An Experimental Analysis of Alarm Calling Behavior in Wild Tufted Capuchin Monkeys (*Cebus apella nigritus*)

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Abstract of the Dissertation

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Alarm calls are vocalizations given by prey species upon detecting a predator or other threatening stimuli. Because these calls are typically given in moments of potentially significant fitness consequence (i.e., escaping from or falling prey to a predator), they are subject to strong selective pressures. As such, these apparently altruistic calls have received much attention from scientists interested in referential communication, the ontogeny of call production and response, the adaptive significance of the calls, and the potential to use them "deceptively". While such questions have been addressed in a wide range of taxa including birds, rodents, and ungulates, studies of primate alarm calls have been generally limited to the degree to which they contain referential information. Further, these studies have been primarily limited to Old World monkeys and Malagasy lemurs. This study takes a largely experimental approach to investigate the alarm call system of a New World primate, the tufted capuchin monkey (*Cebus apella nigritus*), in Iguazú National Park, Argentina.

Specifically, this dissertation addresses four main questions regarding the alarm calling behavior of tufted capuchin monkeys: 1) Are the alarm calls of this species functionally referential signals? 2) Does learning play any role in the ontogeny of alarm call use or response, or are these anti-predator behaviors innate? 3) What is the adaptive significance of the calls? and 4) Do capuchin monkeys use these calls in a functionally deceptive manner to usurp resources? If so, what ecological and social conditions lead to such uses of alarm calls?

To address these questions, experiments using predator decoys, live predators, vocalization playbacks, and provisioning platforms hoisted into the forest canopy were combined with natural observations. The results indicate that: 1) the capuchin monkeys have a functionally referential aerial predator call, but the call most often associated with terrestrial predators is also given in non-predatory contexts; 2) the contexts in which alarm calls should be used and the appropriate ways to respond to alarm calls from others are mostly (but not completely) under-developed in infants, but the degree to which these behaviors are learned or innate requires additional investigation; 3) the adaptive function of alarm calling varies with predator type - it is largely a selfish behavior that reduces the likelihood of predation for the caller, although callers also seem to benefit by warning offspring and collateral kin of the presence of venomous snakes; and 4) terrestrial predator-associated calls are sometimes used “deceptively” by subordinates to elicit anti-

predator reactions in call receivers, allowing them to usurp contestable resources from conspecifics.

Taken together, these results indicate that the alarm call system of tufted capuchin monkeys in Iguazú has been largely shaped by several features of their ecology, including the predator guild of the study site, the monkeys' arboreal habits, and the density of vegetation in their habitat. However, additional research is needed to understand the roles that emotion, cognition, and physiology play as proximate mechanisms driving alarm calling behavior.

For my dad, to whom in one moment I said ‘goodbye’.
And for Barbara, to whom in the next moment I said “hello’.

Table of Contents

Chapter 2: Situationally Variable Alarm Call Production in Tufted Capuchin Monkeys: Functionally Referential or Urgency-Based?

Chapter 3: The Ontogeny of Alarm Call Use and Response in Wild Tufted Capuchin Monkeys (*Cebus apella nigritus*)

Chapter 4: Selfish or Altruistic? The Adaptive Significance of Alarm Calling in Wild Tufted Capuchin Monkeys (*Cebus apella nigritus*)

Chapter 5: Are Tufted Capuchin Monkey Alarm Calls Pursuit Deterrent Signals? Insights from Hawk Eagle Behavior

Chapter 6: Monkeys crying wolf? Tufted Capuchin Monkeys Use Functionally Deceptive Anti-Predator Calls to Usurp Resources from Conspecifics.

List of Figures

List of Tables

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Chapter 1

Introduction

Group-living in primates, as well as many other species of mammals and birds, is thought to be an adaptive strategy to reduce individual predation risk (Alexander, 1974; van Schaik, 1983). Several non-mutually exclusive hypotheses aim to explain how the threat of predation can be reduced for a group-living individual relative to a solitary one. These include the “selfish herd” effect, in which individuals occupy spatial positions within the group which offer safety from predator (normally in the center of the group; Hamilton, 1971; Vine, 1971); the “dilution effect”, in which individual predation risk decreases with an increase in group size, reducing the probability that any one individual will fall victim to the predator (Bertram, 1978); the “many eyes effect”, in which the chances that a predator will be detected early enough to escape an attack increases with the number of individuals on the lookout for such threats (Pulliam, 1973); and the “cooperative defense effect”, in which group members can deter predation by cooperatively attacking the predator (e.g., mobbing; see Curio, 1978a). While the “selfish herd” and “dilution effect” can decrease an individual’s predation risk without any intraspecific communication, the “many eyes effect” and the “cooperative defense effect” require that individuals be able to communicate the presence of a potential predator to conspecifics (Lima, 1995). In these latter cases, non-detectors must rely on the detector to indicate that a predator has been spotted. The use of particular anti-predator vocalizations (so called “alarm calls”) serves as an efficient means for detectors to communicate to conspecifics that a predator has been detected and appears to have evolved independently in a number of gregarious mammals and birds. Alarm calling behavior has been the subject of considerable scrutiny be evolutionary biologists for the last half century, with a strong focus on why individuals produce these calls, how they perceive them, how they develop, and the potential to use them “dishonestly”.

A brief history of the study of alarm calls: function, meaning, ontogeny, and deception

Function

Alarm calls began to receive attention from biologists in the 1960s (Maynard Smith, 1965; Williams, 1966) because, although they facilitate some anti-predatory benefits of group living, they also present what appears to be an evolutionary paradox: an individual who altruistically produces a conspicuous vocalization in the presence of a predator may decrease its own fitness by drawing the predator's attention to itself (e.g., Ivins & Smith, 1983; Sherman, 1977; Alatalo & Helle, 1990). How does such an altruistic behavior evolve given the potentially high costs?

In the intervening years, a number of empirical studies have shown how callers can benefit despite these costs. For example, the costs born directly by the caller could be outweighed by the indirect benefits received by alerting kin that a predator is present and allowing them a chance to escape (e.g., Sherman, 1977; Hoogland, 1996). Other studies have shown that callers may increase their direct fitness by warning conspecifics, such as offspring or mates, of an impending attack (e.g., Dunford, 1977; Witkin & Ficken, 1979; Blumstein et al., 1997). Still other studies have shown that the calls may not function primarily to communicate with conspecifics, but rather with the predator itself (e.g., Zuberbühler et al., 1999); this may benefit the caller if, by alerting the predator that it has been seen, it gives up its pursuit of the detecting prey.

Meaning

Also in the 1960s, it was noted for the first time that some primates have multiple alarm calls that they use in different situations. In a study of vervet monkeys (*Chlorocebus aethiops*), Struhsaker (1967) noted that these primates give three acoustically distinct alarm calls, one solely in response to terrestrial carnivores such as leopards (*Panthera pardus*), a second solely in response to snakes, and a third solely in response to raptors, which attack from the air (reviewed in detail in Cheney & Seyfarth, 1990). Furthermore, production of each of these calls elicits unique, predator-specific responses: leopard calls cause listeners to run into trees, eagle calls cause listeners to look up towards the sky or run into dense bushes, and snake calls cause listeners to stand bipedally and scan towards the ground. Because this seemed to be an example of the use of arbitrary sounds to denote the existence of external referents in the environment, and because listeners responded to these sounds as if they understood that the referent was present, it was interpreted by some as an example of semantic communication in a non-human animal (Altmann, 1967, Marler 1977).

These findings presented a challenge to the long-held view that animal signals reflect their internal ("emotional") state and only humans were capable of using vocalizations with a "meaning" (e.g., Premack, 1975), although not all ethologists agreed that this was truly an example of referential communication. For example, variation in call production could be explained simply as variation in the level of fear that different predators elicit (Marshall, 1970); and listeners may employ distinct reactions when these different calls are given, not because of the calls, but because they have also seen the predator and are reacting to its presence (Cheney & Seyfarth, 1990).

A decade later, Seyfarth and colleagues (1980a, b) addressed these issues by playing back audio recordings of the calls when no predators were present. These experiments revealed that the calls alone were sufficient to elicit predator-appropriate reactions, and that variation in acoustic features related to urgency did not affect the types of responses employed by listeners. These findings bolstered the argument that the calls may indeed share similarities to the human words for "leopard", "eagle", and "snake". Studies conducted in subsequent years have shown that such "functionally referential" communication exists in the alarm call systems of a number of primate, carnivoran, avian, and (possibly) rodent taxa; others studies, primarily in rodents and birds, have demonstrated that variation in alarm calling behavior in some species functions to communicate the urgency of the threat present, but not the type of threat (see reviews in Fichtel & Kappeler, 2002; Zuberbühler, 2003; Caro, 2005; Blumstein, 2007a).

Still, the idea that functionally referential alarm calls are similar to human words has continued to receive criticism (e.g., Owren et al., 2003). Notably, the notion that the sounds animals produce in response to particular predators are arbitrary has been challenged on the grounds that there is remarkable similarity in the acoustic structure of alarm calls across distantly related taxa, with calls being characterized by features that elicit attention and arousal (Owren & Rendall, 2001). Indeed, most researchers now agree that, despite the fact that emotion alone does not likely explain the use of different calls for different predators, the use of functionally referential signals says little about the cognitive abilities of the caller (Zuberbühler, 2003; Cheney & Seyfarth, 2007). Nevertheless, there remains a strong argument that the mental processes associated with the perception of these signals offer an example of an evolutionary stepping stone in the gulf that exists between the between humans and other animals in terms of communication capabilities (Zuberbühler, 2003; Cheney & Seyfarth, 2007; but see Owren & Rendall, 1997, 2001; Owren et al., 2003 for an alternative view).

Ontogeny

Along with the findings that the alarm calls of vervet monkey are seemingly more than reflections of the caller's internal state and that different calls can necessitate different reactions if one hopes to survive, came interest in the ontogeny of alarm call use and response in this species (Seyfarth & Cheney, 1980, 1986). An examination of the contexts in which individuals of different age classes used the various alarm call types showed that infants and juveniles produced these calls in response to a wider range of stimuli than did adults, with younger individuals more frequently calling in response to non-dangerous stimuli which were in some way similar to the predators that elicited the same call types from adults. Further, playback experiments conducted with individuals of different age classes showed that infants were less likely than adults to react "appropriately" upon hearing a particular predator-specific alarm call. These findings were argued to provide evidence that young vervet monkeys likely learn both which stimuli are dangerous and what the appropriate response to a particular call type is (reviewed in Cheney & Seyfarth, 1990). Indeed, the roles of learning and experience are widely accepted as important in the development and refinement of these anti-predator behaviors, but whether the learning process leads individuals to conjure up mental images of a carnivore when they hear one alarm call type and a raptor when they hear another type is debated (cf., Owren et al., 2003; Zuberbühler, 2003).

Deception

Around the same time that arguments were being made that vervet monkey alarm calls contain referential information, came a new paradigm for understanding the evolution of signaling behavior (Dawkins & Krebs, 1978; Krebs & Dawkins, 1984). Under this new school of thought, it was argued that signals evolved not to provide reliable information to signal receivers, but rather to provide unreliable information as an attempt to deceive receivers and manipulate their behavior in a way that benefits the signaler, a view contended to be more grounded in Darwinian natural selection. Further, Dawkins & Krebs (1978; Krebs & Dawkins, 1984) argued that such attempts to manipulate receivers are inherently incompatible with providing reliable information, a view that conflicted not only with the traditional thinking of ethologists at the time (e.g., Marler, 1977**)**, but also with the empirical data on vervet alarm call production and perception. However, cogent arguments have been made that the informational and manipulation paradigms are not actually incompatible and can in fact be incorporated (Cheney & Seyfarth, 1985; Smith, 1986a). Indeed, signals must be reliable to a certain extent, otherwise they will simply be ignored and manipulation will be impossible (Smith, 1986a). But so long as the "dishonest" use of signals does not exceed a certain threshold, they can theoretically be used to "deceive" listeners.

Alarm calls offer an ideal opportunity for callers to manipulate listener behavior through "deceptive" uses of the signals, because the calls are ignored at the risk of great peril. Perhaps not surprisingly, some of the best evidence for functionally deceptive signaling in non-human animals comes from studies of some avian and mammalian taxa which demonstrate the use of alarm calls outside of a predatory context (Munn, 1986 a,b; Møller, 1988, 1990; Tamura, 1995). For example, Munn (1986 a,b) noted that some species in mixed species flocks of Amazonian birds serve as sentinels, frequently giving alarm calls when predators are spotted, creating flee reactions in conspecific and heterospecific listeners. The sentinel species benefit from these polyspecific associations by catching falling arthropods flushed out by the foraging behaviors of the other species of the flock. This oftentimes leads to more than one individual pursuing the same falling insect, which will be eaten by whichever individual catches it first. Such situations frequently elicit alarm calls from the sentinel species, even if there is no predator to be seen. Just as when predators are present, these alarm calls cause other individuals, potentially including those foraging competitors pursuing the same insect as the caller, to flee to safety, increasing the likelihood that the caller will obtain the food resource. Thus, it seems that these species are using alarm calls in a functionally deceptive manner; by providing unreliable information, signalers are able to increase their feeding success by eliciting anti-predator behaviors in receivers while simultaneously *not* employing additional anti-predator behaviors themselves. Similar use of alarm calls outside of predatory contexts has been shown to successfully manipulate the behavior of receivers in mating contexts as well (Møller, 1990; Tamura, 1995).

Open questions regarding the alarm calling behavior of primates

While a number of studies have examined alarm calling behavior in primates, previous investigations have been taxonomically limited (focusing primarily on Old World monkeys and lemurs), and have been largely limited to studies of alarm call meaning, with few studies examining either the ontogeny of alarm call use and response or alarm call function. Alarm call meaning has been best studied in Old World monkeys including vervets (*Chlorocebus aethiops*; Seyfarth et al., 1980a, b), Campbell's monkeys (*Cercopithecus campbelli*; Zuberbühler, 2001), Diana monkeys (*Cercopithecus diana*; Zuberbuhler, 2000a), putty-nosed monkeys (*Cercopithecus nictitans*; Arnold & Zuberbühler, 2006; Arnold et al., 2008), Barbary macaques (*Macaca sylvanus*; Fischer et al., 1995; Fischer, 1998; Fischer & Hammerschmidt, 2001), and chacma baboons (*Papio cynocephalus ursinus*; Fischer et al., 2001). Among lemurs, alarm call meaning has been addressed in ring-tailed lemurs (*Lemur catta*; Macedonia & Evans, 1993), black-and-white ruffed lemurs (*Varecia variegata*; Macedonia & Evans, 1993), redfronted lemurs (*Eulemur fulvus*; Fichtel & Kappeler, 2002), and Verreaux's sifakas (*Propithecus verreauxi*; Fichtel & Kappeler, 2002). In contrast, alarm call meaning has been addressed in only two genera of New World primates, white-faced capuchin monkeys (*Cebus capucinus*; Digweed et al., 2005; Fichtel et al., 2005), moustached tamarins (*Sagunius mystax*; Kirchhof & Hammerschmidt, 2006), and saddleback tamarins (*Saguinus fuscicollis*; Kirchhof & Hammerschmidt, 2006). Furthermore each of these studies with New World primates examined only one of the two aspects considered vital in understanding call meaning: production and perception (Macedonia & Evans, 1993). Indeed, many of the more complete studies conducted with Old World monkeys and lemurs did not properly address call production, examining only whether different predator types elicited different types of calls, but not examining whether or not these call types were produced in any additional contexts (Owren & Patel, 2008). Despite these shortcomings, the available studies have demonstrated considerable diversity in the degree to which functionally referential alarm calls are used among primates, even among closely related species (e.g., Macedonia & Evans, 1993). Thus, detailed studies of the contexts in which anti-predator calls are produced are needed in primates generally, while additional research on both call production and perception are needed to understand the diversity of alarm communication in New World primates.

