

Risky Business? Lethal Attack by a Jaguar Sheds Light on the Costs of Predator Mobbing for Capuchins (*Cebus capucinus*)

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Received: 13 October 2011 / Accepted: 28 November 2011
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Abstract While some primates attempt to avoid predation by fleeing or hiding, others actually approach, harass, and sometimes attack potential predators, a behavior known as mobbing. Mobbing seems to invite obvious risks, but predators have rarely been observed to injure or kill animals that harass them. The true costs of predator mobbing and the functional significance of this behavior remain poorly understood. Here, we report a fatal attack by a jaguar (*Panthera onca*) on a mobbing capuchin (*Cebus capucinus*) that we observed on Barro Colorado Island, Panama. This rare observation illustrates that mobbing predators such as large felids can, indeed, be costly. However, to understand fully the costs of mobbing, the energetic and opportunity costs that primates incur when they harass predators must also be considered.

Keywords Antipredator strategies · Barro Colorado Island · *Cebus capucinus* · Mobbing · *Panthera onca*

Introduction

Predation is an important selective pressure for many primate species (Cheney and Wrangham 1987) and thus it is not surprising that primates show a wide range of antipredator strategies, including crypsis (Rahlfs and Fichtel 2010), vigilance, and the

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production of context-specific alarms calls that alert groupmates to the presence of danger (Digweed *et al.* 2005; Fichtel *et al.* 2005; Seyfarth *et al.* 1980; Zuberbuhler *et al.* 1997). Keeping in mind that most animals go to great lengths to avoid predators, it is interesting that some species, instead of fleeing, actually confront potential attackers. This strategy of harassment, known as mobbing, consists of several patterns of behavior including approaches, loud vocalizations, and physical attacks. Despite the fact that mobbing is known in numerous species of birds and mammals (Curio and Regelman 1985; Dugatkin and Godin 1992; Graw and Manser 2007), and is a dramatic component of the behavioral repertoire of many primate species (Bartecki and Heymann 1987; Boesch 1991; Chapman 1986; Cowlshaw 1994; Eberle and Kappeler 2008; Gursky 2005; Lloyd *et al.* 2006; Passamani 1995; Perry *et al.* 2003; Ross 1993; Schulke 2001), it has been the subject of surprisingly little systematic research (but see Gursky 2005, 2006; Wheeler 2008), and its adaptive significance remains poorly understood (for a review of the hypothesized benefits of predator mobbing, see Caro 2005; Curio 1978).

Approaching and mobbing predators appears to invite obvious risks, including injury and death. However, estimating the true costs of predator mobbing poses a significant challenge. Presumably, mobbing is costly because it decreases the distance between predator and prey, and thereby increases the risk of a successful predatory attack. However, reports of primates being injured or captured while mobbing a predator are exceedingly rare (but see Cowlshaw 1995). Variation in primates' propensity to mob different types of predators may reflect the risk they pose. Of the species that provoke mobbing behavior in primates, snakes appear to be common targets (Eberle and Kappeler 2008; Ferrari *et al.* 2004; Gursky 2005; Perry *et al.* 2003). Many snakes are cryptic but, once discovered, can be mobbed with relatively little risk (but see Correa and Coutinho 1997). Mobbing of other types of predators, especially of felids, has been reported less frequently (Boesch 1991; Cowlshaw 1995; Lloyd *et al.* 2006; Passamani 1995), perhaps because it is more dangerous (*cf.* Wheeler 2008). Predators such as large cats continue to pose a significant threat to terrestrial primates even after they have been discovered, and are known to at least occasionally capture individuals that mob them (Cowlshaw 1994). However, mobbing mammalian predators is thought to be less risky for forest-living primates, because they can escape to safety in the trees (Hart 2000; Ouattara *et al.* 2009).

Here, we describe a rare observation of a fatal attack by a jaguar (*Panthera onca*) on a white-faced capuchin (*Cebus capucinus*) that was engaged in mobbing behavior.

