

Why Mob? Reassessing the Costs and Benefits of Primate Predator Harassment

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Key Words

Predators · Mobbing · Primate · Move-on hypothesis · *Cebus capucinus* · *Tarsius spectrum*

Abstract

While some primate species attempt to avoid predators by fleeing, hiding or producing alarm calls, others actually approach, harass and sometimes attack potential threats, a behavior known as ‘mobbing’. Why individuals risk their safety to mob potential predators remains poorly understood. Here, I review reports of predator harassment by primates to (1) determine the distribution of this behavior across taxa, (2) assess what is known about the costs of mobbing, and (3) evaluate hypotheses about its function. Mobbing is taxonomically widespread and is used against a wide range of predator species. However, inconsistent use of the term ‘mobbing’ within the primate literature, the lack of systematic studies of primate mobbing, and the likelihood of systematic biases in the existing data pose significant obstacles to understanding this puzzling behavior. Although difficult to quantify, the costs associated with harassing predators appear nontrivial. Many benefits that have been proposed to explain mobbing in birds may also be important in primate systems. There are puzzling aspects of primate mobbing, however, that existing hypotheses cannot explain. Future research should consider the within-group signaling potential of this costly behavior, as well as the ability of behavioral syndromes to explain the distribution of mobbing in primates.

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[A]n eagle seized a young Cercopithecus, which, by clinging to a branch, was not at once carried off; it cried loudly for assistance, upon which the other members of the troop, with much uproar, rushed to the rescue, surrounded the eagle and pulled out so many feathers, that he no longer thought of his prey, but only how to escape. This eagle assuredly would never again attack a single monkey of a troop.

Darwin [1871]

Introduction

The literature on primate behavior and ecology is littered with accounts of group mates acting in concert to face down, harass, cow and even kill potential predators. These attacks are impressive both in their intensity and in the seemingly large risks that participants take in approaching, pestering and sometimes physically assaulting predators as large as leopards and jaguars [Cowlshaw, 1994; Lloyd et al., 2006; Tórréz et al., 2012]. The cooperative nature of the attacks is also intriguing: despite the apparent danger, group mates often rush to join the mob surrounding a potential predator and frequently threaten it in a highly coordinated fashion. As predator harassment seems to pose a classic collective action problem [Olson, 1965], how is this cooperation maintained?

Relatively little theoretical or empirical research has focused on primate predator harassment. Existing reports are largely anecdotal and descriptive, and generally draw parallels to the mobbing behavior exhibited by many avian species. While the hypothesized benefits of avian predator mobbing may be sufficient to explain the patterns of behavior observed in primates, significant differences exist in ecology, social organization and style of predator-prey interaction of these taxa. Currently, the paucity of systematic behavioral data on the interactions between primates and their predators presents an important obstacle to understanding the function of primate mobbing behavior. Furthermore, the shy and cryptic habits of most predator species mean that the very presence of a human observer likely influences both the frequency with which primate study groups encounter threats [Isbell and Young, 1993; Perry and Manson, 2008] and the outcome of mobbing events [Passamani, 1995; Burney, 2002; Matsuda and Izawa, 2008]. Finally, because predator mobbing is rarely observed, published accounts are primarily descriptive [but see Gursky, 2005, 2007] and significant publication biases likely exist. For example, reports of exceptionally intense mobbing events or of encounters with enigmatic predators like large cats are more likely to be written up and published than observations of unenthusiastic harassment of commonly encountered threats. Keeping these cautions in mind, in this paper I gather reports of predator harassment by primates from the literature to (1) review the distribution of this behavior across primate taxa, (2) assess what is known about the costs of mobbing behavior, and (3) evaluate hypotheses about the function of predator mobbing.

What Is Mobbing?

The term mobbing is generally used to describe prey animals approaching, gathering around, intently observing and harassing a predator. This harassment encompasses a suite of behaviors that may include vocalizations specific to the mob-

bing context (i.e. distinct from general alarm/warning calls) and advances towards the predator to inspect, follow, harangue or attack. Mobbing generally denotes a group activity, although it can be initiated by solitary individuals [Eberle and Kappeler, 2008]. However, the term has been used to describe antipredator behaviors as distinct as baboons attacking and sometimes killing hunting leopards [Cowlshaw, 1994], capuchins lunging towards, biting and dropping sticks on boas that had captured group mates [Chapman, 1986; Perry et al., 2003], and tamarins approaching, peering at, vocalizing and excitedly hopping around a pair of mating vine snakes [Bartecki and Heymann, 1987].

According to Caro's review of antipredator strategies [2005, p. 383], mobbing was originally defined as 'a demonstration against a potential or supposed enemy belonging to another and more powerful species [that] is initiated by the member of the weaker species, and is not a reaction to an attack upon the person, mate, nest, eggs or young of the bird which begins it' [Hartley, 1950, p. 315]. A key feature of this definition is that it explicitly excludes counterattacks against active threats; to be considered mobbing, an animal's behavior must be a *proactive* response to an encounter with a predatory species that does not pose an immediate risk. Thus, of the examples of primate antipredator behavior described above, only the last case involving tamarins, would be considered mobbing. Other definitions of avian mobbing are less stringent with regard to the proactive versus reactive nature of the behavior. For example, Shields [1984] focused on the structural components of mobbing, which he defined as 'approach[es] towards a potentially dangerous predator (whether it is actively hunting or not), followed by frequent position changes with most movements centered on the predator'. His definition drew attention to the '[r]elatively stereotyped visual displays and loud localizable vocal displays [that] usually accompany the locomotion' and specifically noted that mobbing could 'involve physical contact by the mobber'.