Although much more limited than studies of call meaning, studies of the ontogeny of conspecific alarm call perception have been conducted with both wild Old World monkeys (Seyfarth & Cheney, 1980; Ramakrishnan & Coss, 2000) and lemurs (Fichtel, 2008), but such studies with New World primates are thus far limited to investigations conducted with captive subjects (Herzog & Hopf, 1984; McCowan et al., 2001). Like the vervets (Seyfarth & Cheney, 1980, 1986), infant Verreaux's sifakas do not demonstrate adult-like perception of alarm calls (Fichtel, 2008), but instead seem to be develop these behaviors during infancy. A study of bonnet macaques (*Macaca radiata*) showed that juveniles did not differ from adults in their reactions to alarm calls from adult conspecifics (Ramakrishnan & Coss, 2000b), but because infant's reactions to alarm calls were not examined in this study, it is unclear if the ontogeny of call response in this species differs from that of vervet monkeys or sifakas. Among New World primates, studies of captive squirrel monkeys (*Saimiri sciureus*) indicate arousal responses to alarm calls are innate, but that development of fully adult-like responses are learned over the first year of life (Herzog & Hopf, 1984; McCowan et al., 2001). However, whether or not such trends characterize squirrel monkeys in wild conditions is unknown.

Studies of the ontogeny of alarm call use among primates are extremely rare, with the only study to date to address this with wild primates being the now classic study of vervet monkeys by Seyfarth & Cheney (1980, 1986). Thus, little is known about the ontogeny of alarm call use in primates in general, while nothing is known in this regard for wild Neotropical primates. However, while not focused exclusively on alarm call use, a number of studies of captive primates, including some New World monkeys, have tested whether such subjects, having never been exposed to predators, exhibit anti-predator behaviors upon encountering decoys of felids, raptors, and snakes (e.g., Vitale et al., 1991; Caine, 1998; Koenig, 1998). For the most part, these studies have shown that even these predator-naive individuals seem to recognize these stimuli as dangerous, (although the reactions might not be as well-developed or intense as in their wild counterparts: Hayes & Snowdon, 1990; Koenig, 1998), indicating that predator recognition may be innate. However, because these studies did not focus on age differences in predator recognition, it is unknown if such behavior is present in infants or if it develops over time.

Studies of alarm call function are even more limited, with only two in-depth studies having been conducted with primates, both with Old World monkeys (Cheney & Seyfarth 1981, 1985; Zuberbühler et al., 1999). These studies showed that alarm calls may serve to warn offspring or even unrelated group members (Cheney & Seyfarth, 1985) or to deter pursuit by the predator (Zuberbühler et al., 1999). Unfortunately, the data collected in these previous studies limited the ability to test more than a few of the many possible hypotheses regarding alarm call function; thus, additional, non-mutually exclusive hypotheses may also explain the existence of alarm calls in these species. Limited evidence suggests kin selection may play a role in some aspects of anti-predator signaling in white-handed gibbons (*Hylobates lar*; Tenaza & Tilson, 1977) and the Neotropical black-handed spider monkey (*Ateles geoffroyi*; Chapman et al., 1990). None of these previous studies, however, collected all of the necessary data to test the many competing hypotheses of alarm call function: 1) differences between individuals in their propensity to call in response to different threat types, 2) whether there is an audience effect for alarm calling, 3) the response of conspecifics to alarms, and 4) the responses of predators to alarm calls. Additional research with primates is therefore needed to elucidate how this apparently altruistic behavior may have evolved in our closest relatives.

The least studied of these four aspects of primate alarm calling is the "deceptive" use of anti-predator calls. In Byrne & Whiten's (1990) attempt to document all known anecdotal observations of "tactical deception" in primates, such use of alarm calls was reported only twice, once in a captive *Saguinus fuscicollis* and once in a wild white-faced capuchin (*Cebus capucinus*). An investigation of the literature published since Byrne & Whiten (1990) has revealed anecdotal observations of the use of false alarms to usurp resources in only one additional primate species, the rhesus macaque (*Macaca fuscata*; Gouzoules et al., 1996). Other potentially deceptive uses of alarm calls have been described anecdotally for tufted capuchin monkeys, which appear to frequently use alarms to distract aggressors during agonistic interactions (Di Bitetti, 2001a), and vervet monkeys, which may use alarms to gain ground against other groups during intergroup interactions (Cheney & Seyfarth, 1990). There are also numerous examples of chimpanzees (*Pan troglodytes*) using alarm calls to distract individuals (although not in a feeding context; de Waal, 1986) or using other "deceptive" tactics to acquire resources that would otherwise be consumed by other group members (e.g., Goodall, 1986). Despite a plethora of anecdotal observations of purported deception among primates, systematic studies of such behaviors are scant. To date, two studies have systematically examined passive deception (i.e., the withholding of information), one in rhesus macaques (Hauser, 1992) and one in tufted capuchins (Di Bitetti, 2005), while only one (Slocombe & Zuberbühler, 2007), a study of the use of exaggerated agonistic screams in chimpanzees, has examined active deception (i.e., providing false information) . However, no study has examined the production of signals outside of their "appropriate" context as a form of deception among primates.

Goals of this study

This dissertation attempts to fill the taxonomic and empirical gaps mentioned above by examining the alarm call system of a wild Neotropical primate, the tufted capuchin monkey (*Cebus apella nigritus*), in Iguazú National Park, Argentina. This study employs a largely experimental approach to address these questions, relying on the use predator decoys, audio playbacks, and controlled provisioning. Specifically, questions related to call meaning are addressed by investigating the contexts in which anti-predator calls are given (both in natural contexts and in response to decoy predators) and the responses of individuals of to audio playbacks of these calls. Likewise, the ontogeny of call use and response are addressed by examining age-related differences in the responses to predator decoys and conspecific alarm call playbacks. Hypotheses related to the adaptive function of alarm calling are tested by examining the vocal responses of capuchins to visual and acoustic models of predators as well as by examining the responses of a bird of prey to capuchin anti-predator calls. Finally, the potential functionally deceptive use of alarm calls in a competitive context is addressed by experimentally manipulating a high value food resource using wooden platforms suspended in the canopy.

Tufted capuchin monkeys in Iguazú are ideal for such a study for several reasons. The monkeys face threats from at least three distinct categories of heterospecifics: vipers, carnivores, and raptors (Di Bitetti, 2001a). Previous investigation has shown that they produce at least two call types in response to these threats (Di Bitetti, 2001a), but it is unclear if these calls are functionally referential, as are their food-associated calls (Di Bitetti, 2003), or urgency-based. Previous studies of tufted capuchins (e.g., Custance et al., 1999; Gunst et al., 2008; Ottoni & Izar, 2008) have indicated that the individuals of this species socially learn foraging skills (see also Perry et al., 2003b for similar findings in the congeneric *Cebus capucinus*), but little is known regarding learning about predators in this species. The social organization and structure of the species, with female philopatry, male dispersal, and linear dominance hierarchies, make them ideal system in which to test hypotheses for alarm call function that require variation in kinship and dominance status among individuals to properly address. There is systematic evidence favoring passive deception (the withholding of food calls) in this species (Di Bitetti, 2005), as well as anecdotal observations indicating that tufted capuchins may use functionally deceptive alarm calls to disrupt aggressive encounters (Di Bitetti, 2001a). Studies in captivity have shown further evidence that tufted capuchins can, under certain conditions, actively engage in functionally deceptive behaviors (Mitchell & Anderson, 1997; Fujita et al., 2002). Thus, the species is ideal for studying the meaning, ontogeny, function, and deceptive uses of alarm calls.

Figure 1.1 The location of the study site, Iguazú National Park, in northeastern Argentina, South America.

Description of the study site and subjects

Study site

Data for this study were collected during August-September 2003, July-September, 2004, and May 2005-December 2006 in Iguazú National Park, Argentina (25°40'S, 54°30'W; Figure 1.1) in the sections of forests to the north and northwest of the waterfalls of the Iguazú River. The site is part of the Upper Paraná Atlanta Forest Ecoregion, the southwestern-most portion of the South American Atlantic Forest complex (Di Bitetti et al., 2003). The area is characterized by humid, semi-deciduous, sub-tropical forest (Crespo, 1982). There is a marked seasonality in day length and temperature although, with an average annual rainfall of 2000 mm, there is no marked dry season (Di Bitetti & Janson, 2001a). Productivity also varies seasonally, with fruit and insect abundance highest during the austral spring and lowest during the winter months (Di Bitetti & Janson, 2001a).

Iguazú National Park is a 67,000 ha protected area with very low incidences of illegal hunting (Di Bitetti et al., 2006). It is contiguous to the 170,000 Iguaçu National Park of Brazil and is part of the “Corredor Verde” (Green Corridor) of Misiones, Argentina, which is a sustainable use conservation area encompassing nearly 709,000 ha. These protected areas contain the largest tracts of forest remaining in the Atlantic Forest complex (Di Bitetti et al., 2006). The Green Corridor hosts a full complement of avian and carnivoran predators, although some are absent in Iguazú and densities for others are quite low (see below). Two species of howler monkeys (*Alouatta caraya* and *A. guariba clamitans*) are also found in the Green Corridor and are sympatric in some regions (Agostini et al., 2008). While there are reports of *A. caraya* in Iguazú National Park (Crespo, 1954 cited in Crockett, 1998), they are absent from the area around the waterfalls where this study was conducted.

The study area has been subjected to various degrees of logging over the past several decades, especially prior to the establishment of the park in the 1930s. Areas left to regenerate since then now contain many tall trees and a dense understory (Di Bitetti et al., 2000). Other areas were subjected to human disturbance until the 1960s and are now dominated by only smaller trees. A third habitat is characterized by very dense bamboo (predominantly *Merostachys clausenii* during the study period, but also *Guadua trinii*) and very few tall trees. Additional descriptions of the site's habitat, climate, and productivity patterns can be found in Crespo (1982), Placci et al. (1994), Di Bitetti et al. (2000, 2006), Di Bitetti (2001a,b), and Di Bitetti & Janson (2001a,b).

Likely primate predators

Among the potential terrestrial predators of capuchin monkeys at the site are three felid species (jaguars, *Panthera onca*; pumas, *Felis concolor*; and ocelots, *Leopardus pardalis*), tayras (*Eira barbara*; Di Bitetti, 2001a). Ocelots are estimated to live at a density of 13 to 20 individuals/100 km^2 in Iguazú National Park (Di Bitetti et al., 2006), while jaguar densities are estimated at only 0.9 to 1.7 individuals/100 km^2 (Paviolo et al., 2008). Puma densities for the Park are unavailable, but at a neighboring site in the Green Corridor (Yabotı´ Biosphere Reserve), densities are estimated at only 0.7 individuals/100 km^2 (Kelly et al., 2008), considerably lower than at other sites. During the study period, one encounter each between the capuchin monkeys and a puma and an ocelot were observed (M.A. Vidal & P. Cooper, pers. comm.). Additional reports of such interactions have been reported by Di Bitetti (2001a) and B. Tiddi (pers. comm.). Puma and ocelot tracks were seen throughout the study area on several occasions during the course of the current study, and in one case the author came across a vocalizing puma. On several additional occasions, the capuchin monkeys reacted very strongly as if they had just seen a carnivoran predator, although because no such predators were observed it is unclear if these represented actual primate-predator interactions.

At least two species of raptors (crowned hawk eagles: *Spizaetus ornatus* and *S. tyrannus*) are found in Iguazú. Density estimates for these aerial predators are not available, but they are quite rare. There were no observed interactions between these species and the capuchins during the study period. On one occasion, the author may have observed a *S. ornatus* soaring high above the monkeys (although this could have been a smaller raptor species with a similar color pattern under the wings); the subjects did not react in any noticeable way, although it was unclear if the raptor had even been detected. There was also an observed attack on a capuchin group, in 2005, by a crested eagle (*Morphnus guianensis*) within Iguazú National Park, some 30 km from the study site. (A.

Paviolo, pers. comm.). This species is otherwise not reported to be present at the site. Harpy eagles (*Harpia harpia*) are known in adjacent parks of the Green Corridor, but are not reported to live in Iguazú (although this is likely a recent phenomenon; J. Anfuso, pers. comm.). In the years prior to the current study, two predation attempts on the study animals by *S. ornatus* were observed, one of which was immediately followed by the disappearance of an infant (Di Bitetti, 2001a; M. Di Bitetti, pers. comm.). On one afternoon during the current study, the monkeys were observed to consistently react with anti-predator behaviors to many innocuous aerial stimuli, including small passerine birds flying in the understory. Such anti-predator behaviors are common after a group has been attacked by an aerial predator (C. Janson, pers. comm.). However, because the group had not been followed during the two days preceding these observations, it is unclear if such an attack had occurred.

In addition to these predators, there are several venomous snakes at the study site. These include both vipers (*Bothrops neuwiedii, B. jararaca,* and *Crotalus durissus*) and coral snakes (*Micrurus frontalis* and *M. corallinus*; Martinez et al., 1992). While these are unlikely to prey upon capuchin monkeys (given that capuchins are likely far too large), they nevertheless pose a mortal threat for individuals who approach too closely. It is possible, however, that the very largest vipers could prey upon infant capuchins, although no such reports exist. Boas do not appear to be present in Iguazú National Park (Di Bitetti et al., 2000), although they are reported to live in other portions of the Green Corridor (Giraudo & Scrocchi, 2002). At approximately 2 m in length, mussuranas (*Boiruna maculate*) are the likely the largest constricting snakes present in Iguazú, but these are specialized at preying upon other snakes and rodents (da Costa Pinto & de Lema, 2002) and are unlikely to be able to prey upon even infant capuchins (D. Fabius, pers. comm.).

