BRIEF REPORT

Captive-Born Cotton-Top Tamarins (*Saguinus oedipus*) Respond Similarly to Vocalizations of Predators and Sympatric Nonpredators

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What types of cues do callitrichid primates use to detect and respond to predators? Do they respond to predator-specific cues or to more general cues? The evidence for these questions remains conflicting. We presented captive-born and reared cotton-top tamarins with no previous exposure to predators (or predator cues) with vocalizations from three potential predators of cotton-top tamarin in the wild (white hawk, jaguar, and tayra) and with vocalizations from sympatric nonpredators (black-faced antthrush and red howler monkey). Vocalizations from predators and from nonpredator mammals elicited equivalent arousal, fear, and vocal responses. Howler monkey roars produced the strongest responses. The results suggest that predator-naïve cotton-top tamarins do not recognize specific predator vocalizations, but may respond to vocal qualities (low-frequency, noisy sounds) that indicate large body size, threat, or aggression. On the other hand, tamarins responded much more strongly to the higher frequency calls from the hawk than the antthrush, suggesting another mechanism must also be involved. The failure of captive-reared tamarins to distinguish between vocalizations of predators and nonpredator mammals has important implications for reintroduction studies. Am. J. Primatol. 70: 707-710, 2008. © 2008 Wiley-Liss, Inc.

Key words: cotton-top tamarins; predator vocalizations; nonpredator vocalizations; fear; arousal; reintroduction

INTRODUCTION

Avoiding predation is a major task for a species and the mechanisms of predator recognition have been the subject of many studies. For example, Mineka et al. [1980, 1984] found that captive-born rhesus macaques (Macaca mulatta) displayed no initial fear of a live boa constrictor (Boa constrictor) compared with wild-caught macaques. However, naïve macaques could readily learn fear of snakes through observational learning of a wild-caught monkey reacting fearfully to the snake. Subsequent studies using edited visual images found that rhesus macaques could be conditioned to fear snakes and snake-like objects (toy snakes and lizards) but not flowers [Cook & Mineka, 1989], suggesting that recognition and appropriate responses to predators are learned, but that perceptual constraints also limit the types of stimuli conducive to fear conditioning.

Known and suspected predators on wild callitrichid primates include snakes [Heymann, 1987; Shahuano Tello et al., 2002], raptors [Heymann, 1990; Izawa, 1978], ocelots (*Felis pardalis*) [Emmons, 1987], and tayras (*Eira barbara*) [Peres, 1993], among others. Several studies have looked at responses of captive callitrichids to various predator cues (visual, olfactory, and auditory). Barros et al. [2002] presented captive *Callithrix penicillata* living in indoor-outdoor cages with a taxidermized rattlesnake, hawk, and Oncilla cat, all potential predators. Marmosets vocalized and increased alarm behaviors to all the three stimuli during presentation. Marmosets increased proximity to the hawk and snake, but moved away from the cat. Only the cat elicited persistent vocal and alarm behavior on removal of the stimulus. Castro [1990] reported that three species of lion tamarins (*Leontopithecus* sp.) in captive indoor-outdoor environments in Brazil showed reactions to predators similar to what would be expected in the wild.

Studies of responses of captive callitrichids to fecal odors from predators have suggested that

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captive animals respond with greater anxiety and fear-like behavior to fecal scents from natural predators than from sympatric nonpredator species [Buchanan-Smith et al., 1993; Caine & Weldon, 1989]. Searcy and Caine [2003] also found that Geoffroy's marmosets (*C. geoffroyi*) housed in indoor-outdoor enclosures in the USA responded to playbacks of red-tail hawk (*Buteo jamaicensis*) (a locally present raptor) vocalizations with increased alarm and vigilance behavior compared with playbacks of calls of ravens (*Corvus corax*).

Captive-born, indoor-housed cotton-top tamarins (Saguinus oedipus) that have never had any exposure to natural predators failed to distinguish visually between predators and nonpredators. Hayes and Snowdon [1990] found low-level arousal reactions to a live *B. constrictor* placed in the cage, but responses did not differ from those to a white rat (*Rattus norvegicus*). We have recently replicated these results [Campbell & Snowdon, in review].

We were interested in how captive-born, predator-naive tamarins would respond to vocalizations from natural predators compared with control vocal playbacks from sympatric nonpredator species (not tested previously). Tamarins may have a domainspecific adaptation for calls of natural predators, or alternatively they may respond to general acoustic parameters indicative of body size and aggression. Morton [see Owings & Morton, 1998] has argued that large body size is represented by low-frequency sounds and that aggression is also conveyed through low-pitched, harsh vocalizations. Thus, tamarins might react fearfully to certain types of vocalizations, whether of a predator or not, owing to acoustic effects on motivational systems. The results may have implications for captive reintroduction programs.