When extending the concept of mobbing from avian systems to primates, two main points need to be considered. First, if the best defense against a predatory attack is active, aggressive defense, are these counterattacks functionally equivalent to the harassment of a predator that poses little or no immediate risk? Unlike most avian species, some primates have a reasonable chance of injuring or killing a predator they decide to retaliate against [Boesch, 1991; Cowlshaw, 1994], and thus it may be important to distinguish between cases where prey animals have the capacity and intent to inflict serious damage and cases where their attacks may be stressful and annoying to the predator, but are unlikely to be physically harmful. Second, we need to consider whether aggressive behaviors directed at predators that have captured, but not yet killed a group mate should be considered separately from other types of antipredator attacks [Chapman, 1986; Gursky, 2002; Tello et al., 2002; Perry et al., 2003; Eberle and Kappeler, 2008; Lledo-Ferrer et al., 2009]. In these apparent rescue attempts, primates not only direct intense aggression towards the predator, but have also been observed directly attempting to free their group mate (e.g. grabbing an individual's arms and pulling him free of a constrictor's coils [Perry et al., 2003]). When discussing mobbing behavior in primates, it is sometimes useful to distinguish between rescue attempts, counterattacks and predator harassment. While these are not mutually exclusive categories, rescue attempts can only occur in response to a (partially) successful predatory attack, whereas counterattacks are attempts to aggressively dissuade a hunting predator.

Harassment, in contrast, fits within the classic definition of mobbing, and refers to aggressive displays and attacks on predators who are not actively hunting and pose little immediate risk.

Distribution of Mobbing Behavior in the Primates

Given the lack of an agreed upon definition, the tendency of researchers to use the term ‘mobbing’ without actually describing the behaviors they observed and the potential for significant reporting biases in the literature, it is difficult to assess the distribution of mobbing behavior among primate species. Certainly, it appears to be widespread. According to Hart [2000], of 1,063 instances of antipredator behavior reported in response to a questionnaire sent to field researchers studying a wide range of primate and predator species, mobbing was the third most commonly reported antipredator response (13.5%) following alarm calling (30.7%) and scanning (15.7%). When broken down taxonomically, mobbing was reported in all but one primate family for which survey data were available. Because responses to Hart’s surveys were not evenly distributed across species, it is difficult to draw conclusions about differences in the antipredator behavior of the various primate taxa. However, her data suggest that mobbing may be a more important strategy for New World primates (specifically, members of the Callithricidae and Cebidae) than for other species. It was the second most commonly reported antipredator behavior after alarm calling in these families, whereas flight, counterattack or crypsis were more common strategies in other taxa. This overall picture is upheld by a review of published accounts of predator mobbing by primates; I found many more reports of mobbing by New World monkeys than by Old World monkeys or apes (table 1). Interestingly, there have been numerous reports of mobbing behavior in nocturnal primates (e.g. *Galago moholi* [Bearder et al., 2002]; *Tarsius spectrum* [Gursky, 2002, 2005, 2007]; *Microcebus murinus* [Eberle and Kappeler, 2008]), and even solitary foragers are frequently able to recruit conspecifics to join them in harassing potential threats [Bearder et al., 2002; Eberle and Kappeler, 2008].

Taxonomic differences in mobbing behavior appear stronger when counterattacks and rescue attempts are considered separately from pure harassment. Counterattacks appear to be more common in Old World monkeys and apes (table 2); baboons, geladas and chimpanzees all respond to certain kinds of predatory threats by launching aggressive counterattacks that can seriously wound potential predators [Boesch, 1991; Cowlshaw, 1994; Iwamoto et al., 1996]. For example, the aggressive interactions between baboons and leopards reviewed by Cowlshaw [1994] often ended in the leopard being chased, injured or killed (9 of 12 instances) whereas in only one of these cases was a counterattacking baboon killed. In contrast, among the New World primates, contact aggression seems to be primarily restricted to cases where a predator has already captured a group member (i.e. rescue attempts, but see Boinski [1988]).

The effectiveness of particular antipredator strategies likely differs for arboreal versus terrestrial primates due both to the hunting style and relative size of their major predators, and the primate’s ability to flee to safety. Counterattacking is expected to be a better strategy when the asymmetries in body size and weaponry between predator and prey are small and flight is risky, as is likely to be the case for terres-

trial primates. Mobbing, on the other hand, may be a more viable strategy for small forest-living species that, even if unable to inflict serious injury on many of their predators, can escape into the trees. It is therefore interesting that there are relatively few reports of mobbing by arboreal Old World primates (although red colobus counterattack when hunted by chimpanzees [Stanford, 2002]), and those that exist [Lloyd et al., 2006] do not describe the lunging, energetic jumping, and stereotyped threat behaviors that characterize predator mobbing in species like capuchins [Perry et al., 2003], tamarins [Bartecki and Heymann, 1987], tarsiers [Gursky, 2002] and mouse lemurs [Eberle and Kappeler, 2008]. Similarly, while larger, diurnal lemurs are known to approach and vocalize at predators [Burney, 2002; Pyritz and Andrianjanahary, 2010], they have not been described as harassing predators. Overall, the patterns of mobbing behavior observed in New World monkeys and in some of the small, nocturnal primates seem more directly analogous to avian mobbing than the antipredator responses that have been described among the diurnal lemurs, Old World monkeys and apes. However, it is not clear whether these phylogenetic patterns represent true differences in primates' propensity for mobbing, or whether they instead reflect reporting biases and/or differences in terminology.

Who Gets Mobbed?

It seems logical that primates might target snakes for harassment more frequently than other classes of predator. Snakes pose a significant threat to many primate species [Isbell, 1994, 2006], but their hunting strategy relies heavily on the element of surprise [Montgomery and Rand, 1978; Slip and Shine, 1988]. Once discovered, primates may be able to approach and mob constricting snakes with comparatively little risk, and because of their reduced sensitivity to auditory stimuli, visual and mechanical signals may be needed to alert snakes that they have been seen. However, there are a number of reasons why, regardless of its relative frequency, snake mobbing might be observed more often than the mobbing of mammalian or avian predators. First, many cases of snake mobbing reported in the literature appear to be rescue attempts that were precipitated by a group mate being captured [Eberle and Kappeler, 2002; Perry et al., 2003]. Constricting snakes take a long time to kill their victims compared to mammalian or avian predators, and are more likely to remain visible while doing so. This not only makes the rescue of group mates a feasible strategy, but also increases the likelihood that a human observer, attracted by mobbing vocalizations, will see the snake with its victim. Second, mammalian predators tend to be cryptic and shy, and may actively avoid humans [Isbell and Young, 1993]. This should decrease the number of encounters between habituated primates and their mammalian predators, and reduce the likelihood that researchers will observe mobbing events. Finally, many sites where primates are studied do not host intact predator communities; large mammalian and avian predators are particularly likely to have been extirpated from sites with heavy human presence.