Study subjects

Tufted capuchin monkeys (*Cebus apella nigritus*, also referred to as the black horned capuchin; Figure 1.2) are small to medium-sized (2.5-3.6 kg; Smith & Jungers, 1997), diurnal, and omnivorous primates that feed primarily on fruits but spend a large proportion of time engaged in destructive foraging for insect prey (Terborgh, 1983;

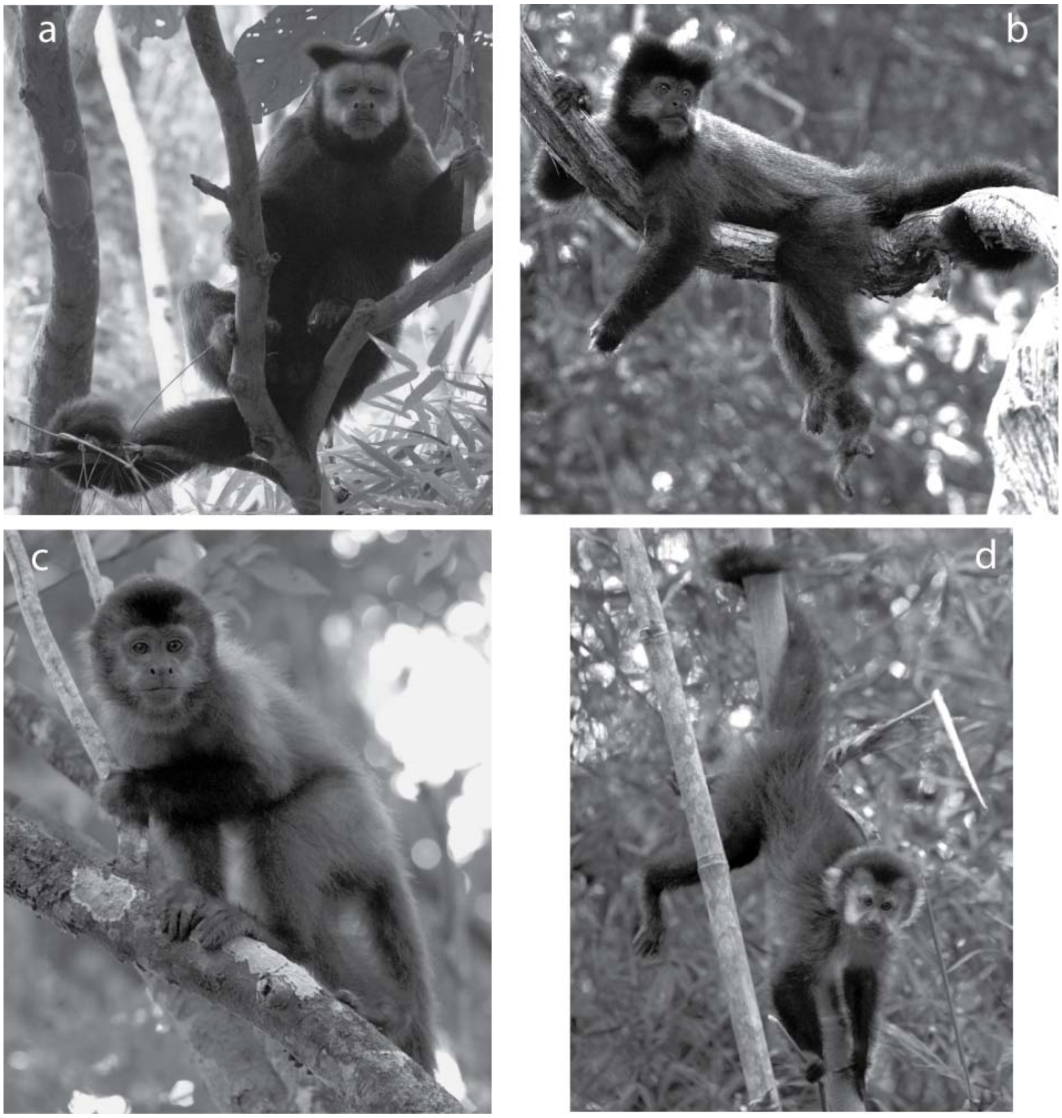

Figure 1.2 The study species, the tufted (or black horned) capuchin monkey (*Cebus apella nigritus*). a) an adult male; b) an adult female, c) a juvenile male, d) an infant female.

Brown & Zunino, 1990). The species is highly arboreal, with individuals spending most of their time in the mid to lower canopy and the understory (Fleagle & Mittermeier, 1980; Fleagle et al., 1981). In the current study, the capuchin monkeys spent 1.9% of their time (in non-experimental conditions) on the ground, 15.3% in the trees at a height of 0.1 to 3.0 m, 20.5% at 3.1 to 6 m, 42.5% at 6.1 to 10.0 m, and 19.7% in the canopy at a height of greater than 10 m (Wheeler, unpublished data). In Iguazú, groups tend to consist of 7-30 individuals, including a dominant male, several other adult males, several adult females, and offspring (Di Bitetti, 2001b), but groups of up to 45 individuals have been observed (pers. obs.). Females remain in their natal groups while males disperse upon reaching sexual maturity (Di Bitetti, 1997). While the alpha male is the likely sire of most offspring during his tenure (Escobar-Páramo, 1999), non-alpha males do secure some matings (Janson, 1994), especially when alpha males experience long tenures, as these dominant individuals tend to avoid inbreeding with their own offspring (Escobar-Páramo, 1999). Births at the site are quite seasonal, occurring exclusively from October to February (Di Bitetti & Janson, 2001a).

The vocal behavior of this species has been studied in-depth by Di Bitetti (2001a), with acoustic parameters and contexts of call production described for over 30 different call types, and evidence that tufted capuchin food calls are functionally referential (Di Bitetti, 2003). Di Bitetti (2001a) described two anti-predator calls for this species: one that appears to be associated with felids and possibly snakes (the "ground predator alarm call"; GPAC) and a second that appears to be associated with flying stimuli (the "aerial predator alarm call"; Di Bitetti, 2001a). The GPAC is also frequently produced by subordinate individuals in response to aggressive interactions; this may constitute functional deception given that the call seems to cause the aggressive encounter to end suddenly (Di Bitetti, 2001a). Di Bitetti (2001a) also noted the use of a call (the "hiku") which was not distinguishable from the GPAC based on the acoustic parameters examined, but which he classified as a distinct call type because it was produced in non-predatory contexts (primarily when using suspensory feeding postures) and did not elicit anti-predator reactions in conspecifics as did the GPAC. A study of captive tufted capuchins by Boinski et al. (1999) has indicated that production of this call type may be associated with elevated cortisol production, a hormone associated with stress (Sapolsky, 2002).

Study groups

Data were collected on three groups including a large group (“Macuco”: 23-28 individuals), a medium-sized group (“Gundolf”: 15 individuals), and a small group (“Guenon”: 9 individuals). During the 2003 and 2004 study periods, these three groups comprised a single group (the Macuco Group) that ranged in size from 38 to 45 individuals. In August of 2004, most of the females of one matriline and the group’s beta male began to split off from the main group and established a home range in an area adjacent to that of the main group; this group became the Gundolf Group (Ramirez-Llorens et al., 2008). In the first months of 2005, following a male takeover and an episode of infanticides by the former gamma male (Ramirez-Llorens et al., 2008), a second matriline split off with what was at that point the group’s beta male (Ramirez-Llorens, pers. comm.). Although the home range of this group (the Guenon Group) greatly overlapped that of the Macuco Group, and the two groups were observed to forage together for up to an hour on a few occasions until mid-2006, most interactions between the groups were aggressive and followed similar patterns to intergroup encounters between groups known to have been separated since at least 1991. All individuals were easily recognizable based on facial characteristics. Maternal relationships for individuals born after 1991 are known, while those of individuals born prior to this date were determined based on affiliative relationships (C. Janson, pers. comm.).

These study groups have been the subject of near continuous investigation since 1991 (see Janson, 1996). Primate studies at the site have been largely experimental, using: 1) feeding platforms to manipulate food type, abundance, and distribution to investigate aspects of foraging behavior (see Janson, 1996; Janson & Di Bitetti, 1997; Janson, 1998; Di Bitetti & Janson, 2001b; Di Bitetti, 2003, 2005; Agostini & Visalberghi, 2005; Janson, 2007a), 2) audio playbacks of recordings of capuchin vocalizations to study aspects of vocal perception (Di Bitetti, 2003), and 3) predator decoys to examine aspects of capuchin anti-predator behavior (Janson, 2007b; Janson et al., 2008).

Organization of the dissertation

This dissertation is divided into five main chapters (Chapters 2-6) which individually address aspects of the meaning, ontogeny, function, and deceptive uses of capuchin anti-predator vocalizations.

Chapter 2 focuses on the "meaning" of tufted capuchin alarm calls by examining aspects of call production and perception. I first identify the types of calls that can be considered alarm calls by examining the vocal responses of the monkeys to visual models of predators (felids and raptors) and other threats (snakes). I then test whether variation in call production better supports a functionally referential call system (i.e., one based on threat type) or an urgency-based (affective) call system. Finally, call perception is examined through analysis of responses to playbacks of audio recordings of alarm calls.

In Chapter 3, I examine the ontogeny of the two aspects of alarm calling that were presented in the previous chapter: call use and call perception. Ontogeny of alarm call use is examined through analysis of 1) the types of calls that capuchin monkeys of different age-classes (infants, juveniles, and adults) use in response to venomous and non-venomous snakes, and 2) differences between these age-classes in the propensity to alarm call in response to each of these two stimulus types. The ontogeny of call perception is examined by comparing the qualitative reactions of infants, juveniles, and adults to playbacks of different alarm call types.

Chapters 4 and 5 investigate the adaptive function of capuchin alarm calls. In Chapter 4, I test multiple hypotheses regarding the adaptive significance of alarm calling behavior by examining variation among individuals in propensity to call to different threat types, the responses of non-detecting individuals after group members have spotted a predator decoy, and whether or not there is a conspecific audience effect on the production of alarm calls. In Chapter 5, I test the responses of tamed crowned hawk eagles to playbacks of capuchin alarm calls and other call types. These experiments allow for a test of whether or not capuchin alarm calls can effectively deter pursuit by potential predators.

Chapter 6 tests whether capuchins use alarm calls “deceptively” during feeding to distract group members and increase their own feeding success. This was tested by experimentally manipulating the quantity and distribution of a high value food resource (banana pieces) and examining whether or not differences in the likelihood of alarm calling existed based on dominance rank, food distribution, food quantity, and spatial location relative to the location of the food.

In Chapter 7, I summarize the major results, offer an explanation of how the ecological factors such as the predator guild and habitat have shaped the alarm call system of tufted capuchins. I also point towards questions that remain open and suggest future research directions.

Chapter 2

The Alarm Call System of the Tufted Capuchin Monkey: Functionally Referential or Urgency-based?

Abstract

Many mammalian and avian prey species produce conspicuous vocalizations upon encountering a predator or other threat, but vary their calling based on the context of the encounter. For example, the alarm calls of some species vary based on risk-urgency (high vs. low). In other species, individuals vary their calling based on predator type (e.g., carnivore vs. raptor). Calls such as these, given only in specific contexts, have been termed "functionally referential" if they also elicit predator-specific reactions in listeners. Functionally referential alarm calling has been well studied in a number of Old World monkeys and lemurs, but less so in New World primates. This study investigates the alarm call system of the tufted capuchin monkey (*Cebus apella nigritus*), in Iguazú National Park, Argentina. Predator decoys (felids, vipers, and raptors) encountered at various distances were used to determine the type of call that subjects give in different predatory contexts. Observations in natural situations were conducted to note whether or not these call types are given in any additional contexts. Results indicate that the species produces a unique call type (the "bark") in response to aerial threats, but the call type most commonly associated with terrestrial threats (the "hiccup") is frequently given in non-predatory contexts. The rate an individual gives this latter call seems to reflect risk-urgency, with only a single call given in low risk or non-urgent situations, but several calls given in higher-risk situations. Playbacks of these two call types indicate that they each elicit both predator-specific and generalized anti-predator behaviors. These observations demonstrate that the bark is a functionally referential aerial predator call while the hiccup is better seen as a non-functionally referential disturbance call which

reflects the caller's risk-urgency. Additional work with a third call type, the "peep", is needed to determine if this call is a functionally referential terrestrial predator call.

Introduction

Many gregarious birds and mammals produce alarm calls upon encountering a predator. These calls have the potential to alert conspecifics to the presence of danger and/or communicate to the predator that it has been detected (Klump & Shalter, 1984). While some species have a generalized alarm call system, producing similar calls in different threatening situations, other species demonstrate "situationally variable" alarm calls (reviewed for mammals in Fichtel & Kappeler, 2002). In the latter case, individuals may produce acoustically distinct call types, vary the number of calls given, and/or vary the intensity of calls based on the specific situation in which they are produced (Blumstein, 1999a). Such situationally variable calls can potentially evoke reactions in call receivers that are appropriate for the context in which they were given (e.g., Seyfarth et al., 1980a, b; Blumstein, 1999b; Rainey et al., 2004). Among those species that produce situationally variable alarm calls, two distinct types of call systems have been identified: those that vary based on the degree of urgency posed by the threat (e.g., high *versus* low) and those that vary based on threat type (e.g., carnivore *versus* raptor; termed "functionally referential": Macedonia & Evans, 1993).

In species with an urgency-based alarm call system, individuals vary their alarm call production based on their perceived degree of risk (Macedonia & Evans, 1993). For example, variation in alarm calling among yellow-bellied marmots (*Marmota flaviventris*) is explained by a combination of the distance from the caller to the predator and the type of predator that is present, but not strictly by predator-type (Blumstein & Armitage, 1997). Such risk is also reflected in call perception; high-risk alarms evoke high arousal responses (e.g., flee to burrow) in marmots more often than low-risk alarms, although the different calls do not evoke distinct reactions (Blumstein & Armitage, 1997; see also Warkentin et al., 2001; Leavesley & Magrath, 2005). While urgency-based alarm call systems have been recognized in the sciurid rodents for some time (reviewed in Fichtel & Kappeler, 2002; Caro, 2005; Blumstein, 2007a), such alarm call systems have more recently been reported in birds (Baker & Becker, 2002; Leavesley & Magrath, 2005; Templeton et al., 2005), suricates (*Suricata suricatta*; Manser, 2001), and, recently, bonnet macaques (*Macaca radiata*; Coss et al., 2007). In addition, Fichtel & Kappeler (2002) argued that the terrestrial predator-associated alarm calls of redfronted lemurs (*Eulemur fulvus*) and Verreaux's sifakas (*Propithecus verreauxi*) may reflect the caller's perceived threat-urgency because these calls were also given in non-predatory contexts characterized by high arousal.

Functionally referential alarm calls, in contrast to urgency-based calls, show both *context specificity* of call production and *stimulus independence* in call response (also referred to as perception specificity; Marler et al., 1992; Macedonia & Evans, 1993). Context specificity of production is demonstrated if only a narrow range of stimuli elicit the calls; this range can be as specific as a single species (e.g., leopard) or as general as group of species with common characteristics (e.g., any terrestrial threat; Blumstein, 1999a). However, the degree to which the calls should be context specific has not been quantitatively defined, and many studies claiming evidence of functionally referential signaling have not provided quantitative data on the contexts in which the calls are produced (e.g., Zuberbühler, 2000; Fichtel & Kappeler, 2002; Kirchhof & Hammerschmidt, 2006). Stimulus independence of call reaction is shown if the call alone evokes a reaction that would be appropriate if the supposed referent were present . Such perception specificity can be demonstrated through playback experiments conducted in the absence of the supposed referent (e.g., Seyfarth et al., 1980a, b; Kiriazis & Slobodchikoff, 2006). Based on this production and perception specificity, functionally referential calls in non-human animals have been argued to offer parallels to the semantics of human words (Evans & Marler, 1995), although the application of linguistic terminology to non-human vocalizations has been criticized (Owren & Rendall, 2001; see Zuberbühler, 2003 for review).

The two criteria of functionally referential signals are illustrated by the now classic studies of vervet monkeys (*Chlorocebus aethiops*) which indicated that not only do raptors, carnivores, and constricting snakes each elicit an acoustically distinct call type in this prey species (Struhsaker, 1967), but also that playbacks of each call type alone are sufficient to evoke predator-specific responses in receivers of the call (Seyfarth et al., 1980a, b). While referential alarm calls are more common in primates than other taxa (reviewed in Fichtel & Kappeler, 2002; Caro, 2005), there is support for such alarm call systems in both suricates (Manser, 2001; Manser et al., 2001) and several avian taxa (Evans et al., 1993; Seddon et al., 2002; Gill & Sealy, 2004). However, in at least one case (domestic chickens, *Gallus gallus*) it appears that callers may respond more to predator location than to predator type (Evans & Marler, 1995). Among primates, alarm calls that show both context specificity of production and stimulus independence of call response have been documented only in lemurs (Macedonia & Evans, 1993; Fichtel & Kappeler, 2002) and Old World monkeys (Cheney & Seyfarth, 1990), but not New World monkeys or apes.

