed group 1: a breeding pair (female 7 years, male 5 years), an adult daughter (5 years) and twin subadult daughters (2 years). Group 2 consisted of 11 animals, 9 of which served as focal animals: an adult female (5 years) and her 4 sets of twin offspring (each pair having 1 male and 1 female, 27, 22, 11 and 3 months old). The youngest twins were not intended to serve as focals; however, the breeding male died just prior to serving as a focal animal and was replaced in the randomization schedule with the youngest male. All subjects were born in captivity.

The marmosets were housed in large outdoor enclosures, $3 \times 3 \times 2.4$ m each, made of 1.3×2.5 cm galvanized wire mesh, except for the shared aluminum wall that separated the two groups. The groups did not have visual contact, but could hear each other. The enclosure floors were dirt with naturally growing weeds, piles of leaves and palm branches that encouraged insect foraging. Several potted plants and trees of various sizes were maintained within the enclosures and were frequently used by the monkeys as perches, play areas, foraging areas and hiding places. Tree branches of various sizes provided a network of aerial pathways throughout the enclosures.

For reference purposes, the cages were divided into 4 quadrants and 3 levels (high, medium and low). Quadrant 1 in both enclosures provided the most overhead cover. In this quadrant there was corrugated aluminum covering the roof, as well as the upper third of the cage sides. Of the remaining ceiling area of the enclosure, half was uncovered and half was covered with shade cloth, through which the marmosets could see. Wooden nest boxes in which the marmosets slept were located in the upper level of quadrant 1.

The enclosures are located off-exhibit at the Center for Reproduction of Endangered Species (CRES) at the San Diego Wild Animal Park. In this remote area of chaparral valley, wildlife could be seen, heard and/or smelled by the marmosets and included a variety of Falconiformes. Most common in the area were red-tailed hawks *(B. jamaicensis),* red-shouldered hawks *(B. linaetus),* turkey vultures *(Cathartes aura),* American kestrels *(Falco sparverius)* and, occasionally, golden eagles *(Aquila chrysaetos).* Common non-raptorial birds in the area included ravens *(C. corax)* and other corvids, herons (e.g. *Casmerodius albus*) and a large variety of smaller birds.

Apparatus

Taped bird calls, provided by the Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, N.Y., USA (© 1996, all rights reserved), were played using a portable stereo recorder with detachable speakers (Sanyo M-9300). The territorial calls of a wild red-tailed hawk *(B. jamaicensis),* recorded around its nesting area, served as the exemplar of a predator. The playback consisted of a naturally occurring series of 3 calls of a red-tailed hawk emitted over a period of 8 s. The calls of a common raven *(C. corax)* near its nesting site were used as a non-predator exemplar. The playback of the raven call consisted of three 3-part calls spanning a period of 10 s. The calls of both hawks and ravens are frequently heard around the marmosets' enclosures. A taped recording of a power drill served as a non-animal comparison sound. The power drill playback consisted of 3 quick bursts of the drill (6 s). The sound of a power drill was not novel to the marmosets. The frequency range of the raven calls (0.5–5 kHz) was similar to the frequency range of the hawk calls (2–6 kHz) and the power drill (1.5–9 kHz). In figure 1, spectrograms of the stimuli are presented.