Given these potentially confounding factors, what can we say about the targets of primate mobbing behavior? First, primates mob a wide array of predators. A large survey on predation and antipredator behaviors in primates yielded reports of primates mobbing raptors, reptiles, felids, canids, hyaenids and other small carnivores [Hart, 2000]. Unfortunately, the form of these data (presence/absence) precludes any

analysis of the frequency with which primates mobbed different classes of predator. We would like to be able to compare the rate at which primates encounter different kinds of predators with rates of mobbing versus other antipredator responses. Data from long-term field studies could shed light on this question, but the potential impact of observer presence on predator encounter rates remains a concern. Studies that present wild primates with models of predators provide an alternative for investigating how primates modify their behavior in response to different kinds of threats [Fichtel et al., 2005; Fichtel, 2007; Wheeler, 2008; Ouattara et al., 2009; Rahlfs and Fichtel, 2010]. For example, wild capuchin monkeys (*Cebus apella*) mobbed ocelot and snake models more frequently than raptor models: ocelot in 15/20 (75%) experiments; viper in 9/13 (69%) experiments; raptor in 5/22 (23%) experiments [Wheeler, 2008]. These types of experiments can tell us about primates' initial reactions to various predators but, as with so many questions surrounding the interactions between predators and prey, it is hard to imagine that we will be able to achieve a nuanced understanding of the functional significance of mobbing behavior without simultaneously studying how primates react to their predators, and how predators react to harassment by primates.

You Only Die Once: Evaluating the Costs of Predator Mobbing

At least 3 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. Fatal (or injurious) attacks on mobbing individuals do occur. For instance, Sordahl [1990] found 30 reports in which mobbing birds had been attacked, captured, killed or had died of stress. Among primates, such reports are exceedingly rare – I found only 3 reports of primates being killed while mobbing (table 2). In a review of the interactions between baboons and their predators, Cowlishaw [1994] reports 1 case in which mobbing proved fatal for the baboon involved. My colleagues and I have reported a fatal attack by a jaguar on a mobbing capuchin monkey [Tórriz et al., 2012], and observers have also reported a case in which an infant tamarin monkey died as a result of a bite it sustained while mobbing a venomous snake [Correa and Coutinho, 1997]. These lethal attacks demonstrate that mobbing *can be* extremely costly. However, 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 mobs versus when it does not mob, it is impossible to assess the overall cost of mobbing as an antipredator strategy.

In addition to the risk of injury or death, primates also face direct energetic costs and opportunity costs when they engage in antipredator mobbing. As Ross [1993] commented: 'Even if the leopard represented no immediate danger [to the Hanuman langurs], the energy expended and feeding time lost presumably represented some cost to the individuals concerned.' Given the long duration of many mobbing events (>2 h [Boesch, 1991; Lloyd et al., 2006]; see table 2), and the vigorous physical threats that characterize primate mobbing behavior, these costs may be substantial. However, they have not been quantified for any species [Caro, 2005].

A review of the literature suggests that most primate mobbing events are relatively short (mode = 15 min; table 2). However, in many instances, observers did not arrive until after the start of the event and, particularly in cases of mammalian and

avian predators, expressed concern that their presence may have caused the predator to flee [Passamani, 1995; Matsuda and Izawa, 2008; Perry and Manson, 2008]. When predators do not flee and perhaps especially when they cannot flee because they have been trapped by their tormentors, mobbing can be protracted [Boesch, 1991; Perry and Manson, 2008]. In addition to the time that is directly lost to mobbing, encounters with predators can affect primates' behavioral patterns for hours and even days [Izawa, 1978; Heymann, 1987; Peres, 1993; Boinski et al., 2000; Perry and Manson, 2008]. Red-fronted lemurs, for example, are reported to show increased levels of vigilance for at least 30–60 min following encounters with fossa (*Cryptoprocta ferox*) [Pyritz and Andrianjanahary, 2010], presumably with some cost to their foraging efficiency. Few attempts have been made to directly assess the physiological costs of mobbing. An experimental study in captive marmosets found that mobbing a model snake was associated with low levels of chronic physiological stress (as assayed by cortisol levels found in hair), but did not investigate acute responses to the predatory stimuli [Clara et al., 2008].

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, as it first appears, harassing predators is highly costly, this suggests that the benefits animals gain by mobbing must be large. Hypotheses that posit more modest benefits appear more plausible if mobbing is not actually as risky as it seems. Establishing the relative contribution of the risk of bodily harm, energetic costs and opportunity costs to the overall expense of mobbing behavior is difficult because their impact occurs at such disparate scales. The energy spent while mobbing and the time lost to other activities may be relatively minor, but they are paid regularly. The risk of being killed, in contrast, is relatively small, but its cost is absolute.

Hypothesized Benefits of Predator Mobbing

Is mobbing an effective antipredator strategy for primates? Mobbing has been proposed to reduce predation pressure in a variety of different ways, and it is important to note that these hypothesized benefits are not mutually exclusive and can accrue simultaneously [Owings and Coss, 1977; Graw and Manser, 2007]. As with birds, however, where reduced predation in colonially nesting species is the primary evidence of the effectiveness of mobbing [Caro, 2005], no one has ever demonstrated that mobbing, per se, reduces predation pressure on primates, independent of other possible group-related antipredator benefits (e.g. increased vigilance or the selfish-herd effect).