A number of additional studies of situationally variable alarm calls in primates and rodents have tested only one of the two criteria of functionally referential calling, or have only partially tested for context specificity (by testing only whether different predator types elicit distinct call types, but not whether or not those calls are given in additional contexts; e.g., Zuberbühler, 2000, 2001). Among primates, both white-faced capuchins (*Cebus capucinus)* and white-handed gibbons (*Hylobates lar*) show some degree of context specificity in alarm call production (Digweed et al., 2005; Fichtel et al., 2005; Clarke et al., 2006; see also Crockford & Boesch, 2003; Notman & Rendall, 2005 for evidence of context specific call production in chimpanzees, *Pan troglodytes*), but the evidence of stimulus independent responses in these cases is limited because playback experiments were not conducted (see also Blumstein, 2007a for a review of similar cases among sciurid rodents). Fichtel et al. (2005) concluded that the observed variation in call production in white-faced capuchins could actually reflect variation in risk urgency. In another study of New World primates, alarm call playbacks conducted with two sympatric species of tamarins indicated that *Saguinus mystax* responded to each of the two call types commonly evoked by aerial and terrestrial stimuli respectively with predator-specific and stimulus independent reactions, while only aerial predator alarm calls elicited such responses in *S. fuscicollis* (Kirchhof & Hammerschmidt, 2006). While quantitative data regarding context specificity of alarm call production were not given for either of these tamarin species, the authors did report that the terrestrial predator alarms of *S. fuscicollis* were sometimes given in non-predatory contexts, including aggressive encounters with conspecifics (although this could potentially be attributable to "deceptive" alarm calling; see Chapter 6). Thus no previous study of the alarm call system of any New World primate has demonstrated that the calls meet both of the criteria to be considered functionally referential.

Demonstration of both production and perception specificity is important because situational variation in call production does not necessarily lead to distinct responses in call receivers (Blumstein, 1995) and predator specific responses to alarms can be elicited by calls that are not specific to predator encounters (e.g., Fichtel & Kappeler, 2002). In addition, because urgency-based call systems may have been misidentified as functionally referential systems due to the differences in risk typically associated with different predator types (cf., Davis, 1991; Blumstein & Armitage, 1997), it is important to explicitly consider risk urgency when investigating a species' alarm call system. It should also be noted that functionally referential and urgency-based call systems are not mutually exclusive (Marler et al., 1992). Combined functionally referential and urgency-based alarm call systems have been identified in suricates, who produce different call types in response to aerial and terrestrial predators respectively, but with also vary the acoustic structure of alarm calls based on the urgency of the threat (Manser, 2001; Manser et al., 2001).

This study experimentally tests whether variation in alarm call production and response in a New World primate, the tufted capuchin monkey (*Cebus apella nigritus*), in Iguazú National Park, Argentina supports the existence of an urgency-based and/or a functionally referential alarm call system in this species. Previous research has documented that the food calls of capuchins in this population show both production and response specificity and are therefore functionally referential (Di Bitetti, 2003). A comprehensive investigation of alarm calling in this species thus provides the opportunity to determine the degree to which this species uses functionally referential calls.

To address questions regarding alarm call production, the study subjects were observed in experimental contexts wherein they were presented with models of raptors, felids, and snakes (including both vipers and non-venomous snakes) to determine the types of calls and rates of calling within a bout in response to these three stimulus types. These experiments were complemented with observations in natural contexts to determine if these call types are produced in any additional contexts. If the alarm calls of tufted capuchins are functionally referential, then individuals should vary their calling in reaction to different threat categories (i.e., aerial vs. terrestrial or raptor vs. carnivore vs. snake), and these calls should not be given in additional contexts (i.e., production should be context specific). If capuchin monkeys have an urgency-based alarm call system, then it is predicted that calling behavior will vary with the immediacy of the threat facing the caller.

To address questions related to call perception, playbacks of the call types elicited by the predator models were conducted. If capuchin alarm calls are functionally referential, then playbacks of calls given in response to particular threats should elicit anti-predator behaviors appropriate for that threat-type. Alternatively, if capuchin alarm calls are purely urgency-based (i.e., not functionally referential), then qualitatively distinct responses should not be elicited by playbacks of these calls. Although a number of studies have shown that high-risk calls in urgency-based alarm systems evoke high-arousal responses in listeners (e.g., Warkentin et al., 2001; Leavesley & Magrath, 2005; Templeton et al., 2005), a lack of such findings does not necessarily indicate a lack of support for urgency-based alarm calls; a call receiver’s perceived risk-urgency may differ from that of the caller’s if additional contextual information (e.g., the receiver’s distance to the caller or height from the ground) affects such urgency (see Leger & Nelson, 1982; Fischer & Hammerschmidt, 2001). This study thus aims to identify the factors that affect a call receiver’s perceived risk.

Methods

Study Site and Subjects

Data were collected from July through September 2004 and May 2005 through December 2006 in Iguazú National Park, Argentina (25°40'S, 54°30'W). The site sits at the southwestern edge of the South American Atlantic Forest and is characterized by semi-deciduous and sub-tropical forest (see Chapter 1; Di Bitetti et al., 2000 for further description of the study site).

Tufted capuchins are small-bodied (2.5-3.6 kg; Smith & Jungers, 1997), diurnal, and omnivorous primates (Terborgh, 1983; Brown & Zunino, 1990) that live in groups of 7-30 individuals (Di Bitetti, 1997). The population is highly arboreal, with individuals spending most of their time in the mid to lower canopy and less than 3% of daytime activity occurring on the ground (Wheeler unpublished data). Data were collected on three fully habituated groups ("Macuco": 23-28 individuals; "Gundolf": 15 individuals;"Guenon": 9 individuals). All individuals were easily recognizable based on physical characteristics and were of known age and sex.

Capuchin monkeys at Iguazú face a number of aerial and terrestrial threats. The likely predators include three felid species (jaguars, *Panthera onca*; pumas, *Felis concolor*; and ocelots, *Leopardus pardalis*), tayras (*Eira barbara*), and two species of raptors (hawk eagles: *Spizaetus ornatus* and *S. tyrannus*; see Hirsch, 2002; Di Bitetti et al., 2006 for further descriptions of predators at the study site). Three species of vipers (*Bothrops neuwiedii, B. jararaca,* and *Crotalus durissus*) are also found at the site (Martinez et al., 1992); while these venomous snakes pose a mortal threat to capuchins, they are unlikely to prey upon them.

Tufted capuchins produce at least three acoustically distinct call types in response to predators and snakes (Figure 2.1), each of which is easily distinguishable by ear. Two of these, the "bark" (Figure 2.1a) and the "hiccup" (Figure 2.1b.), were described by Di Bitetti (2001a) and labeled the "aerial predator alarm call" (APAC) and the "ground predator alarm call" (GPAC) respectively. *Ad libitum* observations by Di Bitetti (2001a) indicated that individuals normally produced only a single APAC in a bout and that the calls were elicited exclusively by flying stimuli, although the possibility that the calls reflect risk-urgency cannot be eliminated based on these observations. In contrast, the bouts of GPACs are characterized by repeated calling and are elicited not only by felids but also in response to conspecific aggression and, possibly, venomous snakes (Di Bitetti, 2001a). Di Bitetti (2001a) also noted that a call not significantly different in acoustic structure from the GPAC (although categorized as a separate call, the "hiku", due to differences in context of production and responses by conspecifics) is frequently produced while an animal forages in suspensory positions. Because of the lack of acoustic variation between the GPAC and the hiku, they are here considered a single call

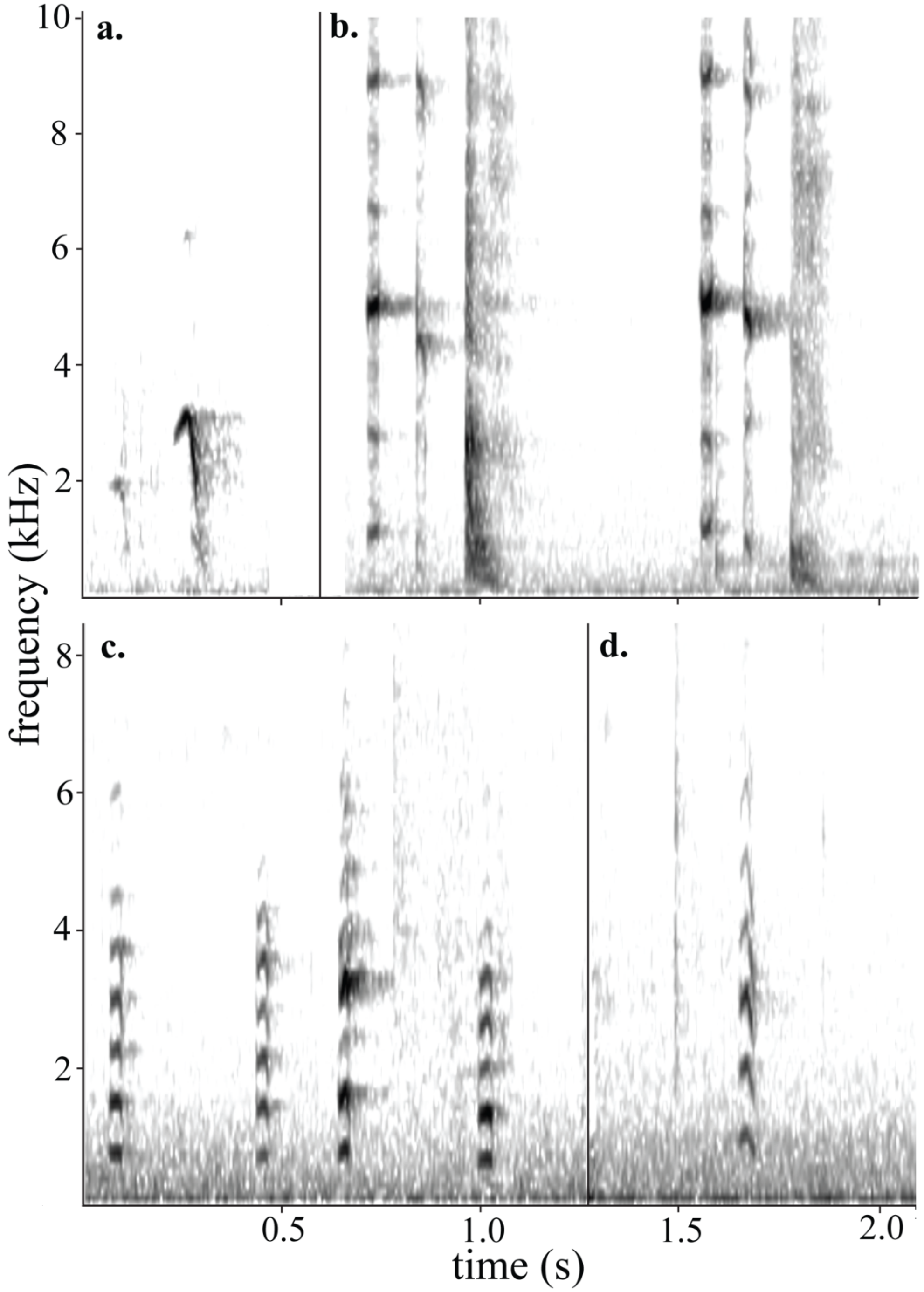

Figure 2.1. Spectrograms of characteristic alarm calls: a) one bark given by an adult male in response to a flying eagle model, b) two hiccups given by a juvenile female in response to an ocelot model, and c) four peeps given by an adult female in response to a venomous snake model; d) a single contact note given by an adult female while foraging. Additional descriptions and spectrograms of calls a, b, & d are provided in Di Bitetti (2001).

type (i.e., the hiccup). In addition to these two alarm call types identified by Di Bitetti (2001a), a third call type, the "peep" (Figure 2.1c), was identified during the course of the current study. While this call appears to be acoustically similar to the species' contact note (CN; Figure 2.1d), it is differentiated from the CN by the rapid repetition of calls over a period of a few seconds to several minutes (as opposed to a single CN given on average every 20 seconds, although considerable variation exists in this regard; Di Bitetti, 2001a). Peeps and hiccups were often given together as a single call series in response to potentially threatening stimuli. For these reasons, a call was considered a peep rather than a contact note if an individual produced four or more notes in a two second period, or if the call was given between two hiccups separated by less than five seconds. Although no quantitative data are available on call amplitude, both the bark and hiccup appear to vary considerably in call intensity, while peeps are always relatively low-intensity calls.

Call production

To determine if alarm call production by tufted capuchins varies situationally, indicating either an urgency-based or a functionally referential call system, the contexts in which all alarm call types were given by focal animals were noted during experimental predator encounters. During experiments, study subjects were presented with models of perched or flying hawk eagles, ocelots, vipers, or non-threatening snakes (see Figure 2.2). During most experiments, audio recordings were made and analyzed to determine the number of calls of each type that were given following the detection (described in further detail below).

Predator model experiments were conducted when the group was moving in a consistent direction. Models were placed 50-150m in front of the group in the direction of movement. Perched raptor models were hung from tree branches at a height of 4 to 12m by a rope thrown over the branch. Experiments with flying eagle models were conducted at sites prepared beforehand; the model glided down a fishing line tied between two tree trunks from a height of 10-15m down to 1.5m as the group approached the site, but before any individuals detected the model. Ocelot models were placed on the ground or in trees at a height of up to 5m while snake models were always placed on the ground.

Figure 2.2. Photographs of predator and snake models (top) and the live animals (bottom): a) *Leopardus pardalis*; b) *Bothrops neuwiedi*, and c) *Spizaetus ornatus*. Photograph of live ocelot: J. Warwick. Photographs of live snake and raptor: C. Janson.

Models were normally placed in dense vegetation in order to ensure that the individuals in the vanguard position were not always the first to detect. Because such a placement normally resulted in detections from short distances, thereby mimicking high-urgency situations (see below), the models were sometimes positioned in areas with greater visibility to increase the likelihood of detection from a greater distance. To prevent the monkeys from habituating to the models, a particular model type (e.g., raptor, felid, snake) was not used for one week following a detection, while a specific model was not used more than once in any fifteen day period; in most cases, each model was used only once per month with each group.

Continuous focal sampling (Martin & Bateson, 2007) was employed by three observers during the predator model experiments to note all vocalization types the study subjects gave in response to the predator models as well as the caller's height and horizontal distance to the model when the vocalizations began. Focal animals were any adult individuals likely to detect the model (individuals within 15m). Focal animals were followed until they moved more than 15m from the model or a non-focal individual approached closer to the model, at which point that second individual became the focal animal. A vocalization was considered to be in response to the model if the caller was looking at the model or employing an appropriate escape response while calling.

Vocalizations given during the predator model experiments were recorded onto a Sony MZ-NH 900 Hi-MD MiniDisc recorder or a Marantz PMD-660 digital audio recorder (with a Lexar 2 GB Compact Flash memory card) using either a Sennheiser ME-67/K6 or MKH-60 directional microphone. In nearly all cases, vocalizing animals were 5-10m from the microphone. All calls were recorded at a sampling rate of 44.1 kHz with a 16 bit resolution and saved in an uncompressed digital format. Recordings were analyzed to determine the number of each alarm type that was given in the 10 second period beginning with the initiation of the first call. A 10 second period was chosen for two reasons. First, the initial calls given should be the most likely to reflect the caller's perceived risk (see Blumstein & Armitage, 1997). Second, because alarm calling among tufted capuchins tends to attract conspecific mobbers (Wheeler, 2008) who often produce alarms once they have detected the predator model, calls given after this initial period could not always be easily assigned to the first caller. Only those call bouts that did not overlap with calls from other group members and which were of sufficiently high quality (e.g., with low background noise) were used to determine how many calls were given.