METHODS

Subjects

We studied ten heterosexual nonbreeding pairs of cotton-top tamarins (*S. oedipus*) at the University of Wisconsin, Madison from 2005 to 2006. All monkeys were born in captivity. None had ever lived outdoors or been exposed to any vocalizations of the species used in this study. Each pair was housed in a cage (160 cm deep by 236 cm high by 93 cm wide). Cages were equipped with branches, ropes, and other structures to simulate an arboreal environment. Multiple pairs were housed in the same colony rooms with visual separation between cages, but animals were in auditory and olfactory contact with other pairs. Further husbandry details are in Ginther et al. [2001].

Materials

We obtained recordings of Neotropical birds and mammals from the Cornell Laboratory of

Ornithology Library of Natural Sounds and selected calls of three species known or suspected to prev on cotton-top tamarins in their native environment in Northern Colombia. These included a white hawk (Leucopternis albicollis) flight call (Voices of Costa Rican Birds, Caribbean Slope), a jaguar (Panthera onca) growl, and tayra (E. barbara) hisses and growls (both from Sounds of Neotropical Rain Forest Mammals). For control stimuli, we selected song from a black-faced antthrush (Formicarius analis) (Voices of Costa Rican Birds, Caribbean Slope) and the roar of a red howler monkey (Alouatta seniculus) (Le Monde des Singe 2: Singes Forestiers). Control species were selected based on the information that they did not prey on tamarins and had similar pitch and duration (27-30 sec) to the calls of predators. Calls were calibrated to be played at 70 dB.

Procedure

We stored sound files on a laptop computer and played them back through hidden speakers placed 76 cm above the floor and 2 m from the cage to be tested. We recorded behavior on a laptop computer using Observer 4.1 software and recorded all vocalizations on an Olympus digital voice recorder (DS-2) (Center Valley, PA).

We conducted tests between 14:00 and 16:00 hr, after the main feed, and played only one stimulus a week to a pair. We tested pairs in five separate colony rooms and we counter-balanced the order of the five stimuli across rooms. Each stimulus was presented once per pair. We first tested one pair in each room and then waited 13 weeks before testing a second pair in the same room to minimize any potential habituation.

Each session consisted of a 5-min baseline period followed by 30 sec of stimulus presentation followed by a 5-min poststimulus period. The observer used 30 sec scan sampling of both pair members to record piloerection, freeze, self-grooming, scratching, location in each vertical third of the cage and the nestbox, and visual fixation to the speaker and toward the top and bottom of the cage. Changes in location from prestimulus to poststimulus periods may indicate movement toward or away from the stimulus. The sum of feeding, grooming, huddling, and play was used as an index of calm behavior. In our colony grooming and huddling are typical of calm, relaxed animals, and we have not seen these behaviors in response to stressors. Vocalizations were identified using Avisoft SASLAB Pro (Berlin, Germany) based on the tamarin vocal repertoire of Cleveland and Snowdon [1982] and supplemented by Campbell and Snowdon [2007]. Calls analyzed included A chirps (low arousal calls in mobbing contexts), H chirps (given to novel stimuli), pulsed calls (moderate arousal calls given in a mobbing

context), and quiet long calls (used for within-group cohesion often after some disturbance or tension). The research protocol was approved by the University of Wisconsin, College of Letters and Science Animal Care and Use Committee and complies with legal requirements of the United States of America.

Data Analysis

We used the pair as the unit in all analyses as the behavior of each mate could not be assumed to be independent of the other mate. Data from the 5 min prestimulus baseline were compared with data from the 5 min poststimulus observations. We analyzed freeze and piloerection with the binomial test, because they occurred at low and variable rates and were best categorized as occurring or not occurring. We analyzed other behaviors and vocalizations with the Wilcoxon, matched-pairs, signed-ranks test. Tied ranks were eliminated from the sample size. All tests were two-tailed with α set at 0.05.

RESULTS

There was no significant change in freezing behavior following playback of any of the stimuli. Piloerection showed a marginal increase only for calls of the hawk and the howler monkey (binomial test, 8 of 10, P = 0.055). Calm behaviors decreased significantly following playback of the hawk (T = 2, N = 9, P < 0.02), the antthrush (T = 0, N = 9, P < 0.01), and the howler monkey (T = 6.5, N = 10, P < 0.05). Increased movement to the upper third of the cage was found only in response to playback of the jaguar (T = 0, N = 9, P < 0.01), an appropriate antipredator response (Fig. 1). No other behavioral measures showed significant changes following playbacks.