Lethal Counterattack

In some instances, mobbing may serve as a lethal counterattack aimed at killing a predator, and thereby eliminating the threat it poses [Meinertzhagen, 1959; Stanford, 1998]. This strategy will only be viable when size and weaponry asymmetries between predator and prey species are comparatively small (i.e. prey are capable of inflicting serious injury) or when a group of individuals, through sheer force of numbers, can collectively overpower a larger, stronger adversary. For example, baboons and chimpanzees, both large-bodied primates with impressive weaponry, are known to launch damaging and sometimes fatal attacks on leopards [Boesch, 1991;

Table 1. Primate mobbing behaviors

Species												Citation	
	Arboreal/terrestrial	Predator	Gather	Approach	Close approach (within 2 m)	Vocalize	Threaten	Lunge/hop around	Peer	Shake/break branches	Pursue		Contact aggression
<i>Galago moholi</i>	A	SM R	+		+		+						Bearder et al., 2002
<i>Loris tardigradus lydekkerianus</i>	A	SM S							+				Bearder et al., 2002
<i>Lemur catta</i>	T	R		+	+	+							Sauther, 1989
<i>Eulemur fulvus rufus</i>	A	S	+	+	+	+		+	+		+		Pyritz and Andrianjanahary, 2010
<i>Propithecus verreauxi coquereli</i>	A	S	+	+	+	+							Burney, 2002; Colquhoun, 1993, 2006
<i>Propithecus verreauxi</i>	A	R				+							Brockman, 2003
<i>Cheirogaleus medius</i>	A	S		+	+	+						+	Dausmann, 2010
<i>Phaner furcifer</i>	A	S	+	+	+				+				Schülke, 2001
<i>Microcebus murinus</i>	A	S	+	+	+	+		+	+		+	+	Eberle and Kappeler, 2008; Fish, 2010
<i>Lepilemur edwardsi</i>	A	S	+	+		+							Scheumann et al., 2007
<i>Lepilemur leucopus</i>	A	S				+			+				Fish, 2010
<i>Tarsius spectrum</i>	A	S	+	+	+	+	+	+			+	+	Gursky, 2002, 2005, 2006
<i>Pithecia pithecia</i>	A	SM S	+			+					+		Gleason and Norconk, 2002
<i>Pithecia aequatorialis</i>	A	R	+	+		+							de Luna et al., 2010
<i>Callicebus discolor</i>	A	R SM				-	+						de Luna et al., 2010
<i>Alouatta belzebul</i>	A	SM				+							Camargo and Ferrari, 2007
<i>Alouatta seniculus</i>	A	R	-	+	+	+	+	-	-	-	+	-	Eason, 1989
<i>Alouatta palliata</i>	A	SM		+		-	-	-	-	-	+	-	Asensio and Gomez-Marin, 2002
<i>Lagothrix lagotricha</i>	A	F	+	+							+		di Fiore, 2002
<i>Ateles belzebuth</i>	A	F	+			+				+	+		Matsuda and Izawa, 2008
<i>Ateles belzebuth</i>	A	R				+				+			di Fiore, 2002
<i>Cebus apella nigrinus</i>	A	F ^m R ^m S ^m	+	+		+	+	+					Wheeler, 2008

Table 1 (continued)

Species	Arboreal/terrestrial	Predator	Gather	Approach	Close approach (within 2 m)	Vocalize	Threaten	Lunge/hop around	Peer	Shake/break branches	Pursue	Contact aggression	Citation
<i>Cebus apella</i>	A	R	+	+	+	+			+	+			van Schaik and van Noordwijk, 1989
<i>Cebus albifrons</i>	A	R	+	+	+	+				+			
<i>Cebus capucinus</i>	A	S	+	+	+	+	+	+	+	+	+	+	Fichtel et al., 2005; Perry et al., 2003; Boinski, 1988; Chapman, 1986
		R					+	+	+				
		F	+	+			+	+			+	+	
<i>Saguinus fuscicollis</i>	A	S	+	+	+	+				+			Bartecki and Heymann, 1987; Buchanan-Smith, 1990
		SM	+	+				+					
<i>Saguinus mystax</i>	A	S	+	+	+	+	+	+	+			+	Tello et al., 2002; Heymann, 1987
<i>Saguinus labiatus</i>	A	SM	+	+		+		+					Buchanan-Smith, 1990
<i>Callithrix aurita</i>	A	S	+	+	+	+			+				Correa and Coutinho, 1997
<i>Callithrix geoffroyi</i>	A	SM	+	+		+			+		+		Passamani, 1995
<i>Callithrix jacchus</i>	A	SM	+	+		+						+	Bezerra et al., 2009
<i>Callithrix flaviceps</i>	A	S	+	+	+	+			+	+			Ferrari and Ferrari, 1990
		SM	+	+									
<i>Procolobus badius tephroceles</i>	A	chimp	+	+	+	+	+	+				+	Stanford, 1995
<i>Presbytis entellus</i>	T	F		+		+			+				Ross, 1993; Srivastava, 1991
		S	+	+	+	+				+			
<i>Trachypithecus phayrei</i>	A	F	+	+		+		+					Lloyd et al., 2006
<i>Cercopithecus c. campbelli</i>	A	F				+	+	+					Ouattara et al., 2009
		R		+	+	+		+					
		S ^m					+	+	+				
<i>Papio</i> spp.	T	F	+	+	+	+	+	+	+	+	+	+	Cowlishaw, 1994, and references therein
		C/H	+	+	+	+	+	+	+	+	+	+	
<i>Papio hamadryas hamadryas</i>	T	R				+		+					Zinner and Pelaez, 1999
<i>Theropithecus gelada</i>	T	C/H		+	+	+		+			+	+	Iwamoto et al., 1996
		F	+	+		+	+	+					
<i>Hylobates lar</i>	A	F	+	+		+							Uhde and Sommer, 2002
<i>Pan troglodytes verus</i>	T	F	+	+	+	+	+		+		+	+	Boesch, 1991
<i>Pan troglodytes schweinfurthii</i>	T	F	+	+	+	+	+	+	+	+	+	+	Hiraiwa-Hasegawa et al., 1986; Pierce, 2009

A = Arboreal; T = terrestrial. Predator type was designated as follows: S = snake, R = raptor, SM = small mammal, F = felid, C/H = canid/hyaenid, ^m indicates a model predator.