Methods

All research received clearance from the Smithsonian Tropical Research Institute Animal Care and Use Committee (assurance no. 2008-03-12-08), and complied with the laws of the Republic of Panama and of the United States of America. Observations took place during a 12-mo study (January 2009–January 2010) of four social groups of habituated white-faced capuchins (*Cebus capucinus*) on Barro Colorado Island (BCI), Panama (9°9'N, 79°51'W). The focal groups ranged in size from 10 to 19 adults and subadults, all of which were individually recognized based on physical characteristics. BCI is a 15.6-km² island of semideciduous lowland

tropical forest that was isolated from mainland Panama in 1914 when the Chagres River was dammed to form Lake Gatun and the Panama Canal. A stable population of between 250 and 300 capuchins in 15 and 20 social groups are thought to live on BCI (M. C. Crofoot, *unpubl. data*; Mitchell 1989; Oppenheimer 1968). BCI is also home to populations of a number of known and suspected capuchin predators including ocelots (*Leopardus pardalis*), tayra (*Eira barbara*), jaguarondi (*Puma yagouaroundi*), margay (*Leopardus wiedii*), and boa (*Boa constrictor*). Larger predators, including puma (*Puma concolor*) and jaguar (*Panthera onca*), though not resident, are known to visit the island (Aliaga-Rossel *et al.* 2006; Moreno and Giacalone 2006). BCI does not, however, host an intact predator community. Except for an 18-mo period from 1999 to 2000 when two subadult harpy eagles (*Harpia harpyja*) were released as part of a reintroduction program that failed (Gil-da-Costa *et al.* 2003; Touchton *et al.* 2002), this major avian predator has not been present on BCI for 50–100 yr (Willis and Eisenmann 1979).

Results

Jaguar Predation of a Mobbing Capuchin

On May 20, 2009 at 07:52 h, the monkeys from FC group were on a hillside in the center of their home range, foraging for invertebrates 0.5–1.5 m from the ground. Two of us (A. González and L. Tórriz) were taking behavioral observations when we heard capuchin alarm vocalizations for a terrestrial predator (Gros-Louis *et al.* 2008) and saw the alpha male and an adult female moving rapidly in the direction of the call. They joined other members of their group including the two other large adult males and at least three subadult males, and directed physical threats, including shaking and breaking and throwing branches, as well as facial and vocal threats, at a dense liana tangle. The alarm calls spread throughout the group. The only adult female with a clinging infant (BT) was *ca.* 20 m behind the rest of the adults in the group and, along with the juveniles, made alarm vocalizations but did not approach the liana tangle or participate in the mobbing. Although we were not able to confirm unequivocally the presence of four adult females and one subadult male, it appeared that all group members except the juveniles and the female with the clinging infant were involved in the mobbing event.

The capuchins' alarm calls intensified and one of us (A. González), located downhill from the liana tangle, smelled the odor of a felid and perceived a large cat sitting in the middle of the dense lianas. A. González was able to see only the right side of the individual, but noted that the pattern of spots on the pelage was quite distinct from that of ocelots (*Leopardus pardalis*), which we regularly see on BCI. A. González also noted that the individual was much larger than an ocelot. Based on the color of the fur, the pattern of markings, and the size, we are convinced that it was a jaguar (*Panthera onca*). We later verified that a jaguar was present on BCI from April 20 to July 20, 2009 using camera trap photographs (J. Giacalone Willis and G. Willis, *pers. comm.*; see Fig. 1), and we have a photograph of the jaguar taken June 2, 2009 (12 d after this event) on a camera located 200 m from where the mobbing occurred.



Fig. 1 Photograph of a jaguar (*Panthera onca*) taken by a camera trap on Barro Colorado Island, Panama on June 1, 2009 (11 d after we observed a jaguar capture a white-faced capuchin). A similar photograph was taken on June 2, 2009 by a camera trap located 200 m from the site of the predation event. (Photo courtesy of J. Giacalone and G. Willis).