Procedure

During playback trials, calls were broadcast through two portable speakers that were placed together, 6.08 m in front of the enclosure approximately 2.12 m above the ground, in bushes that obscured the speakers from view of the marmosets. The amplitude of each stimulus was held constant with the mean sound pressure level at the mid point of the enclosures being 73 dB for the hawk and raven calls and 79 dB for the power drill.
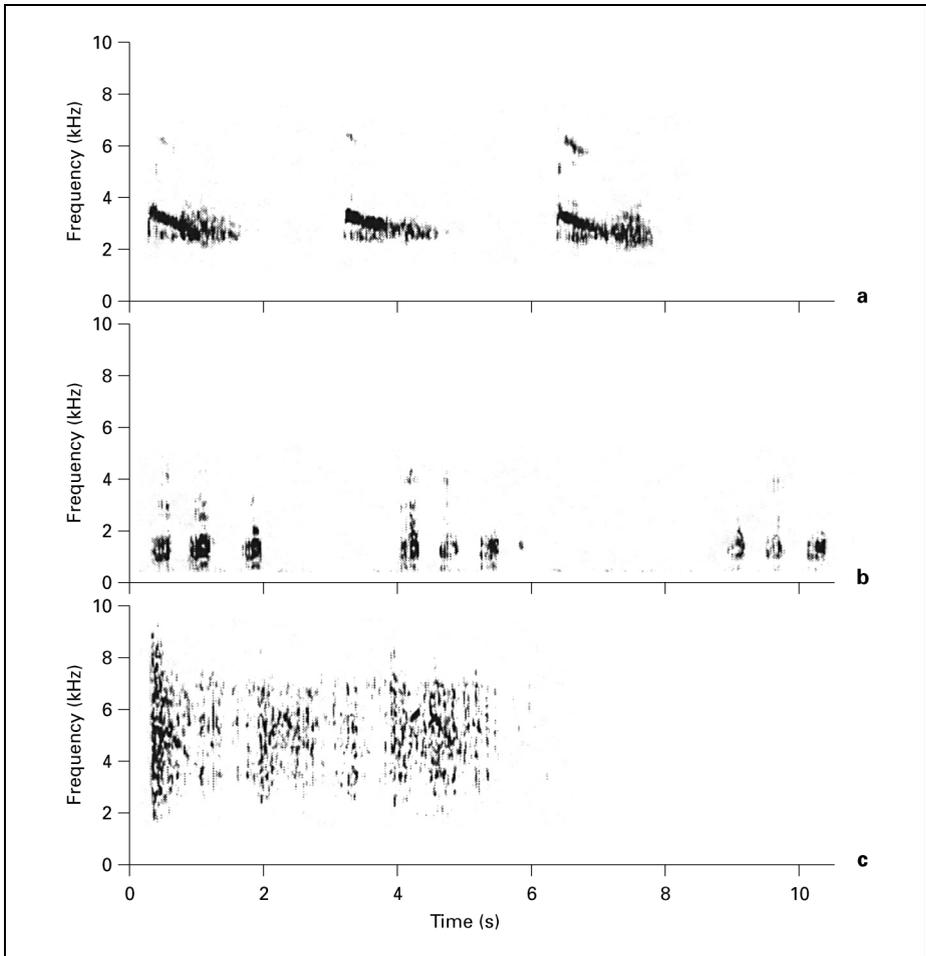
Fig. 1. Sonograms of the stimuli used in the current study. **a** Red-tailed hawk *(B. jamaicensis)*. **b** Common raven *(C. corax)*. **c** Power drill.

Prior to data collection, the inter-rater reliability for 4 observers was calculated. Values of r ranged from 0.89 to 0.94.

Each marmoset was observed as a focal animal once under each of the 3 conditions: hawk call, raven call and power drill. The order in which focal animals were observed, as well as the order of stimuli presentations, was randomized. Either 1 or 2 monkeys served as focal animals during each trial (with either 1 or 2 observers present, respectively), for a total of 8 presentations of each stimulus over the course of 14 weeks. At least 48 h separated the playback trials. Because the playbacks could be heard by the observers, it was not possible for the researchers to be blind to condition or to the timing of the presentation of the stimuli.

The auditory stimuli were presented after 10 min of baseline data collection. Post-exposure data were collected for 30 min following presentation of the stimuli. Continuous

Table 1. Operational definitions of behaviors scored

Alarm call	includes quick calls: short, high-pitched chirp or seet, usually followed by rapid locomotion or taking cover, and repetitive calls: a rapid series of loud short notes
Forage	directing the head and gaze toward a substrate associated with food; manipulating food or objects containing food
Freeze	motionlessness, except for movement of the head associated with still look or visual fixation, that has occurred in response to a startling stimulus
Huddle/groom	sitting in body contact with, or grooming or being groomed by a group mate
Locomote	movement of at least one body length, not including the tail
Play	chasing, being chased and/or wrestling with a group mate in a non-aggressive manner; includes self-play and solitary vigorous locomotor interaction with an object(s)
Self-groom	scratching, biting or otherwise manipulating one's own body
Startle	a sudden cessation of ongoing activity followed by a brief, rapid flight and then freezing in place; on some occasions, the freezing is immediate (i.e. not preceded by brief flight)
Stationary look	visual monitoring of the environment while stationary; does not include visual scans associated with foraging or intense focus on a particular target outside the enclosure
Visual fixation	intense visual orientation toward and inspection of a specific target or area outside the enclosure

behavior sequences were collected using a HyperCard-based computer program that recorded elapsed time in seconds from one key punch to the next. The keys of a laptop computer were labeled with the behaviors observed. Data were gathered on 7 mutually exclusive behaviors: locomotion, foraging, stationary looking, autogrooming, social grooming, playing and visual fixation toward the speakers. A startle event was scored if, upon exposure to the playback, there was a sudden cessation of ongoing activity, followed by brief, rapid flight and then freezing in place. On some occasions the freezing response was immediate (not preceded by flight) (table 1).