Table 2. Cost of predator mobbing

Species	Predator	Group mate captured?	Had predator attacked?	Duration, min	Approach distance, m	Mobber injured?	Outcome	Citation
<i>Galago moholi</i>	genet	n	n	30	n	n	Predator moved away	Bearder et al., 2002
<i>Galago moholi</i>	owl	n	n	30	n	n	Not specified	Bearder et al., 2002
<i>Eulemur fulvus rufus</i>	snake ^c	n	n	15	1	n	Predator moved away	Pyritz and Andrianahary, 2010
<i>Eulemur macaco macaco</i>	snake ^c	n	n	15–20	1	n		Colquhoun, 1993
<i>Propithecus verreauxi coquereli</i>	snake ^c	n	n	15–20	1	n	Primate group left area	Colquhoun, 1993, 2006
<i>Chetrogaleus medius</i>	snake ^v	n	y	0	n	n	Primate bit snake which moved away	Dausmann, 2010
<i>Phaner furcifer</i>	snake ^c	n	n	10	n	n	Primates moved away and resumed feeding	Schülke, 2001
				30	<1	n	Predator moved away	
<i>Microcebus murinus</i>	snake ^c	n	n	29	<0.1	n	Primate moved away	Fish, 2010
<i>Microcebus murinus</i>	snake ^c	y	y	>15	0	n	Predator released captured male (alive), and primates moved away	Eberle and Kappeler, 2008
<i>Lepilemur leucopus</i>	snake ^c	n	n	12	n	n	Primates moved away	Fish, 2010
<i>Tarsius spectrum</i>	snake ^c	y	y	15	<1	n	Primates moved away, predator killed and ingested victim	Gursky, 2002
<i>Pithecia pithecia</i>	oncilla	n	n	20	n	n	Primates pursued predator for >200 m	Gleason and Norconk, 2002
<i>Pithecia pithecia</i>	snake ^c	n	n	20	n	n	Not specified	Gleason and Norconk, 2002
<i>Alouatta seniculus</i>	harpy eagle	n	y	<1.5	n	n	Predator moved away	Eason, 1989
<i>Ateles belzebuth</i>	jaguar	y	y	12	10–20	n	Predator moved away (possibly because of observer)	Matsuda and Izawa, 2008
	puma	n	y	16	n	n	Predator moved away	
<i>Cebus capucinus</i>	snake ^v	n	n	22	<1	n	Predator beaten with stick, killed	Boinski, 1988
<i>Cebus capucinus</i>	snake ^c	y	y	15	<1	n	Primates moved away	Chapman, 1986
<i>Cebus capucinus</i>	snake ^c	y	y	22	0	n	Victim rescued, predator was injured and moved away	Perry et al., 2003
<i>Cebus capucinus</i>	jaguarundi	n	n	<1	n	n	Primates pursued fleeing predator	Rose et al., 2003
<i>Cebus capucinus</i>	ocelot	n	n	>50	1.5	n	Primates tread the predator	Rose et al., 2003; Perry and Manson, 2008
<i>Cebus capucinus</i>	jaguar	n	n	12	2	y	Predator captured subadult mobber, other group members moved away	Torrez et al., 2012

Table 2 (continued)

Species	Predator	Group mate captured?	Had predator attacked?	Duration, min	Approach distance, m	Mobber injured?	Outcome	Citation
<i>Saguinus fuscicollis</i>	tayra	n	n	50	n	n	Predator moved away	Buchanan-Smith, 1990
<i>Saguinus labiatus</i>	tayra	n	n	15	n	n	Predator moved away	Buchanan-Smith, 1990
<i>Saguinus mystax</i>	snake ^c	y	y	2	0	n	Predator released victim and moved away	Tello et al., 2002
<i>Saguinus fuscicollis</i>	raptor	y	y	60	10	n	Predator ignored mobbers and consumed victim	Lledo-Ferrer et al., 2009
<i>Saguinus fuscicollis</i>	snake ^c	n	n	15	1.5–2	n	Predator moved away	Bartecki and Heymann, 1987
<i>Callithrix jacchus</i>	tayra	y	y	1	n	n	Predator moved away with victim	Bezerra et al., 2009
		n	n	10	3	n	Predator moved away	
<i>Callithrix aurita</i>	snake ^v	n	n	10	<1	y	Predator killed victim	Correa and Coutinho, 1997
<i>Callithrix geoffroyi</i>	margay	n	n	22	7	n	Predator moved away (possibly because of observer)	Passamani, 1995
<i>Presbytis entellus</i>	snake ^c	n	n	<10	2	n	Predator moved away	Srivastava, 1991
<i>Presbytis entellus</i>	leopard	n	n	~60	100	n	Predator moved away	Ross, 1993
<i>Trachypithecus phayrei</i>	clouded leopard			20	10	n	Primates moved away	Lloyd et al., 2006
	2 clouded leopards	n	n	120			Primates moved away	
<i>Theropithecus gelada</i>	leopard	n	y	3	3–5	n	Predator moved off	Iwamoto et al., 1996
<i>Papio</i> spp.	leopard	n	y			y	Predator killed mobbing primate	Cowlshaw, 1994
<i>Hylobates lar</i>	tiger	n	n	104		n	Not observed	Uhde and Sommer, 2002
<i>Pan troglodytes verus</i>	leopard	n	n	244	<3	n	Predator trapped, eventually primates moved away	Boesch, 1991
<i>Pan troglodytes</i>	leopard (and cub)	n	n	>45	<5	n	Primates captured and killed the cub, eventually moved away	Hiraiwa-Hasegawa et al., 1996
<i>Pan troglodytes</i>	leopard	n	n	23	10	n	Predator moved away	Pierce, 2009

n = no; y = yes. Venomous and constricting snakes differentiated by superscript v and c, respectively.