To determine if the call types produced in response to the predator models were given in any additional (i.e., non-predatory) situations, two-minute continuous focal samples were conducted in natural contexts. Focal samples were conducted on all adults and juveniles over two years of age throughout the day, but no such data were collected in the two hours following predator model or playback experiments. Focal animals were chosen opportunistically, although an effort was made to choose individuals who were undersampled, and no individual was sampled more than once in a one hour period. If a focal animal gave an alarm call, the number of calls given and the eliciting stimulus were noted. Eliciting stimuli were divided into four main categories: 1) actual/potential aerial threats, 2) actual/potential terrestrial threats, 3) any other stimuli, and 4) unknown. Actual threats included predators and vipers. Potential threats included alarm calls of conspecifics or heterospecific animals as well as stimuli which could be reasonably misclassified as a predator or viper. Stimuli included for the latter category included large, non-predatory birds in flight (including vultures and toucans), medium to large-sized animals in the understory (including large rodents and deer), and non-venomous snakes. Misclassification of non-predatory birds and mammals is expected in a dense forest where callers may not be able to identify the exact nature of the stimulus (Evans, 1997). Such stimuli were classified as “other” (not potential predators) in cases where the focal animal had an unobstructed view of the stimulus, i.e., only if it is reasonable for the animal to have misclassified the innocuous stimulus as threatening. Non-predatory stressors included conspecific aggression, attacks by stinging insects, and precarious positional behaviors; the latter included suspensory positions and the use of unstable substrates (dead vegetation or substrates less than 1 cm in diameter).

Production of each alarm call type was considered to be context specific if at least 95% of the calls were given in response to a particular threat category (e.g., actual or potential terrestrial threats). Calls given by focal animals in both experimental and natural contexts were combined to determine if production was context specific.

Call response

To determine if alarm calls elicit either predator-specific responses or indicate variation in risk perception in call receivers, observations of focal animals following the playback of conspecific alarm calls were made. Only alarm calls produced in response to a known threat (i.e., the predator models or potential predators encountered in natural contexts) were used as playbacks. Recordings of actual call sequences given in response to threatening stimuli were used for playbacks (rather than modified sequences of calls at particular intervals) and only the first calls from the bout were used. Because barks were normally produced singly or in pairs while hiccups were given repeatedly, playbacks of these calls types reflected this, therefore creating what may be an important difference between these playback types. Due to a lack of a sufficient number of recordings of sequences of peeps of sufficient quality for playbacks, I was unable to conduct enough playback experiments to test for responses to this call type. Likewise, due to a lack of quality recording of barks or hiccups produced in low-urgency threats, all recordings played back were from high to medium risk-urgency situations. In addition to playbacks of alarm calls, playbacks of non-alarm vocalizations of sympatric avian taxa and alarm calls played in reverse were conducted as control experiments. Playbacks were conducted with a compact-disc player or an Apple iPod connected to a RadioShack (#277-1008) or Saul Mineroff Electronics (SME-AFS) amplified speaker hidden in vegetation at a height of 2 ± 0.5m. Call intensity was adjusted to mimic that observed during the predator model experiments (75-85 dB as measured by a RadioShack 33-2055 digital sound level meter placed 1 meter from the speaker). Only a single playback was conducted per day and experiments were conducted only in cases when no alarm calls had been heard for at least 15 minutes and when no stimuli which could be mistaken for predators were present (e.g., small terrestrial mammals or low-flying vultures).

While I initially intended to use a unique call sequence for each playback, a lack of recordings of sufficiently high quality prevented this from being possible. Thus some call series were used for more than one playback experiment, although these were spaced out by more than a month in order to ensure that individuals did not habituate to a particular call. A total of 10 distinct bouts of barks and 11 of hiccups were used for the 19 bark and 20 hiccup playbacks.

Adult and juvenile animals resting, grooming, or foraging (with little or no directional movement) within 5-30m of the playback speaker were chosen as focal animals. Focal individuals were videotaped with a Canon Elura 80 MiniDV camcorder for at least 20 seconds prior to the initiation of the playback and for up to one minute following the playback. However, because of the density of the forest and the fact that the playbacks often elicited movement in the focal animals causing them to move out of view, only the first 10 seconds following the initiation of the playback were analyzed; increasing the amount of time analyzed following the playback greatly decreased the number of analyzable experiments. Following the playback, notes were taken on the focal animal's height and distance to the speaker at the initiation of the playback and its qualitative reaction to the playback. In addition, a map was drawn indicating the position of the focal animal, the video camera, and the playback speaker. Videos were analyzed to determine if focal animals performed any appropriate anti-aerial predator (e.g., look up) , anti-terrestrial predator (e.g., run up) , or generalized anti-predator behaviors (e.g., look towards the caller). All behaviors considered are listed and defined in Table 2.1. Latency to these reactions was determined using Microsoft Windows Movie Maker v. 5.1 to count the number of frames (15 frames per second) from the initiation of the playback to the initiation of each behavior.

Statistical analyses

To test the factors that affect call production in experimental contexts, a multinomial logistic regression was used with call type as the dependent variable and stimulus category (raptor, felid, or snake) and risk-urgency (high, medium, or low) as the predictor variables (Tabachnick & Fidell, 2001). Each of the three risk-urgency categories is defined in terms of threat type and detection distance in Table 2.2. Predators which could likely attack immediately from their current position were considered a high urgency threat, while those at greater distances were considered medium or low urgency threats. Venomous snakes were always considered a low urgency threat because these species seem to be extremely unlikely to pursue capuchins, and in no case did a capuchin

Table 2.1. List of behaviors falling into the different anti-predator behavioral categories and their definitions.

	behavior	definition
anti-aerial predator	look up	looking beyond immediate substrate, with head at least 45° above the horizontal
	run into cover	quick movement to an area with a vegetation density greater than that of the point of initiation
generalized anti-predator	run horizontal	quick horizontal movement of at least two meters
	approach speaker	movement within 45° of a straight line between the focal animal and the speaker
	scan	looking beyond immediate substrate in any direction other than up, down, or toward the speaker
	look to speaker	looking beyond immediate substrate, and within 45° of a straight line between the focal animal and the speaker
anti-terrestrial predator	look down	looking beyond immediate substrate, with head at least 45° below the horizontal
	run up	quick vertical movement of at least two meters

Table 2.2. The three level classification of risk-urgency used in this study, and the threat types/distance combinations that define each level. Note that this classification was applied only to threat detections that occurred in experimental contexts, where detection distances could be reliably measured.

threat urgency	threat type/distance
high	flying stimuli at ≤ 25m stationary predators at ≤ 5m
medium	flying stimuli at 25-100m stationary predators at 5-25m snake at ≤ 1m
low	snake at ≥ 1m stationary predators at ≥ 25m

detect a venomous snake within a likely striking distance. Context specificity of call production was determined by categorizing all alarm calls given by focal animals in both natural contexts and during the predator model experiments and assigning them to one of three contexts: actual/potential aerial threat, actual/potential terrestrial threat, or other (defined above). To be conservative, calls produced in unknown contexts were classified as “other”. Production of a call type was considered to be specific for a particular threat category if a binomial test indicated that the number of calls given in that context did not differ significantly from an expected value of 95%; this value was chosen because it requires that call production approaches total specificity, but allows for some observer error in context classification. Non-parametric Mann-Whitney U tests were used to test for differences between two categories (e.g., felids versus snakes) in the number of calls produced in the first 10 s of a calling bout, while Kruskal-Wallis tests were used to test for such differences between three or more groups (e.g., the three levels of risk-urgency). To test for differences in the likelihood of reaction to playbacks based on various contextual variables, either a chi-square test of independence (if all cells had values of five or greater) or a Fisher’s exact test (if some cells had values of less than 5) was used. Variables examined for these analyses included the playback type, the caller’s risk-urgency at the time the playback recording was made, the focal animal’s height in the canopy (low: ≤ 7 m; high: 7 m or higher), and the focal animal’s distance to the playback speaker (near: ≤ 12 m; far: 12 m or more). Because only a single recording of a bark given in a low-urgency situation and no such recordings of hiccups were available, playbacks of medium and low-urgency calls were pooled for these analyses. For cases when focal animals employed an anti-predator behavior following a playback, a Kendall’s correlation was used to test for a relationship between the latency to the caller’s reaction and each of its height and distance to the playback speaker. This was conducted for both the latency to any anti-predator reaction, and the latency to look towards the speaker, which was the most common reaction to all playback types. All analyses were conducted with SPSS 15.0 with the exception of the Fisher’s exact test, which were conducted with the Preacher & Briggs interactive calculator (Preacher & Briggs, 2001).

Results

Call production

Call types given in experimental contexts

Vocal reactions to raptor models were recorded on 13 occasions, to ocelot models on 35 occasions, and to snake models on 48 occasions (Table 2.3; see Wheeler, 2008 for discussion of detections which did not result in a vocal response). The call type (i.e., bark, hiccup, peep, or combination of hiccups and peeps) that an individual produced in response to a model was better explained by stimulus category (i.e., raptor, felid, or snake; multinomial logistic regression: $N=96$, $\chi^2=62.96$, $df=6$, $p<0.0001$) than by risk-urgency (same logistic regression: $\chi^2_6=4.53$, $df=6$, $p=0.606$; Table 2.3, Figure 2.3). Focal animals produced only barks, and never hiccups or peeps, in response to models of flying and perched raptors as well as other flying stimuli in natural contexts (Figure 2.3a). In contrast, focal animals produced hiccups, peeps, or a combination of the two call types in response to both felid and snake models, but barks were never given in this context (Figure 2.3a). The urgency of the threat presented by the predator or snake model and the type of call given were less tightly associated; barks were given at all levels of risk (including the only low-risk raptor detection resulting from the experiments), as were both hiccups and peeps, although peeps given in high risk situations were always accompanied by hiccups (Figure 2.3b).

Anti-predator calls given in natural contexts

In addition to the alarms given in these experimental contexts, another 141 alarm calls were given by focal animals in natural contexts (Table 2.4). When these data are factored in, clear differences between the three alarm calls types emerge in the degree to which the production of the calls is context specific. Seven barks were given by focal animals in natural contexts (Table 2.4). Six of these were in response to flying stimuli; only one of these was a small raptor that may have posed a threat to infants (but not to the adult male who called), while the others fell into the category of potential aerial threats. The eliciting stimulus could not be determined in the seventh case. When these calls are considered together with the calls given in the experimental contexts, 19 of 20 observed

Table 2.3. Vocal responses during experimental exposure to models of raptors, felids, and snakes at different levels of risk-urgency. See Table 2.2 for definitions of risk-urgency.

	perched raptors			flying raptors			felids			vipers		other snakes		total
call type	h	m	l	h	m	l	h	m	l	m	l	m	l	
barks only		7	1	5										13
hiccups only							4	19	1		8		7	39
peeps only								4			14		4	22
hiccups plus peeps							3	4			7		8	22

Shaded cells indicate that no detections of threat type at that particular level of risk-urgency;
h = high risk-urgency, m = medium risk-urgency, l = low risk-urgency

Table 2.4. Stimuli which elicited barks and hiccups in natural contexts. Note that aerial and terrestrial threats include all potential threats as defined in the text.

call type	aerial threats	terrest threats	other	unk	total
barks	6			1	7
hiccups		7	96	31	134

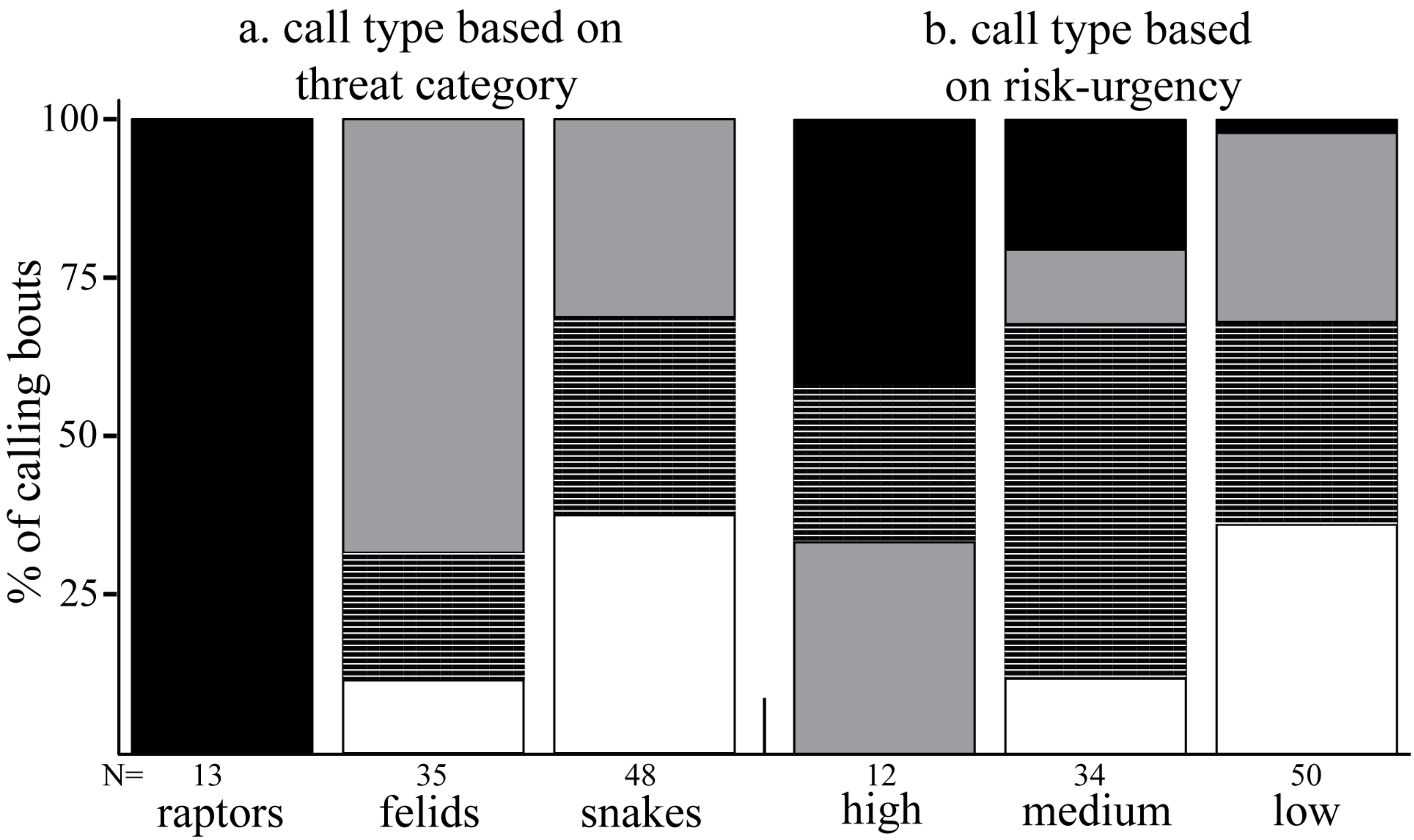

Figure 2.3. Stacked bar graphs showing call types given to: a) different threat types, and b) different levels of risk-urgency. Black bars = barks only, grey bars = hiccups only, lined bars = both hiccups and peeps, white bars = peeps only. The call type given was predicted by the threat category but not by the caller’s risk-urgency.

barks (95%) were associated with an actual or potential aerial threat, a value which does not significantly differ from the expected value for a context specific call (binomial test: $p=0.736$).

Focal animals were observed to produce hiccups in natural contexts on 134 occasions (Table 2.4). Only seven of these (5.2%) were in response to potential threats: one in response to a medium-sized terrestrial rodent (agouti, *Dasyprocta azarae*) which had suddenly burst through the understory, three following hiccups given by other group members, and following agouti grunt vocalizations (which seem to be the species' alarm call). Of the remaining calls, the vast majority (N=95; 70.9%) were given in situations in which the caller was employing a precarious positional behavior; this included using a small (<1 cm diameter) or otherwise unstable (e.g., dead bamboo) substrate, reaching for a food item while in a suspensory posture, and jumping between or bridging a gap. A single bout (0.7%) was given by an individual while receiving aggression from another groupmate. No eliciting stimulus could be identified in 31 cases (23.1%). When the contexts in which these calls were given are combined with those given during the predator model experiments, only 56 of 190 hiccups (35.9%) were in response to actual or potential terrestrial threats, a number significantly less than expected for a context specific call type (binomial test; $p<0.0001$).