A chirps increased following playback of the hawk (T=2, N=9, P< 0.01), jaguar (T=0, N=9, P< 0.01), tayra (T=4, N=10, P< 0.02), and howler monkey (T=0, N=9, P<0.01). The same pattern of results held for H-chirps: hawk (T=0, N=7, P<0.02), jaguar (T=0, N=6, P< 0.05), tayra

(T = 0, N = 8, P < 0.01), and howler monkey (T = 0, N = 8, P < 0.01). Pulsed calls increased significantly following playback of hawk (T = 1, N = 8, P < 0.02), tayra (T = 1, N = 8, P < 0.02), and howler monkey (T = 0, N = 8, P < 0.01, Fig. 1). Only two calls elicited increased numbers of long calls, hawks (T = 3.5, N = 9, P < 0.05), and howler monkeys (T = 1, N = 7, P < 0.05).

Responses to howler monkey roar vocalizations were similar to the responses to predator vocalizations. With 8 behavioral or vocal responses showing significant results with at least one stimulus and the presentation of 3 predator species, there were 24 measures where antipredator behavior could be detected. Only 11 (or 45.8%) of these measures were significant. However, five of eight (62.5%) measures with howler monkey vocalizations were significant. Thus, there appears to be little differentiation in vocal and behavioral responses by captive tamarins to vocalizations of predator species vs. nonpredator howler monkeys.

DISCUSSION

indoor-reared Captive-born and cotton-top tamarins displayed several reactions to playback of calls from both predator and nonpredator species, but showed no evidence of discrimination between calls of predators and nonpredator howler monkeys. In addition, the pattern of responses did not appear to be consistent adaptive responses to predators. There was little evidence of freezing or piloerection to any stimulus. Calm behavior decreased in response to calls from the raptor as well as to the nonpredator antthrush and howler monkey playbacks, but calm behavior did not decrease in response to the calls of the predatory jaguar and tayra. The only behavioral response consistent with expectations was an increased use of the upper third of the cage following jaguar calls (but not following tayra calls). However, there was no significant movement out of the upper part of the cage in response to the raptor call (although for consistency we played all calls at a



Fig. 1. Behavioral (30 sec scans) and vocal responses to vocal stimuli. Open bars indicate prestimulus levels and filled bars indicate poststimulus levels. *P = 0.055 Binomial test, *P < 0.05 Wilcoxon test.

standard height, whereas natural calls from hawks and jaguars would come from different elevations). Vocal responses indicative of mobbing or high arousal to playbacks were relatively consistent across all stimuli except the antthrush, but increases in the cohesive quiet long call were observed only following the playback of the raptor and howler monkey and not to the playback of jaguar and tayra.

As the calls of nonpredator howler monkeys were selected to be similar in acoustic frequency to the calls of mammalian predators, the similar responses of tamarins on many measures to all mammalian calls suggest that some aspects of acoustic variables, rather than implicit knowledge of specific predator calls is responsible for the results. Morton predicts that wide bandwidth, low-pitched and harsh vocalizations should be associated with threat and aggression. Thus, on hearing a playback of a low-frequency, harsh call for the first time tamarins might be expected to exhibit mobbing, fearful and arousing behavior, and vocalizations regardless of whether the calls are from predators or nonpredators. However, the calls of the hawk and antthrush do not have these acoustic features, yet tamarins responded much less to antthrush than to hawk calls. In the wild, responses to nonpredators should habituate rapidly as animals learn to distinguish predators from nonpredators. Searcy and Caine [2003] found vigilance in captive animals to playbacks of raptor calls where previous exposure was likely.

The inability to distinguish between natural predators vs. nonpredators based on vocalizations coupled with findings indicating that captive-born, indoor-housed tamarins did not display species typical alarm or mobbing behavior to viewing a live snake [Campbell & Snowdon, in review; Hayes & Snowdon, 1990] suggest that tamarins do not have a fear of natural predators but must learn socially or individually to fear cues from predators. The findings are supported by Mineka et al. [1980, 1984] showing that captive-born rhesus macaques had no fear of snakes, but rapidly learned such fear through observation of responses from a wild-born macaque. It is likely that multiple cues—visual, vocal, and olfactory—are used to identify predators in the wild.

These findings have important implications for reintroduction programs. If nonhuman primates have no specific recognition of predators, then prerelease training involving not only predator recognition but also appropriate antipredator responses is critical. Soorae and Baker [2002] have suggested that "captive stock should be given the opportunity to acquire the necessary information to enable survival in the wild through training in their captive environment." Increased survival rates in previous reintroduction projects may have been possible with greater attention to prerelease predator training [Beck et al., 1991].

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