Cowlshaw, 1994], while capuchins have been observed beating a poisonous snake to death with a stick [Boinski, 1988]. Whether counterattacks are intended to kill predators, or whether fatal outcomes are merely an accidental by-product of aggressive displays aimed at repelling a predatory attack or encouraging a predator to stop hunting and leave the area (see the move-on hypothesis) is not clear. However, if presented with the opportunity to do so safely, some primates appear highly motivated and even eager to violently assail normally dangerous animals [Teleki, 1974; Hiraiwa-Hasegawa et al., 1986; Boinski, 1988]. The viper (*Bothrops asper*) clubbed to death by a capuchin, for example, had been pinned by a falling branch and was thus unable to escape as the capuchin hit at it at least 55 times over a period of 16 min [Boinski, 1988]. Similarly, Hiraiwa-Hasegawa et al. [1986] report an incident in which a large group of chimpanzees (33 individuals, in all) surrounded a female leopard in her den, attacked the female and killed her cub.

Counterattacks may also be aimed at persuading a predator to release a captured group mate. For example, Eberle and Kappeler [2008] report that encounters they witnessed between mouse lemurs and snakes only elicited mobbing when the snake had successfully captured a conspecific. Rescue attempts seem to primarily be aimed at constricting snakes, perhaps because the time it takes them to kill their prey provides a window of opportunity to effect such a strategy. Janzen [1970] also noted that constrictors cannot strike while killing an animal they have captured, making them vulnerable to attacks by the victim's group mates. As most primates live in groups with at least some close relatives, individuals who participate in such rescue attempts likely gain indirect fitness benefits. Kin selection may also promote cooperation among group mates to realize damaging counterattacks against predators. However, the primary benefits of such counterattacks are probably mutualistic – participants gain direct benefits by cooperating to retaliate against an attacking predator they could not have dissuaded on their own [Caro, 2005].

Move-On Hypothesis

Since many prey species are significantly smaller than their predators, the lethal counterattack hypothesis is not a widely generalizable explanation for predator mobbing behavior. Curio [1978] posited that prey animals persist in harassing predators, even when they have no chance of inflicting significant damage, because doing so can eliminate the threat the predators pose by encouraging them to move-on and leave the area. Mobbing is predicted to deter predators from hunting, drive them away and discourage them from returning to the area [Curio, 1978]. The move-on hypothesis is an intuitively appealing explanation for primate mobbing behavior because mobbing events often end with the predator leaving the area [Passamani, 1995; Matsuda and Izawa, 2008; Perry and Manson, 2008]. However, the key question is if predators that are mobbed leave the area *sooner* than they would have if they had not been harassed. Studies of avian mobbing have demonstrated that mobbing distresses predators [Shalter, 1978; Flasskamp, 1994] and that kestrels move further when they are mobbed than when they are not mobbed [Pettifor, 1990]. However, comparable studies have never been conducted with primates. Whether or not mobbing drives predators away and allows primates to more quickly resume their normal activities, and whether it is a quicker or more effective means of accomplishing this goal than the primates simply moving away themselves are critical, but currently unanswered questions.

Perception Advertisement

Many sit-and-wait or stalking predators abandon the hunt when their presence has been noted and they have lost the element of surprise. Mobbing behavior may thus serve to inform predators that they have been discovered [Curio, 1978]. This hypothesis has received relatively little attention, perhaps because it is unable to explain the most distinctive and puzzling features of predator mobbing: why should prey animals approach potentially dangerous animals, rather than using alarm calls to communicate to the predator that it has been seen? Likewise, why would specialized vocalizations and stereotyped movement patterns be necessary? One possibility is that these visual and mechanical cues are primarily targeted at snakes which, because of how they process auditory stimuli [Christensen et al., 2012], are probably not (as) sensitive to alarm calls as mammalian or avian predators.

Selfish-Herd Effect and Confusion Effect

Mobbing behavior often attracts conspecifics, which approach the mob and join in harassing the predator. Curio [1978] thus suggested that mobbing individuals, by gathering others around them, might benefit by diluting their predation risk (i.e. the selfish-herd effect [Hamilton, 1971]). Similarly, rallying a mob of rapidly and erratically moving individuals might confuse a potential predator, and make it difficult to mount a successful attack. While either of these explanations might prove to be incidental benefits of collective mobbing, neither, on its own, can explain why the rallying effect occurs. Why should an individual go out of its way to join a mob if doing so puts them in danger? Recent experiments by Krams et al. [2006, 2008] suggest that reciprocal altruism may support cooperative mobbing in pied flycatchers, and present evidence that this species follows a tit-for-tat-like strategy, with study subjects preferentially joining in predator mobbing with neighbors who had cooperated with them in the past. Whether primates show a similar pattern of reciprocal cooperation remains to be seen.

Attract the Mightier

In addition to attracting conspecifics, noisy mobbing displays may draw the attention of other predators that could drive away or kill the original threat [Curio, 1975; Bourne, 1977]. Fossas, for example, are reportedly drawn to the mobbing vocalizations of several lemur species [Fichtel, 2009]. However, predators drawn in by mobbing vocalizations might also attack the mobbing prey animals, and thus ‘attracting the mightier’ may be an additional cost of mobbing rather than a benefit [Krama and Krams, 2005; Krams et al., 2007].

Warning Signal/Monitoring the Threat

Predator mobbing has also been hypothesized to serve as a warning signal, alerting others to the presence of a threat. However, given the highly complex alarm call systems of many primates [Seyfarth et al., 1980; Zuberbühler, 2000; Digweed et al., 2005; Fichtel et al., 2005; Fichtel and Kappeler, 2011], it is not clear why approaching and harassing a predator would be necessary to accomplish this goal. There is some evidence from the avian literature that mobbing conveys information specifically about the *location* of the predator [Frankenberg, 1981] or about the predator’s motivation to hunt [Dugatkin and Godin, 1992]. This explanation is consistent with many of the design features of primate mobbing, including the ten-

dency of mobbing individuals to approach, circle and peer intensely at potential predators. Mobbing may also be a way to keep group-mates aware of a predator and monitoring its movements [Stanford, 1998]. Initial mobbers benefit by being able to resume feeding (or resting) sooner because they recruited companions to watch the predator, while individuals that join the mob benefit from being able to observe the threat themselves [Cornell et al., 2012] and share the burden of vigilance with others [Caro, 2005].