Focal animals were never observed in a natural context to produce a call series that was perceptively similar to the peeps that were given in response to the ocelot and snake models. However, given the ubiquity of the acoustically similar contact call, and the inconspicuous behavior that normally accompanies the production of contact calls, it is possible that such calls were produced at a rate similar to that observed during bouts of peeps, but that this went unnoticed. If the lack of observations of calls similar to peeps indeed reflects a lack of production of such call series, then it appears that peeps are indeed context specific, with all 49 observed bouts occurring in the context of a terrestrial threat. However, this specificity referred only to terrestrial threats generally, and not specific types of threats; sixteen bouts were given in response to felid models, while 21 were given to venomous snake models and 12 to non-venomous snake models. These calls were most often given together with hiccups; bouts of peeps alone (i.e., without hiccups in the first 10 seconds) were observed on 22 occasions, four of these were in response to felid models, 14 to venomous snake models, and four to non-venomous snakes. However, in all of these cases except four involving non-venomous snakes and one with a viper, hiccups were given within the first 30 seconds following the detection of the model (but not within the first 10 seconds as considered here).

Call rate

In addition to variation in the types of calls that were produced, there was also considerable situational variation in the number of alarm calls produced by a caller in a single calling bout. The number of barks produced by an individual in the first 10 seconds of a calling bout varied from 1 to 9. Although fewer calls tended to be given to high-urgency aerial predators (all of which were in flight; mean ± SE: 1.60 ± 0.24 calls) than to medium or low-urgency aerial predators (all of which were perched; 3.13 ± 1.0 calls), this difference was not significant (Mann-Whitney U test: $Z=-0.971$, $N_{high}=5$, $N_{med/low}=8$, $p=0.332$). The number of hiccups an individual gave in the first 10 seconds of a calling bout varied from 1 to 11. Individuals produced significantly more hiccups in response to felids (4.88 ± 0.8 calls) than to snakes (1.1 ± 0.2 calls; Mann-Whitney U test: $Z=-3.514$, $N_{felid}=26$, $N_{snake}=23$, $p<0.001$; Figure 2.4) and in response to high urgency relative to lower urgency threats or in non-urgent contexts (high risk: 7.40 ± 1.7 calls, N=5; medium risk: 5.50 ± 0.9 calls, N=16; low risk: 1.75 ± 0.2 calls, N=16; non-urgent: 1.04 ± 0.2 calls, N=95; Kruskal-Wallis test: $\chi^2=86.07$; df=4; $p<0.001$; Figure 2.5). The number of peeps an individual gave during the first 10 seconds of a calling bout varied from one to 23, but did not vary significantly across situations. The number of peeps given in response to felids (6.80 ± 1.6 calls) did not differ from that given to snakes (7.33 ± 1.6 calls; Mann-Whitney U test: $Z=-0.334$, $N_{felid}=15$, $N_{snake}=15$, $p<0.739$), and there was no variation in the number of peeps based on the levels of risk-urgency experienced by the caller (high risk: 5.00 ± 3.5 calls, N=3; medium risk: 7.25 ± 1.8 calls, N=12; low risk: 7.33 ± 1.6 calls, N=15; Kruskal-Wallis test: $\chi^2=1.02$; df=2; $p=0.601$). Finally, when considering an entire call series consisting of both hiccups and peeps (as this was the only observed combination of alarm call types), felids elicited significantly more calls in the first 10 seconds (8.9 ± 0.8 calls; N=26) than did snakes (5.9 ± 1.2 calls, N=23; Mann-Whitney U test: $Z=-3.175$, $N_{felid}=26$, $N_{snake}=23$, $p=0.001$) as did higher levels of urgency (high risk:

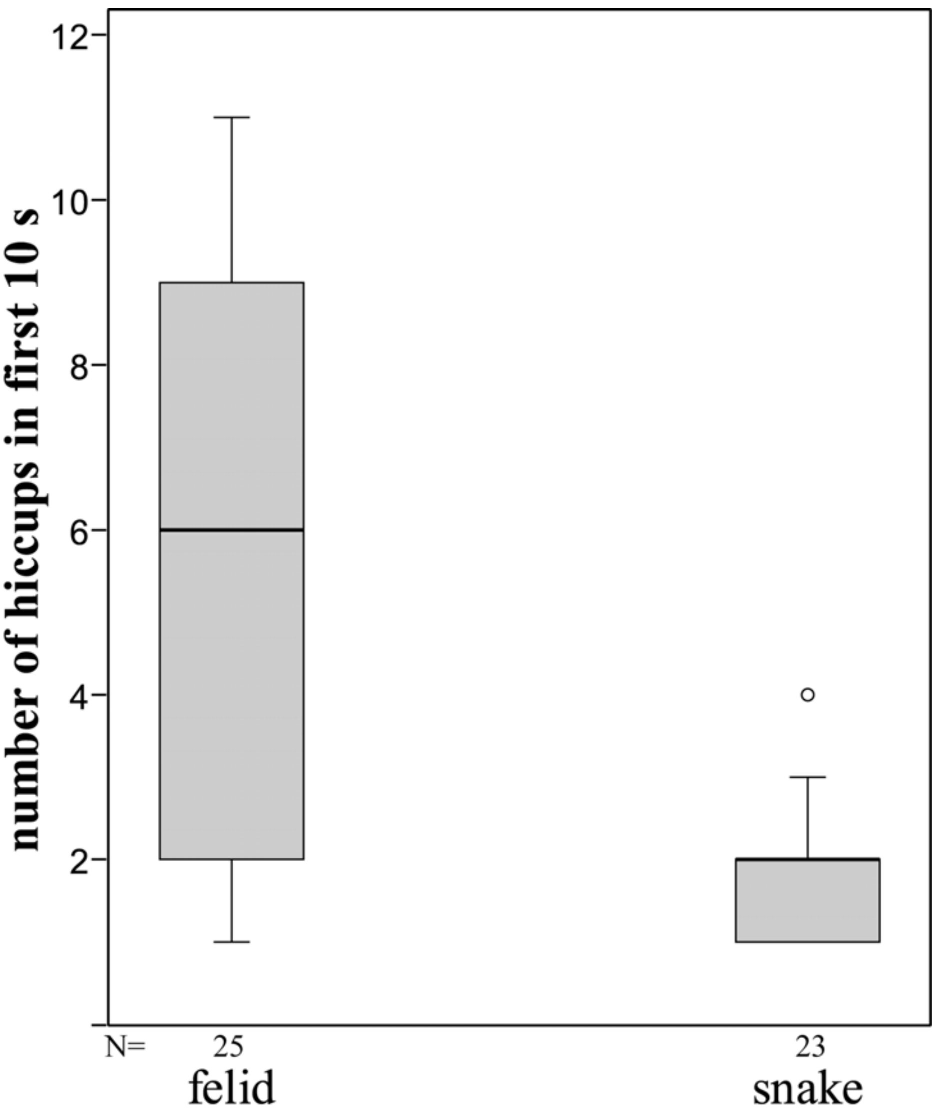

Figure 2.4. Box plots showing the number of hiccups given in the first 10 s of calling bouts elicited by felids versus snakes. Box plots show median (dark line), first and third quartiles (box), range (whiskers), and extreme values (open circles). Felids elicited significantly more calls in the first 10 s than did snakes.

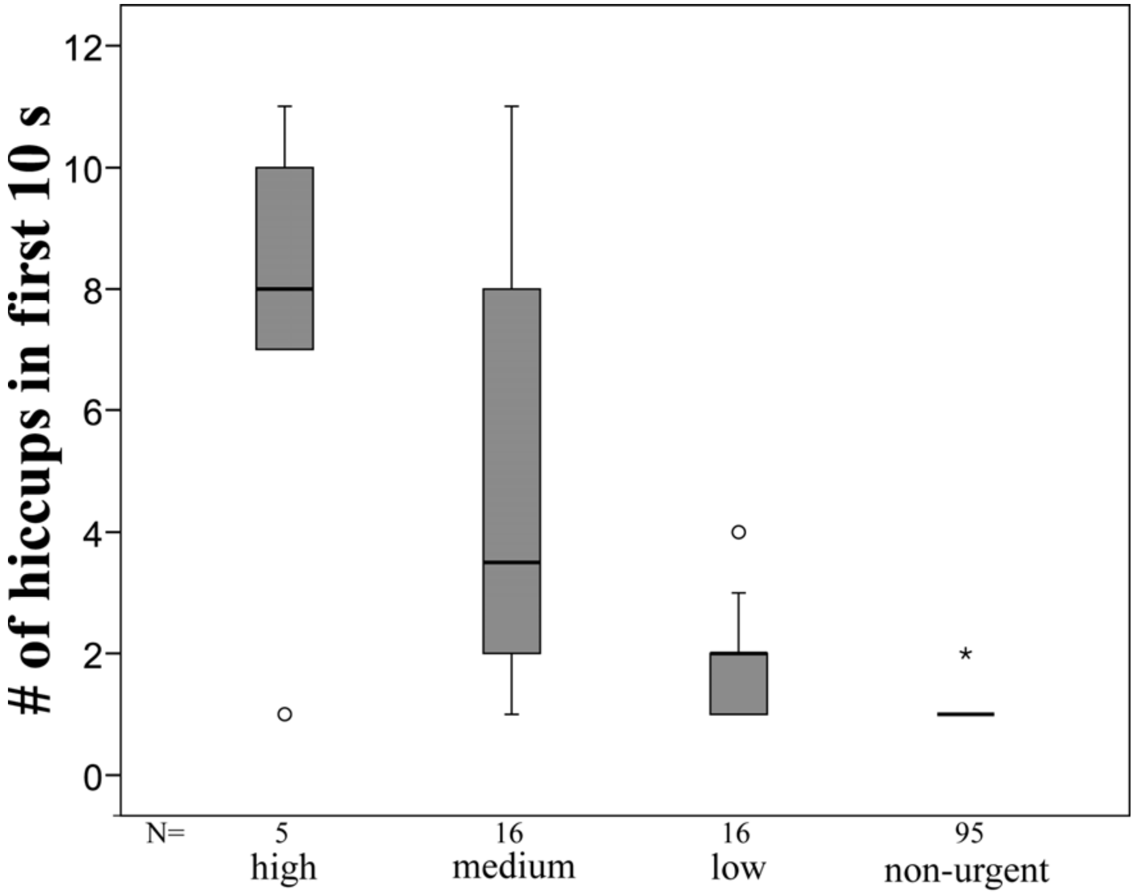

Figure 2.5. Box plots showing the number of hiccups in the first 10 s of calling bouts given in response to stimuli representing the three levels of risk-urgency as well as those given in non-urgent contexts. Box plots show median (dark line), first and third quartiles (box), range (whiskers), extreme values (open circles), and outliers (asterisks). Significantly more calls were produced in the first 10 s in higher risk situations relative to lower risk situations.

10.40 ± 1.2 calls, N=5; medium risk: 9.05 ± 1.0 calls, N=19; low risk: 5.91 ± 1.2 calls, N=23; Kruskal-Wallis test: χ^2=14.74; df=2; p=0.001).

Call response

Anti-predator reactions were employed by focal animals more often following playbacks of alarm calls (i.e., barks and hiccups; 32 of 39 experiments) than following control playbacks (9 of 18 experiments; chi square test of independence: N=57; χ^2_1=6.27, p=0.016). However, there was no difference in this regard between the two alarm call types; focal animals employed an anti-predator behavior following 16 of 19 bark playbacks, and 16 of 20 hiccup (Fisher's exact test; p=1.0). The urgency faced by the caller when the playback call was recorded did not affect the likelihood that the listener would respond; focal animals did not respond more often to barks and hiccups given when the caller faced a high risk-urgency (18 of 20 playbacks) than when facing a medium or low risk-urgency (12 of 17 playbacks; Fisher's exact test: p=0.140). The same was true when the two alarm call types were examined individually. The number of responses to barks from high-urgency situations (12 of 13 playbacks) did not differ from that of low and medium-urgency situations (4 of 6 playbacks; Fisher's exact test: p=0.222), nor did they respond to hiccups produced in high-urgency contexts (6 of 7 playbacks) more than those given when the caller faced a medium risk-urgency (10 of 13 playbacks; Fisher's exact test: p=0.561). Although the trend in both of these latter cases is in the direction predicted if higher urgency calls are more likely to elicit reactions than lower urgency ones, the difference remained non-significant even when combining these two results using Fisher's method for combining probabilities (Sokal & Rolf, 1996; χ^2=4.184; df=4; p=0.382)

Types of reactions

Playbacks of barks and hiccups elicited qualitatively distinct reactions in the first 10 seconds following the playback (Figure 2.6; Table 2.5). When compared to the control experiments, focal animals responded to playbacks of barks with aerial predator-specific behaviors (one-tailed binomial test: p=0.002) and generalized anti-predator behavior (p=0.009) more often than expected, but these calls never elicited anti-terrestrial predator behaviors. In contrast, hiccups evoked terrestrial predator-specific (p=0.004) and

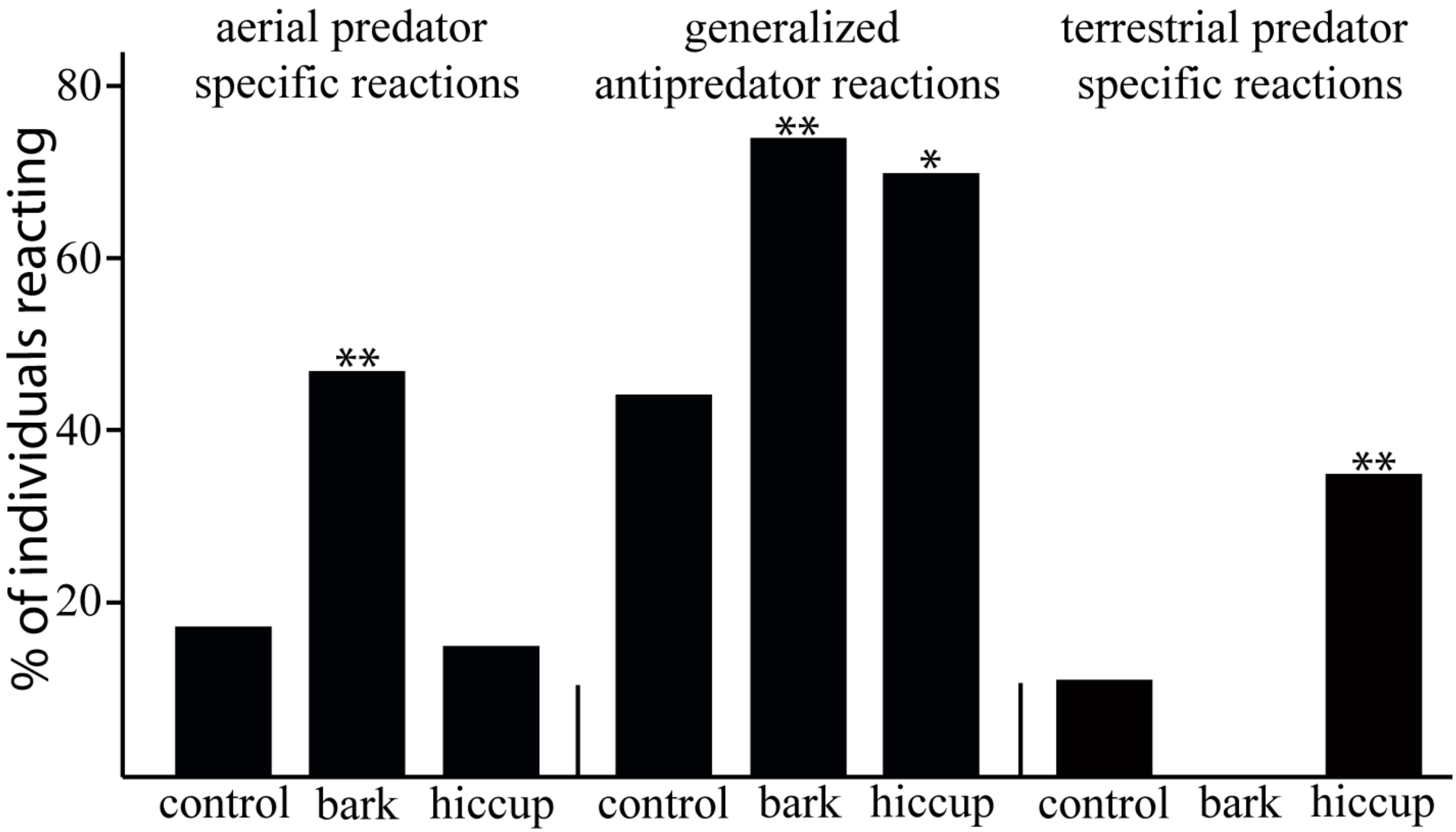

Figure 2.6. Bar graphs showing the percent of playbacks of controls (N=18), barks (N=19), and hiccups (N=20) which elicited one or more aerial predator-specific behaviors, generalized anti-predator behaviors, and terrestrial predator-specific behaviors within 10s of playback initiation. Asterisks indicate cases in which barks or hiccups elicited a particular type of reaction significantly more than expected based on the reactions to controls: *p<0.05, **p<0.01.