At 07:55 h, we heard the low growls of a cat, and the capuchin alarm calls increased in intensity. At 07:59 h, the jaguar made a very loud vocalization that appeared to make the capuchins extremely nervous. They glanced repeatedly at one another and one of the adult females retreated to where the juveniles and BT and her infant were waiting. Together, they moved away from where the jaguar was hiding. We could hear the jaguar move in the dry leaves, and most of the rest of the capuchin group retreated, following BT and the juveniles. As far as we could see, only three adult males and three subadult males remained near the liana tangle where the jaguar was hiding. Their vocalizations had decreased in both frequency and intensity. The six capuchins looked back and forth at one another, notably nervous, and then moved silently away from the jaguar, following the route taken by their groupmates. As they did this, we could hear terrestrial alarm vocalizations from a single capuchin that had remained behind. Although we were unable to see this individual well enough to determine its identity, by process of elimination, based on our observations as the other capuchins retreated, it was a subadult male (LK).

We tried to get close enough to verify the identity of the capuchin but, at 08:04 h, an aggressive vocalization indicated that we needed to back up and not disturb the cat. We retreated *ca.* 40 m, and from that distance we could still hear the capuchin that had remained alone near the jaguar making alarm calls. We heard sudden movements, the alarm calls stopped, and *ca.* 30 s later we heard two weak vocalizations, similar to a moan, after which there was only silence.

We encountered the rest of the group *ca.* 100 m from the place where the mobbing had occurred. The capuchins were very quiet, but had returned to their normal activities and were foraging for insects. We conducted a group count and confirmed that the subadult male LK was absent. All other group members were accounted for, and LK has not been seen since this event.

Discussion

This report of a fatal attack by a jaguar on a mobbing capuchin provides the first direct evidence that mobbing terrestrial predators can be risky for arboreal primates. Quantifying the costs of mobbing is important because the price that primates are willing to pay to harass their predators informs our understanding of the benefits they gain from this strategy (Dugatkin and Godin 1992). If the costs are large, the benefits must be likewise. However, if mobbing does not actually impose much of a cost, the benefits primates gain may be relatively modest. At least three main types of cost contribute to the overall price that primates pay when they mob. The most striking of these is, of course, the risk that a mobbing individual runs of being injured or killed by the predator it is harassing. Mobbing may also impose significant energetic and opportunity costs although, as far as we know, these have never been quantified for any primate species. Determining the relative contribution of these factors to the overall expense of mobbing behavior is difficult because their impacts occur at such disparate scales. Our observation of a lethal attack on a mobbing capuchin demonstrates that harassing predators *can be* extremely costly. Without information on how often such lethal outcomes occur, or data that would allow us to compare the probability of a fatal attack when a primate does vs. does not mob, however, it is impossible to weigh the relative importance of the risk of injury, the energy spent while mobbing, and the time lost to other activities.

Capuchins are pugnacious (Perry and Manson 2008) and regularly mob a wide variety of both dangerous and innocuous animals (Rose *et al.* 2003). Perry and Manson (2008) have suggested that this apparently generalized tendency to harass is part of a behavioral syndrome (Sih *et al.* 2004) that stems from selection for a bold, tenacious temperament in other contexts. However, the extreme risks that capuchins take when mobbing predators, illustrated by the fatal outcome we describe, suggest that additional explanations for the functional significance of predator mobbing in this species need to be considered.

Acknowledgments We thank the Autoridad Nacional del Ambiente (ANAM) and the government of the Republic of Panama for permission to conduct this research. We thank the Smithsonian Tropical Research Institute, the Wenner-Gren Foundation for Anthropological Research, Princeton University, and the Max Planck Institute for Ornithology for funding. We also thank the staff of the Barro Colorado Island research station, whose daily help and support was critical to the success of this research. We extend special thanks to Jacalyn Giacalone, Ben Hirsch, Sara Pinzon, Roland Kays, and Oris Acevedo for their helpful comments and suggestions on a previous version of this manuscript. Two anonymous reviewers and Joanna Setchell provided thoughtful and constructive comments and criticisms that we gratefully acknowledge.

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