Cultural Transmission

A series of well-known experiments with captive blackbirds demonstrate that individuals learn to fear objects that they have witnessed other birds mob [Curio et al., 1978b, a]. Mobbing may thus serve to ‘teach’ naïve individuals what constitutes a threat. In primate groups, initiators of mobbing events (‘teachers’) would likely gain indirect fitness benefits from helping offspring or other closely related individuals learn to recognize and avoid predators. However, they could also gain direct fitness benefits if teaching increases the size of mobbing groups and the level of predator harassment, or if pupils recognize future threats and warn their teacher [Caro, 2005]. Evidence for the cultural transmission hypothesis in wild primates is equivocal. Correa and Coutinho [1997] report that in 7 cases of snake mobbing by buffy tufted-ear marmosets (*Callithrix aurita*), infants always approached the snakes more closely than other group members, as the authors predicted would occur if mobbing was being used to direct their attention towards potential dangers. However, another study of the same species reported the opposite pattern [Ferrari and Ferrari, 1990]. Avoidance of predators by infants during mobbing events has also been reported for common marmosets (*Callithrix jacchus*) [Bezerra et al., 2009] and red-fronted lemurs (*Eulemur fulvus rufus*) [Pyritz and Andrianjanahary, 2010]. Experiments testing the cultural transmission hypothesis show mixed results as well. Captive-born, predator-naïve rhesus macaques (*Macaca mulatta*) learned to fear snakes simply by watching a wild-born individual behave fearfully in the snake’s presence [Mineka et al., 1984; Cook et al., 1985], but attempts to induce a snake-mobbing response in captive-born tamarins (*Saguinus oedipus*) using playbacks of mobbing vocalizations failed [Campbell and Snowdon, 2009]. Auditory stimuli alone are sufficient to provoke a mobbing response in naïve birds [Maloney and McLean, 1995; McLean et al., 1999; Griffin and Galef, 2005], but the results of the tamarin experiments suggest that visual and/or social cues may be necessary for the acquisition of predator mobbing behavior in primates [Campbell and Snowdon, 2009].

Costly Signaling

Like the cultural transmission hypothesis, the costly signaling hypothesis posits that mobbing behavior is primarily directed at conspecific observers, rather than the predator that is being harassed. Mobbing is proposed to act as a demonstration of fitness [Dugatkin and Godin, 1992; Zahavi, 1995], aimed either at prospective mates [Ellis, 2009] or potential coalition partners [Maklakov, 2002]. This hypothesis helps explain the mobbing of inappropriate (i.e. nonthreatening) targets [Arnold, 2000], a behavior which is commonly observed in some monkey species (e.g. *Cebus capucinus*) [Rose et al., 2003; Fragaszy et al., 2004; Perry and Manson, 2008]. If the costly signaling hypothesis is correct, we would expect to find a strong audience effect in

patterns of mobbing behavior (animals should be more likely to mob when group mates are around to see them), and mobbing should primarily be conducted by particular age/sex classes.

Investment in Future Defense

A final hypothesis, hinted at by Darwin [1871] in the quote that opens this paper, is that mobbing dissuades future attacks either by causing predators to avoid the area [Trillmich, 1996; Stewardson and Brett, 2000] or by teaching them that attacks are costly and/or unprofitable [Baker and Parker, 1979]. To be effective, this strategy requires that prey repeatedly encounter the same predators – a condition which is likely to be true for most primates, given their tendency to live in relatively stable home ranges. The idea that, by mobbing predators, primates are investing in their future safety helps explain why harassment often persists long after a predator has ceased to pose any real threat. For example, Perry and Manson [2008] describe an ocelot being harassed by the capuchin monkeys in one of their study groups as looking ‘pitifully distressed’. Similarly, at our study site in Panama, my colleagues and I observed a capuchin group tree a juvenile ocelot and mob it intensely for almost 1 h. The ocelot was trembling and looking around wildly, apparently seeking an escape route. The mobbing capuchins, in contrast, including individuals of all age/sex classes, did not appear afraid, and threatened the ocelot from distances of less than 0.3 m. A subadult male went as far as to pull the ocelot’s tail [L. Torrez and A. Gonzalez, pers. commun.]. Incidents such as this cannot easily be explained by any of the preceding hypotheses, suggesting that additional functional explanations for primate mobbing behavior need to be explored.

Evaluating the Hypothesized Benefits of Predator Mobbing

Predator mobbing behavior has been studied systematically in few primate species. To evaluate hypotheses about the benefits of predator mobbing, I therefore chose to focus on the two species – spectral tarsiers (*T. spectrum*) and white-faced capuchins (*C. capucinus*) – for which the most information was available.

Spectral Tarsiers

Both observational and experimental studies of snake mobbing have been used to provide insight into the function of predator harassment in spectral tarsiers [Gursky, 2002, 2003, 2005, 2006, 2007]. Gursky [2006] found that tarsiers did not always mob the snakes they encountered; mobbing was observed in only 11 of 43 encounters with real snakes (25%) and in 31 of 73 encounters (42%) with model snakes. However, mobbing events directed at both real snakes and models were intense, lasting from 15 to 52 min (average = 33.7 min), and involving 3–10 individuals, oftentimes including extragroup males from nearby territories [Gursky, 2006]. The overall intensity of mobbing behavior, including the duration and number of mobbers, influenced the behaviors of the predators that were being targeted. Consistent with the move-on hypothesis, the more mobbers a snake faced, the more quickly it moved away from the area [Gursky, 2005, 2006].