Table 2.5. Anti-predator behaviors elicited by the alarm call playbacks. Note that the rows do not sum to 100% because some playbacks elicited more than one anti-predator behavior.

		anti-aerial predator				generalized anti-predator					anti-terrestrial predator		
	# of PBs	no rxn	lk up	run to cover	≥1 AAP	run horiz	apr spkr	scan	lk spkr	≥1 GAP	run up	look down	≥1 ATP
control	18	9	3	0	3	1	1	2	6	8	0	2	2
bark	19	3	7	2	9	1	0	6	8	14	0	0	0
hiccup	20	4	2	1	3	0	5	0	14	14	3	5	7

PBs = playbacks; no rxn = no reaction; lk up = look up; AAP = anti-aerial predator specific behavior; apr spkr = approach playback speaker; lk spkr = look towards playback speaker; GAP = general anti-predator behavior; ATP = anti-terrestrial predator specific behavior generalized anti-predator behaviors ($p=0.017$) more often than expected, but the number of aerial predator-specific responses did not differ from the control ($p=0.550$).

Latency to react

When considering only those cases when individuals did react to the playbacks, there were differences between the playback treatments in the latency in which they reacted (Figure 2.7). Focal animals responded more quickly to alarm calls (i.e., barks and hiccups; mean ± SE: 1.59 ± 0.32 s) than to controls (mean ± SE: 3.44 ± 0.87 s; two-tailed Mann-Whitney U test: $Z= -2.443$, $N_{alarm}=32$, $N_{control}=9$, $p=0.013$). The latency of response to barks (mean ± SE: 0.96 ± 0.17 s) did not differ from that to hiccups (mean ± SE: 2.23 ± 0.58 s ; two-tailed Mann-Whitney U test: $Z= -1.131$, $N_{bark}=16$, $N_{hiccup}=16$, $p=0.258$), but was significantly less than that to controls (mean ± SE: 3.44 ± 0.87 s ; two-tailed Mann-Whitney U test: $Z= -2.950$, $N_{bark}=16$, $N_{control}=9$, $p=0.003$). In contrast, there was no difference between hiccups and controls in latency to respond (two-tailed Mann-Whitney U test: $Z= -1.448$, $N_{hiccup}=16$, $N_{control}=16$, $p=0.148$). The latency of response to each of barks and hiccups did not depend on the caller's risk-urgency. The latency to respond to playbacks of hiccups originally produced in high risk-urgency situations (mean ± SE: 1.98 ± 1.01 s) did not differ from those produced in medium-urgency situations (mean ± SE: 2.37 ± 0.74 s; one-tailed Mann-Whitney U test: $Z= -0.976$, $N_{high}=6$, $N_{low}=10$, $p=0.165$). Likewise, latency to respond to playbacks of barks recorded in high-urgency contexts (mean ± SE: 1.04 ± 0.21 s) likewise did not differ from barks recorded in medium and low-urgency situations (mean ± SE: 0.73 ± 0.24 s; one-tailed Mann-Whitney U test: $Z= -0.789$, $N_{high}=12$, $N_{med/low}=4$, $p=0.215$). While the trends in these latter two cases are in the direction predicted if higher urgency calls elicited anti-predator reactions more quickly than lower urgency calls, the difference remained non-significant even when using Fisher's method for combining probabilities (Sokal & Rolf, 1995; $\chi^2=6.68$; $df=4$; $p=0.154$).

Other contextual factors affecting call response

The importance of additional contextual factors beyond call type - the call receiver's height in the canopy and distance to the playback speaker - on call response were also investigated. Individuals did not respond significantly more to playbacks of

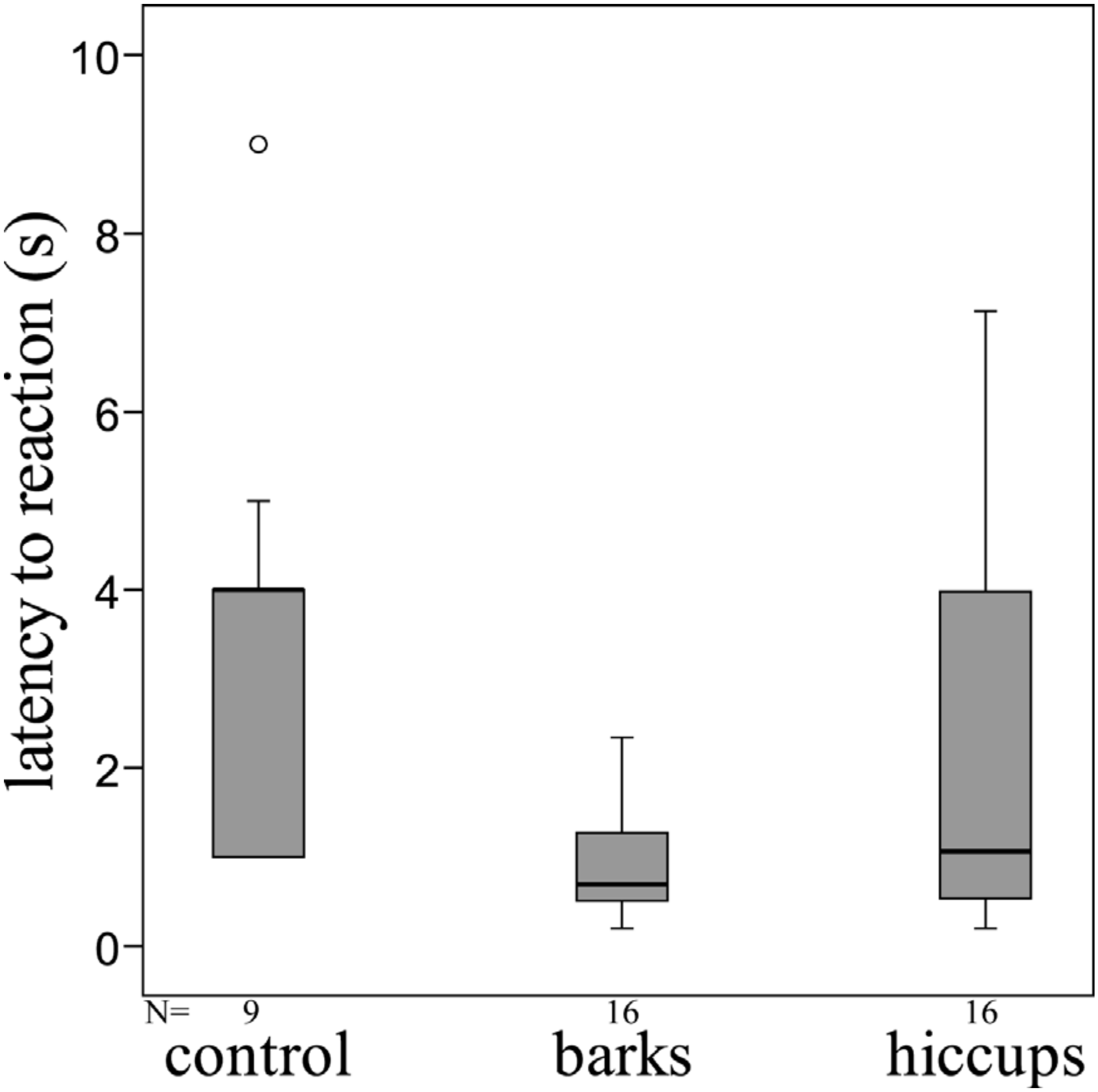

Figure 2.7. Box plots showing the latency to employ an anti-predator behavior following playbacks of controls, barks, and hiccups. Note that these exclude those playbacks when no anti-predator behavior was observed within 10 s of the initiation of the playback. Box plots show median (dark line), first and third quartiles (box), range (whiskers), and extreme values (open circles). Focal animals responded significantly faster in response to barks than to controls, but there was no significant difference between hiccups and controls or barks and hiccups in latency to respond.

barks when they were high in the canopy (6 of 7 playbacks responded to) than when they were low (9 of 11 playbacks; Fisher's exact test: P=0.470), nor did they respond more when close to the speaker (7 of 9 playbacks) relative to when they were farther (8 of 9 playbacks; Fisher's exact test: p=0.397). When examining responses to playbacks of hiccups, there was also no effect of height (low: 9 of 12 playbacks responded to; high: 7 of 8 playbacks; Fisher's exact test: p=0.363) or distance to the speaker (near: 6 of 7 playbacks; far: 10 of 13 playbacks: p=0.413) on the likelihood of responding to playbacks of hiccups.

In the cases when individuals did respond to the playbacks, height and distance did in some cases affect latency to respond. Following playbacks of barks, there was a non-significant trend for individuals at greater distances from the speaker to be slower to look towards it (Kendall's tau= 0.45, N= 7, one-tailed p=0.083), and a significant, positive correlation between the distance to the speaker and the latency to employ any appropriate anti-aerial predator behavior (Kendall's tau= 0.35, N= 15, one-tailed p=0.039). In contrast, there was no significant relationship between the animal's height in the canopy and latency to either look to the speaker (Kendall's tau= -0.29, N= 7, one-tailed p=0.181) or employ any appropriate anti-aerial predator behavior (Kendall's tau= -0.23, N= 15, one-tailed p=0.126). Following playbacks of hiccups, the focal animal's distance from the speaker was positively correlated with its latency to look towards the speaker (Kendall's tau= 0.384, N= 14, one-tailed p=0.033), but not with its latency to employ any appropriate anti-terrestrial predator behavior (Kendall's tau= 0.134, N= 16, one-tailed p=0.245). Height in the canopy did not affect latency to look to the speaker following hiccup playbacks (Kendall's tau= 0.25, N= 14, one-tailed p=0.112), but there was a nonsignificant trend for individuals higher in the canopy to be slower to employ any appropriate anti-terrestrial predator behaviors (Kendall's tau= 0.30, N= 16, one-tailed p=0.056).

Discussion

Situationally variable alarm calls may reflect the caller's perceived risk-urgency (high versus low) or the category of threat it has detected (e.g., aerial versus terrestrial;

Blumstein, 1999a). In this study, the three different alarm call types produced by tufted capuchins showed varying degrees of production specificity: only the bark and perhaps the peep demonstrated production specificity, being elicited almost exclusively by aerial and terrestrial threats, respectively, while the hiccup was given both in response to terrestrial threats and when experiencing non-predatory stress, but was never given in response to aerial threats. However, the number of hiccups given during the first 10 seconds of a calling bout varied with the degree of risk faced by the caller, with more calls being given in higher-urgency situations. Playbacks of barks indicated that these calls elicit appropriate anti-aerial predator and generalized anti-predator behaviors, while playbacks of hiccups elicited generalized anti-predator behaviors and those specific to terrestrial threats. Because playbacks of peeps were not conducted, it is unclear if this call type elicits anti-predator behaviors that would be appropriate for the contexts in which they are produced. The caller's risk urgency had, at best, a weak effect on the perceived risk-urgency of call receivers, whose reactions were more affected by additional contextual cues, especially their distance to the caller. Together, these results suggest that situational variation in alarm call production by tufted capuchin monkeys reflects both functionally referential and urgency-based alarm calls, but responses to calls are more linked to the types of threats that are likely to elicit the calls rather than the degree of risk faced by the caller.

Urgency-based alarm calls

The type of call(s) produced does not seem to uniquely indicate threat urgency as has been demonstrated in some sciurid rodents (e.g., Blumstein & Armitage, 1997). All three alarm call types were observed to be given at least once in each of high, medium, and low-urgency situations. Hiccups were also frequently produced in non-urgent situations in which the caller was likely to have experienced some degree of stress. However, based on these data, the possibility that the different call types represent different levels of risk-urgency cannot be eliminated completely, although this seems unlikely. Because there was only a single observed vocal reaction to a low-urgency aerial threat, it is unknown if barks are indeed the typical response in this context. In addition, it is possible that the classes of risk-urgency used in this study are flawed. However, it seems unlikely that the study subjects would perceive felids in ambush positions at close distances as less threatening than perched eagles at relatively greater distances. Given that there was complete differentiation in the types of calls given in these situations, it seems more likely that threat type (i.e., aerial or terrestrial) explains the type of alarm call an individual gives when faced with such a danger.

While the available evidence points against the different call types reflecting different levels of risk-urgency, there is some indication that call rate, at least in regards to bouts which contained hiccups only or both hiccups and peeps, varied with risk-urgency. In a previous study of captive tufted capuchins, Boinski et al. (1999) found that rates of hiccup (referred to as terrestrial predator alarms) production correlate with the degree of (non-predatory) stress experienced by the caller, as measured through cortisol levels. Since higher levels of risk-urgency are likely to be more stressful for the caller, this provides a plausible proximate explanation for the observed increase in call production in the current study. Increases in rates of calling within alarm call bouts with increases in risk have been previously documented in sciurid rodents and birds (Blumstein & Armitage, 1997; Warkentin et al., 2001; Baker & Becker, 2002; Leavesly & Magrath, 2005), and there are unpublished reports that tufted capuchins in Manu National Park, Peru produce more barks in response to high urgency aerial threats relative to lower risk encounters with raptors (C. Janson, pers. comm.). In addition, although call intensity was not measured quantitatively in this study, it is possible that the intensity of barks and hiccups also varied with risk-urgency: flying raptors tend to elicit higher amplitude barks than do perched raptors, felids tend to elicit higher amplitude hiccups than do snakes, and hiccups given in non-urgent contexts are almost always relatively low in amplitude. Such variation in call type based on levels of arousal is expected (Marler, 1992; Marler et al., 1992; Seyfarth & Cheney, 2003) and has previously been shown in suricates (Manser, 2001). However, firm conclusions regarding the relationship between call amplitude and risk-urgency in capuchin monkeys cannot be drawn without quantitative data on sound amplitude.