In addition to collecting continuous behavior sequences via computer, the focal animals' location, as determined by quadrant and level in the enclosure, was noted by hand on a data sheet every 30 s throughout the 40-min observation period. If an alarm reaction occurred upon presentation of the stimulus, we recorded the quadrant and level occupied by the focal animal at the time of the startle and the quadrant and level to which it fled, the direction fled (up, down, same), whether or not alarm calls were given by any group member and the freeze time of the focal animal.

Data Analysis

Freeze times were compared between conditions (hawk call, raven call, power drill) using Wilcoxon's matched-pairs signed rank tests (the test statistic of which is presented as a Z score). While Wilcoxon's test is a non-parametric procedure that makes no assumptions about the shape of the distributions of the two variables [Rosenthal and Rosnow, 1991], we provide the means and standard deviations as a measure of central tendency.

Changes in utilization of the enclosure were examined within each of the 3 conditions using Wilcoxon's tests. For each quadrant and level of the enclosure, the percent of each marmoset's time spent there during the 10 min following exposure to the stimulus was compared with baseline rates of usage. If no significant differences emerged from these comparisons, analyses went no further. However, if a significant difference from baseline was re-

Table 2. Behavior and enclosure use during playback conditions (mean ± SD)

	Hawk call	Z	Raven call		Power drill	
Quadrant 1						
Baseline	18.8±21.4		33.4±20.2		26.6±29.2	
0–10 min after	52.6±38.2*	2.68	41.9±35.3	n.s.	25.0±29.6	n.s.
11–20 min after	47.6±37.1*	2.04				
21–30 min after	33.4±36.8	n.s.				
Lower level						
Baseline	20.7±22.6		1.1±3.0		10.3±17.0	
0–10 min after	3.9±6.8*	2.32	3.0±6.0	n.s.	9.6±16.8	n.s.
11–20 min after	15.7±23.3	n.s.				
Locomotion						
Baseline	7.7±4.2		5.9±2.4		5.8±2.9	
0–10 min after	4.3±2.7*	2.59	5.2±3.3	n.s.	5.2±3.2	n.s.
11–20 min after	2.3±1.7*	3.11				
21–30 min after	3.6±2.1*	2.76				
Visual fixation						
Baseline	0.03±0.1		0.00±0.0		0.10±0.36	
0–10 min after	1.78±2.2*	2.55	0.00±0.0	n.s.	0.58±0.91	n.s.
11–20 min after	0.00±0.0	n.s.				
Freeze times	111.3±125.1*	2.97	no freezing		5.8±12.6	

Data (except freeze times) are reported as the mean percent of the marmoset overall time budget, and statistical comparisons are to baseline rates. Freeze times (seconds) are compared across conditions. n.s. = Not significant; * $p < 0.05$. Also, recall that quadrant 1 was the part of the enclosure offering overhead cover, and the lower level of the enclosures offered less in the way of cover than other levels.

vealed during the 10 min after exposure, behavior was further examined by comparing data obtained from 11–20 min after exposure with baseline data. If differences persisted at the 20-min comparison, longer-term changes in enclosure use were investigated by comparing baseline usage with that during 21–30 min after exposure.

Finally, Wilcoxon's tests were used to compare baseline values of the remaining 6 behaviors to the corresponding values of those behaviors during the first 10 min after being exposed to the stimuli. Significant differences were explored further as described above for enclosure use.

The α level was set at $p < 0.05$ for all comparisons.

Results

Startle Reactions and Freeze Times

All 13 focal animals startled during the playback of the hawk call and maintained significantly longer freeze times (mean = 111.3 s, SD = 125.1) compared to the raven call, which never caused a startle (mean = 0, SD = 0; $Z = 3.2$), and the power drill, which caused only 3 focal animals to startle (mean = 5.8 s, SD = 12.6; $Z = 2.97$) (table 2).

To test whether or not habituation to the hawk calls occurred, the freeze times of the marmosets observed as focal animals in the first 4 presentations were compared to the freeze times of the marmosets observed as focal animals in the second 4 presentations. The mean freeze time for trials 1–4 was 108.4 s; for trials 5–8, the mean was 114.6 s. Thus, there is no evidence that the marmosets became habituated to the calls after repeated presentations.

Alarm Calls

Upon exposure to the taped hawk call, alarm calls were emitted by at least 1 group member in 25% of trials, while alarm calls were never emitted following exposure to the raven call or the control sound.