Repeated observations of mobbing in tarsier groups without immature offspring suggest that teaching offspring to recognize dangers in their environment

cannot be the primary function of predator harassment [Gursky, 2006]. The fact that infant tarsiers less than a week old alarm-called in response to snakes, even if they had never encountered them before provides further evidence against this cultural transmission hypothesis [Gursky, 2003, 2006]. Gursky [2006] also argues that her results – specifically the fact that the extragroup males recruited to mobbing events are not bigger than resident males – provide evidence against the ‘attract the mightier’ hypothesis. This conclusion, however, is based on a misunderstanding of Curio’s original hypothesis [1978]. He proposed that conspicuous mobbing displays might attract other, more powerful predators who, by attacking the original threat might provide the mobbers with a chance to escape. Thus, Gursky’s results do not provide evidence either for or against this hypothesis. The fact that extragroup males were more likely to join mobbing events if the group contained subadult females is intriguing and, as Gursky [2006] suggests, may indicate that males use such events to advertise their quality as potential mates [Zahavi and Zahavi, 1997; Ellis, 2009].

White-Faced Capuchins

Given their pugnacious temperaments [Perry and Manson, 2008] and their willingness to harass just about every animal in their habitat [Rose et al., 2003], it is surprising that no one has ever undertaken a systematic study of the function of mobbing behavior in capuchin monkeys. Despite many observations of capuchin mobbing, in only 1 case was the predator actually killed [Boinski, 1988], suggesting that mobbing is probably not intended to be a lethal counterattack. There is strong evidence, on the other hand, that some mobbing events are rescue attempts aimed at forcing a predator (usually a snake) [Chapman, 1986; Perry et al., 2003] to release its prey. The claim that these incidents are rescue attempts, rather than simply aggression directed at potential predators, is supported by the fact that some of the capuchins’ efforts are focused directly on the captured group mate (e.g. grabbing a juvenile’s arms and pulling it free of the boa’s coils) [Perry et al., 2003]. These rescues, however, comprise a small proportion of all capuchin mobbing behavior; most mobbing events are unprovoked, and appear to stem from encounters with animals that, though potentially dangerous, do not pose an immediate threat.

Consistent with the move-on hypothesis, capuchins often mob until their target departs, and even then will sometimes follow behind them as they vacate the area, alarm calling and shaking and dropping branches at them. When the target of a mobbing event does not leave, capuchins will continue with their harassment for periods of 1 h or more, oftentimes with periods of high-intensity mobbing punctuated by intervals of relative calm that end when a group member reprises mobbing and recruits others to join [Crofoot, pers. observation]. Even after a group has stopped mobbing and moved off, individuals will sometimes return periodically, as if to check on the location and behavior of their target [Perry and Manson, 2008; Crofoot, pers. observation]. It thus seems that mobbing may serve a dual function of encouraging potentially dangerous animals to leave the area (move-on hypothesis) while simultaneously monitoring the threat and keeping group mates alert to its presence (monitoring the threat hypothesis). Continued harassment of specific predators might also represent an investment in future defense, if intense mobbing discourages predators that may be encountered again from attempting predatory attacks. For example, over the course of a year, one capuchin group routinely mobbed a large spectacled owl (*Pulsatrix perspicillata*) living in their range. Additionally, once a

threat has been neutralized, capuchins appear to relish the opportunity to attack and terrify their victims with impunity (i.e. a poisonous snake pinned by a fallen branch [Boinski, 1988]; a treed ocelot whose escape routes have been cut off [Crofoot, pers. observation; Perry and Manson, 2008]).

Perhaps the most intriguing and puzzling aspect of capuchin mobbing behavior is their motivation to harass many animals that clearly pose no threat to them and are too large to be considered potential prey. Capuchins seem to go out of their way to provoke other animals, even if their targets must be awakened before they can be tormented. For example, Perry and Manson [2008, p. 85] recount that, when pestering sleeping porcupines, the capuchins typically ‘move forward cautiously and gingerly grasp a quill between thumb and fingers to give it a hard tweak before darting back’. What explains the time and energy that capuchins invest in harassing animals ranging from frogs to sloths to cows and, upon occasion, even pestering inanimate objects like large rocks [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] which stems from selection for a bold, tenacious temperament in other contexts. Alternately, because capuchins often attempt to redirect group mates’ aggression by soliciting them to join in coalitions against third parties (often human observers) [Perry, 1996, 1997, 1998], it is possible that the mobbing response has been co-opted to serve a secondary social function within groups, perhaps related to strengthening coalitional relationships.

Discussion

As with most antipredator strategies, we know far too little about primate mobbing behavior. If broadly defined (i.e. including harassment, counterattacks and rescue attempts), mobbing is taxonomically widespread and is used against many different types of predators. However, inconsistent use of the term ‘mobbing’ within the primate literature makes cross-species and even cross-site comparisons of behavior problematic. Given the duration of many mobbing events, the opportunity costs it imposes appear nontrivial. No information is currently available on the energetic costs of predator harassment, but it is clear that it involves a small, but nonetheless significant risk of injury and death. While the costs of predator mobbing remain poorly understood, the benefits it confers are even more obscure. Numerous hypotheses have been proposed to explain predator mobbing, but due to the logistical problems of studying predator-prey interactions, few studies have systematically tested among them. It has proven difficult to formulate mutually exclusive predictions [Gursky, 2006] because some or all of the proposed benefits of predator mobbing may accrue simultaneously.

To improve our understanding of primate predator mobbing, two main avenues of research need to be pursued. Experimental studies using models to simulate encounters between primates and their predators can elucidate the contexts in which mobbing occurs [Wheeler, 2008; Ouattara et al., 2009]. However, studies which simultaneously monitor the behavior of both predators and their prey will be needed to really shed light on the costs and benefits of mobbing.

Curio’s influential paper on the benefits of avian mobbing proposed 9 potential benefits of predator harassment [1978]. These hypotheses have served as a guide for most subsequent studies of mobbing behavior in both avian and mammalian taxa. It is

clear, however, that there are aspects of primate mobbing behavior that cannot be explained by any of these original hypotheses (e.g. capuchins' tendency to mob non-threatening animals). Future research should consider the ability of behavioral syndromes [Sih et al., 2004] to explain the distribution of mobbing behavior in primates. New hypotheses focused on the potential social benefits of mobbing behavior (e.g. costly signaling) [Dugatkin and Godin, 1992; Zahavi, 1995] should also be considered. While not necessarily its original function, mobbing may have been co-opted into serving one or more secondary functions related to within-group signaling in primates.

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