Direction Fled

During the hawk call condition, the startle reactions of 11 of the 13 focal animals were accompanied by brief and rapid locomotion prior to freezing. The marmosets most often fled upward (7 times) versus staying at the same level (3 times) or fleeing downward (1 time; $\chi^2 = 5.09$, $p < 0.10$). Of the 3 focal animals that startled to the sound of the power drill, 2 fled upward, and 1 fled downward. (Recall that there were no startles to the raven call.)

Enclosure Use

As shown in table 2, the percent of time that the marmosets spent in quadrant 1, the only quadrant with overhead cover, more than doubled compared to baseline for 20 min following the hawk call. Marmosets spent an average of 18.8% of their time in quadrant 1 before the hawk call; this percentage increased significantly (mean = 52.6%, $Z = 2.68$) during the 10 min following the hawk call and remained significantly higher (mean = 47.6%, $Z = 2.04$) during the 11–20 min following the hawk call. In contrast, there were not significant changes in quadrant use in response to the raven call or the control sound. In addition to causing changes in quadrant use, the hawk call was followed by changes in the marmosets' use of the lower level of the enclosure. Compared to baseline (mean = 20.7%), the marmosets were significantly less likely to use the lower level of their enclosure for 10 min following the hawk call (mean = 3.9%, $Z = -2.32$). There were no such changes following the raven call or the control sound.

Other Behaviors

Rates of behavior were converted to and are presented as a percentage of the marmosets' time budget. Because play behavior was not observed in all focal animals and accounted for a very small percentage of the overall time budget of the animals who did exhibit the behavior, 'play' was omitted from analyses.

The marmosets significantly reduced their locomotor activity compared to baseline (mean = 7.7%) for 30 min after exposure to the hawk call: during the first 10 min (mean = 4.3%, $Z = -2.59$), during 11–20 min (mean = 2.3%, $Z = -3.11$) and during 21–30 min (mean = 3.6%, $Z = -2.76$). There were no such changes following the raven call or control sound. Visual fixation increased significantly from baseline (mean = 0.03%) during the first 10 min following exposure to the hawk call (mean = 1.78%, $Z = 2.55$). Visual fixation did not occur following the raven call, and rates remained close to zero following the control sound (table 2). Station-

ary looking, foraging, social grooming and self-grooming did not differ from baseline following the hawk call, raven call or power drill.

Discussion

Geoffroy's marmosets consistently reacted to the tape-recorded calls of a red-tailed hawk *(B. jamaicensis)* with high-intensity antipredator behaviors that included alarm calling, brief and rapid locomotion to a safe location, freezing and intense visual monitoring. The behavior of the marmosets suggests that the hawk calls were recognized as coming from a threatening predator, as patterns of marmoset behavior following the taped calls of the hawk were similar to how both captive and wild tamarins reportedly behave after visual encounters with aerial threats, that is with rapid escape to protective cover, spending more time in protected areas [Izawa, 1978; Pook and Pook, 1981] and reducing locomotor activity [Heymann, 1990]. The immediate reactions we observed are also similar to those reported for captive and wild lemurs that were exposed to playbacks of raptor vocalizations [Macedonia and Yount, 1991; Karpanty and Grella, 2001]. To our knowledge, however, this is the first study to systematically record a range of behavioral effects for up to 30 min following exposure to a raptor call.

The antipredator behavior of the marmosets following the hawk calls was different from their reaction to the taped calls of a raven (nonraptorial bird) and the taped sound of a power drill. The hawk calls elicited more startle reactions, more alarm calls, longer freeze times, increased use of safe areas of the enclosure and greater disruption in ongoing behavior. Having heard the hawk call, but being unable to visually locate the hawk or determine if the hawk had left the area, it was reasonable for the marmosets to limit their activities to the safety of quadrant 1 (which provided overhead cover) for a period of time. In the confines of that area, the marmosets did continue to forage and groom at baseline rates. This is an efficient response to a potentially dangerous situation: safety is maximized while time lost for other important activities is minimized [Caine, 1998].

During startle reactions in the present study, the marmosets tended to flee upward to a higher location in the enclosure. These findings appear to contradict those of Ferrari and Lopes-Ferrari [1990] who found that in the presence of birds of prey overhead, free-ranging marmosets fled downward (see also Peres [1993] and Heymann [1990]). Recall, however, that the upper levels of the enclosures provided the densest overhead cover, while the densest cover in the forest is lower in the canopy. Thus, the direction of the marmosets' flight from danger was appropriate to the particular features of their environment. On the other hand, the stimuli in this study were broadcast from speakers that were set at a height of 2.12 m. The marmosets may have responded with upward flight because they interpreted the threat to be coming from near the ground. In the field studies cited above, the raptor calls probably came from locations well above the monkeys' heads. However, Searcy [2000] found that the marmosets at the CRES almost always fled in an upward direction, toward cover, when startled by naturally occurring raptor calls, all of which originated from far above the marmoset enclosures. Therefore, we favor the explanation that the marmosets are predisposed to flee toward cover (wherever that cover is found) when exposed to raptor calls.

While the playback of the raven call never caused alarm reactions, the marmosets were sometimes surprised by the sudden sound of the power drill and responded with rapid locomotion and freezing. However, the 3 marmosets that startled to the power drill recovered relatively quickly compared to recovery times following hawk calls, suggesting that loud sounds may sometimes be startling but not interpreted as threatening. Searcy [2000] found that, while marmosets did startle to naturally occurring non-animal sounds, and to the sudden or nearby vocalizations of non-raptorial birds, marmoset freeze times following these encounters were relatively short compared to freeze times following startles caused by hawk calls.

All 13 focal animals startled to the presentation of the hawk call, but alarm calls were emitted during only 2 of the 8 hawk call trials. Similarly, Searcy [2000] reported that alarm calls did not accompany 2 observed startle events caused by naturally occurring hawk calls (where no hawk could be seen), while marmoset alarm calls did accompany 3 of 4 startles caused by hawk sightings. Karpanty and Grella [2001] recorded lemur alarm calls after only 15% of 47 raptor playbacks (see also Hauser and Wrangham [1990]). To the extent that one function of alarm calls is to alert group mates to danger, it is redundant (and perhaps unnecessarily risky) to emit alarm calls when the potential threat was probably heard by all group members. Zuberbühler et al. [1999] propose that primate alarm calling may discourage predators that depend on surprise attack. We have often observed marmosets issuing high rates of alarm calls to perched raptors they had seen, but our data suggest that raptor vocalizations alone are much less likely to generate that effect.

Although findings from single examples of a raptor and non-raptor call cannot be generalized to all other calls or to similar calls from other species [Kroodsma, 1989], the present findings are consistent with our observations of marmoset behavior during naturally occurring startling events. Searcy [2000] recorded the causes and consequences of naturally occurring events that elicited startle reactions within the two groups of marmosets used in the current study. These events included raptor calls of various duration, intensity and origin (i.e. different calls, different species and, presumably, different individuals within species). The marmosets' reactions to these events were similar to those we recorded following the playbacks of the red-tailed hawk calls. Likewise, Karpanty and Grella [2001] and Macedonia and Yount [1991] showed that lemur species reacted to calls of several different raptor species with similar antipredator behavior, although there were some interesting differences in strength of response to different calls.

The raptor calls used in the current study were from a resident hawk species. It would be of interest to know if hawk calls from the marmosets' native Brazil would generate the same reactions. Given the similarities in advertisement calls across different species of hawks [Brown and Amadon, 1968], we predict that they would. In pilot trials, we presented the marmosets with the taped call (Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, N.Y., USA) (© 1996, all rights reserved) of a Harpy eagle *(Harpia harpyja),* which ranges across South America. The marmosets responded strongly and with the same behaviors (freezing, fleeing toward cover etc.) observed in response to the red-tailed hawk calls. Macedonia and Yount [1991] concluded that ring-tailed lemurs *(L. catta)* may use certain acoustic characteristics common to the calls of many large hawks (e.g. negative frequency slope) to distinguish between sounds made by large hawks and other sounds. We think it likely that Geoffroy's marmosets use a similar perceptual system for re-

sponding to threatening auditory stimulation from aerial predators. Furthermore, the responses of the marmosets to the Harpy eagle call (an entirely novel auditory stimulus for the monkeys) suggest that the defensive reactions to the red-tailed hawk that we quantified in the current study are more the result of an innate predisposition to react defensively to a class of auditory stimulation than to experience with the hawks, although experience may well have modified the marmosets' reactions in one or more ways (see also Macedonia and Yount [1991]).

In sum, the present study provides evidence that marmosets react to the sudden, nearby calls of a hawk, but not to calls of a raven or non-animal sound, with appropriate antipredator behaviors, including modifications in some behaviors that reduced their vulnerability to aerial predation for up to 30 min. We conclude that, in addition to being visually vigilant, marmosets are able to use auditory cues to detect and avoid aerial predators.

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