Responses to playbacks of barks and hiccups also did not support the hypothesis that these different call types reflect threat urgency, as there were no differences between these two call types in likelihood or latency to respond based on any of the criteria investigated. Likewise, when looking within call types, individuals did not respond more often or more quickly to calls associated with a high risk-urgency than to those associated with lower urgency situations (although all trends were in the predicted direction and a larger sample size may reveal a significant effect of the caller's risk-urgency on receiver responses). Unfortunately, because only hiccups associated with high and medium risk-urgency were used for playbacks in this study, it is unclear whether playbacks of hiccups associated with low-urgency or non-urgent situations would elicit quantitatively distinct reactions. However, because variation in the number of hiccups varies with risk-urgency, some insight into this question may come from examination of latency of response to these calls. Call receivers responded slightly (but non-significantly) more slowly to hiccups than to barks (Figure 2.7); this difference may be due to receivers normally responding to barks following the first call in the playback, but not to hiccups until two or more calls had been played. Thus individuals may not have responded at all if only a single hiccup (indicating lower risk for the caller) had been played. Although further investigation is necessary to determine whether or not this would indeed be the case, receivers react only very rarely to hiccups given in natural contexts by individuals engaged in precarious positional behaviors, and these reactions, when they occur, include only vigilance behaviors (Wheeler, unpublished data). The lack of demonstrated variation in response based on the caller's risk-urgency in the current study differs from that shown in suricates and some sciurids and birds (Weary & Kramer, 1995; Blumstein & Armitage, 1997; Manser et al., 2001; Warkentin et al., 2001; Leavesly & Magrath, 2005, Templeton et al., 2005).

While call type did not affect latency to response, it does seem that call receivers rely on additional factors to determine the urgency of the threat that they themselves face. Receivers' perceived risk-urgency is based to some degree on their distance to the caller (in response to both barks and hiccups), with individuals closer to the caller reacting more quickly, or on their height in the canopy (only in the case of hiccups), with individuals closer to the ground reacting faster. The variation in perceived risk-urgency based on the caller's distance may be associated with average detection distances in this population; given that individuals tend to detect raptors, felids, and snakes only at extremely short distances (Janson, 2007b), group members that are near an individual giving an alarm call are likely to be at greater risk than those that are further from the caller. Similarly, individuals higher in the canopy are likely react to hiccups more slowly because of the decreased risk associated with terrestrial threats. Interestingly, species that have been shown to respond more strongly to high-urgency than low-urgency alarm calls (Blumstein & Armitage, 1997; Manser et al., 2001; Warkentin et al., 2001; Leavesly & Magrath, 2005; Templeton et al., 2005) live in more open environments than do tufted capuchins; because the distance at which prey detect predators is likely greater in more open habitats, individuals farther from the caller are not necessarily at less risk than those closer.

Functionally referential alarm calls

The alarm call system of tufted capuchins is characterized by a functionally referential aerial predator alarm call (the bark), a non-functionally referential general disturbance call which is regularly given in response to felids and vipers but also non-lethal disturbances (the hiccup), and a third call associated with terrestrial threats (the peep), but the degree of context and perception specificity associated with the peep remain unclear. The latter call may or may not be functionally referential, depending on whether or not additional analyses indicate that the call is acoustically distinct from the contact note, and whether playbacks indicate perception specificity in regards to this call type.

Distinct alarm call types for aerial versus terrestrial threats are ubiquitous among primates (Seyfarth et al., 1980a,b; Zuberbühler, 2000, 2001; Fichtel & Kappeler, 2002; Digweed et al., 2005; Fichtel et al., 2005; Kirchhof & Hammerschmidt, 2006). Further, alarm call systems with a functionally referential aerial predator call and non-referential terrestrial predator call may also be common in primates, having been previously documented in redfronted lemurs and Verreaux's sifakas (Fichtel & Kappeler, 2002) and, possibly some New World monkeys as well (Digweed et al., 2005; Kirchhof & Hammerschmidt, 2006). As was found in the current study, Fichtel & Kappeler (2002) found that the terrestrial-predator associated alarm call of two species of lemurs demonstrated perception specificity but was also produced in non-predatory contexts characterized by high levels of arousal. In addition, the current evidence also indicates that both saddleback tamarins (Kirchhof & Hammerschmidt, 2006) and white-faced capuchins (Digweed et al., 2005) may have a similar alarm call system, but evidence of production specificity (in the former case) or perception specificity (in the latter) of the aerial predator-associated alarm calls are needed to determine whether or not this is indeed the case.

The lack of distinct alarm call types for terrestrial mammalian threats and snakes contrasts with that observed in some highly terrestrial species including vervet monkeys and suricates (Seyfarth et al., 1980a; Manser, 2001), but is similar to that described for the more arboreal white-faced capuchins and redfronted lemurs (Fichtel & Kappeler, 2002; Fichtel et al., 2005; Digweed et al., 2005). The greater specificity of call production in the former taxa is likely a result of the different response strategies that are appropriate for a terrestrial species to execute in the presence of a terrestrial carnivore versus a snake. In contrast, it is likely adaptive for tufted capuchins and other arboreal primates to respond in a similar manner to these two distinct types of threats: run up if call receivers perceive the threat to be immediate, and move towards the caller to locate the threatening stimuli if the threat is perceived to be less immediate.

The reactions of individuals to alarm call playbacks of barks and hiccups were appropriate given the contexts in which the two call types were produced, although both calls also elicited generalized anti-predator reactions in addition to appropriate predator-specific reactions. Indeed, the single most common response to both alarm call types was to simply look towards the speaker, with hiccups often eliciting approaches towards the speaker. Such reactions may be adaptive for two distinct reasons. First, examining the behavior of the caller may provide the receiver with additional clues as to what elicited the call (Fischer & Hammerschmidt, 2001). Second, given the short distance in which terrestrial threats are typically detected in the study population (Janson, 2007b), a likely place to locate the threat will most often be near the caller. Since a clear view of the caller would in most cases be impeded because of the typical distance that separated the playback speaker from the focal animal, approaching the speaker may often be necessary to either locate the predator or to obtain addition cues based on the caller's behavior. That individuals never approached the speaker following playbacks of barks may be due to the fact that raptors in flight (which elicit barks far more often than do perched raptors; see

Wheeler, 2008) are unlikely to be located near the caller, as their position would have changed by the time the call receiver arrived.

It is interesting that apparent attempts to locate the predator were far more common reactions to both barks and hiccups than were escape reactions. However, the direction in which an individual looked differed between the two call types. While distinct escape reactions for different predator types have been hypothesized to be necessary for the evolution of predator-specific alarm calls (e.g., Macedonia & Evans, 1993), these findings further support the idea that the ability to quickly locate a predator may also be important (see Kirchhof & Hammerschmidt, 2006). Some previous studies have shown that apparent attempts to locate a predator are more common that escape reactions (Manser et al., 2001; Fichtel & Kappeler, 2002), but this contrasts with trends observed among vervet monkeys (Seyfarth et al., 1980a). In the current study, the low rate of escape reactions may be related to the short distances in which raptors, felids, and snakes are detected (Janson, 2007b). When predators rely on ambush, detection distances may be extremely short, so that the detector is likely in far more danger than are other group members. If this is the case, then an escape response is not necessarily the most adaptive response to an alarm call. In addition, given that a large proportion of the alarms given in natural contexts were to innocuous stimuli, call receivers may lower the costs associated with responding to such false alarms by relying on additional cues before employing a time and energy consuming escape response (Beauchamp & Ruxton, 2007).

The importance of additional acoustic cues

While this study examined only variation in the production of different call types across different situations, acoustic variation within call types may also be associated the context of production and have an effect on listeners' responses (e.g., Manser 2001; Manser et al., 2001). For example, while hiccups are most often a two-syllable call (*hic-cup*), they sometimes contain three syllables (*hic-hic-up*; Di Bitetti, 2001a), as seen in Figure 2.1. Variation in syllable number may be random, but could also be associated with particular threat types (e.g., snakes versus felids) or the caller's risk-urgency (e.g., Templeton et al., 2005). Playbacks of calls that vary in the number of syllables may likewise elicit distinct reactions or different latencies to react. Further investigation will be necessary to draw conclusions in this regard.

The intensity of calls may also be of particular importance. While quantitative data on call intensity is not available from this study, there was clearly variation in this regard for hiccups and barks, although the intensity of peeps seemed to vary little across individuals or situations. Higher intensity calls seem to be associated with more urgent threats. Such trends are similar to that described for vervets, who tend to produce louder alarm calls in higher urgency situations (Cheney & Seyfarth, 1990). Call intensity may thus be an important criteria for listeners in determining, for example, how quickly to react. However, it may be difficult for individuals to correctly perceive a call's intensity given that this will vary with the distance to the caller (see Blumstein & Armitage, 1997; Blumstein, 1999a). Experiments in which the same call is played back at different volumes to individuals at a given distance will provide more insight in this regard.

Conclusions

This study found that the type of call that is given by tufted capuchins to aerial predators (barks) differs from those given to terrestrial threats (hiccups and peeps), but both of these latter two call types are given to both felids and snakes. While production of barks is specific to aerial threats, hiccups are given in a number of stressful contexts and peeps may simply be contact calls given at a higher rate than they are in non-threatening contexts. The degree of risk the caller faces from terrestrial threats is reflected in the number of hiccups the individual produces, but the number of peeps alone does not vary with the degree of risk posed by the terrestrial threat. Likewise, the number of barks given does not reflect the degree of risk posed by the aerial threat based on the risk levels examined in this study. Although a greater number of hiccups tend to be given to felids than to snakes (likely reflecting the difference in the degree of risk each of these threat types poses), there was considerable overlap in the number of calls each of these threat types elicited (Figure 2.4). Even calling bouts characterized by many hiccups are unlikely to be specific to felids. While not recorded in the focal samples in the current study, it is common for individuals receiving aggression to give a bout of hiccups similar to those observed in high-urgency situations (Di Bitetti, 2001a); such aggression-related calling bouts were frequent in experimental feeding contexts (Chapter 6; see also Janson, 1996), but less common in natural contexts.

Both barks and hiccups elicit anti-predator reactions appropriate for the threat types that elicit each call type. Barks thus demonstrate both production and perception specificity and are therefore functionally referential, while the of lack production specificity indicates that hiccups are not referential. Because playbacks of peeps were not conducted, it is unclear whether this call type elicits behaviors that would be appropriate if a terrestrial threat were present. These findings further demonstrate that appropriate anti-predator reactions can be elicited by calls that do not show a high degree of context specificity (see also Fichtel & Kappeler, 2002). However, because this study examined only responses to hiccups given in high and medium-urgency situation, it is unclear whether or not individuals would respond to low-urgency hiccups with similar reactions.

Future directions

Additional contextual factors that may affect responses to alarm calls, such as canopy cover or understory density should be examined (see Boinksi et al., 2003). Playbacks of peeps should be conducted to determine if this call type indicates perception-specificity on the part of call receivers and is therefore functionally referential. Comparisons of acoustic features of peeps and contact notes should be conducted to determine whether or not capuchins could differentiate between these calls based on features other than call rate. Even if there are acoustic differences, it may be more meaningful to determine whether or not the monkeys cue in on these potential acoustic differences; playbacks of contact notes artificially strung together in quick succession to could be used to test if calling rate is the primary criteria that differentiates the perception of these calls from peeps. Likewise, playbacks of multiple hiccups given in non-threatening contexts artificially strung together could be used to determine if capuchins cue in on (potential) subtle acoustic differences between calls given in threatening and non-threatening situations. Playbacks of single hiccups given in high-urgency situations could also be conducted to determine if these calls are responded to more readily than single hiccups given in low-urgency or non-urgent situations. Call intensity could also be varied to test if receivers use sound amplitude as a cue to determine the urgency of the threat. Finally, the proximate mechanisms that drive situational variation in alarm call production and response (e.g., the importance of cognition versus emotion) should be investigated (see Gyger et al., 1988; Blumstein et al., 2006), as an understanding of such mechanisms will provide greater insight into whether variable production and perception of calling in primates indeed parallels language in humans (cf. Evans & Marler, 1995; Owren et al., 2003).

Chapter 3

The Ontogeny of Alarm Call Use and Response in Wild Tufted Capuchin Monkeys (*Cebus apella nigritus*)

Abstract

Infants and juveniles of many mammalian species face a higher risk of predation due to their smaller body size. As such, immature individuals would appear to be at less risk if they possessed adult-like abilities to recognize predators and to respond to conspecific anti-predator signals. Previous research on these behaviors has shown contradictory results, with studies of wild and captive subjects often offering conflicting results. Among New World primates, studies of the ontogeny of anti-predatory behaviors conducted with wild subjects are lacking. This study examines the ontogeny of alarm call use and response among wild tufted capuchin monkeys in northeastern Argentina. Specifically, I examined age differences in: 1) propensity to alarm call in response to threatening and nonthreatening stimuli (venomous and nonvenomous snake decoys, respectively), and 2) responses to playbacks of alarm calls associated with each of aerial and terrestrial predators. The results indicate that juveniles, but not infants, seem to recognize vipers as dangerous, but they do not have the abilities of adults to differentiate between venomous and nonvenomous snakes. In response to the playbacks, both infants and juveniles show adult-like responses to aerial predator-associated calls, but infants ignore terrestrial predator-associated alarm calls more often that do adults. While many of these trends are in the direction predicted if anti-predatory behaviors are not fully developed in immature individuals, larger sample sizes are needed to draw more firm conclusions.

Introduction

Infants and juveniles of many mammalian species face higher rates of predation than do their adult counterparts (e.g., Janson & van Schaik, 1993; Doolan & Macdonald, 1997; Hoogland et al., 2006). This is due in part to the fact that their smaller body size makes immature individuals vulnerable to a greater number of predators than are mature conspecifics (e.g., Vasquez & Heymann, 2001; Bearder et al., 2002). Given this increased risk, immature individuals would seemingly be better off if predator recognition and appropriate anti-predator response behaviors were innate, allowing them to moderate the risk of predation associated with smaller body size. While some studies have lent support to this notion (e.g., Owings & Coss, 1977; Herzog & Hopf, 1984; Caine & Weldon, 1989), others have shown that immature individuals do not demonstrate the same anti-predator abilities as adults (e.g., Seyfarth & Cheney, 1980, 1986; Hollén & Manser, 2006; Hollén et al., 2008). These latter studies indicate that learning and experience play a role in the development of predator recognition and anti-predatory behaviors, and the lack of experience likely further increases their predation risk beyond that caused by small body size. This study investigates the development of alarm call use and response among wild tufted capuchin monkeys (*Cebus apella nigritus*) by examining the stimulus types which elicit the calls and the responses to these calls among different age classes.

Many insights into the development of anti-predatory behaviors have come from studies of captive primates that have never been exposed to predators and therefore have not had the opportunity to learn of the dangers that they pose, most of which support the idea that such behaviors are innate. For example, predator-naive red-bellied tamarin (*Saguinus labiatus*) adults and juveniles react more strongly to the scents of predators than to the scents of non-threatening animals (Caine & Weldon, 1989; see also Caine, 1998; Koenig, 1998; Barros et al., 2002; Hollén & Manser, 2007). Captive tufted capuchins (*Cebus apella*) have also been shown to exhibit fear responses upon encountering snake models without any prior exposure to such stimuli (Vitale et al., 1991; see also Smith 1975, 1977 for similar findings with avian taxa). Similarly, infant squirrel monkeys (*Saimiri sciureus*) raised in social isolation respond to conspecific alarm calls with anti-predator behaviors even if they have never heard the calls in association with threatening stimuli or conspecific anti-predator reactions (Herzog & Hopf, 1984). However, another study showed that these behaviors differ somewhat from those of adults and become more adult like over time (McCowan et al., 2001; see also Masataka, 1983). In addition to these studies of New World primates, similar findings have been reported for some captive Old World primates (e.g., Vitale et al., 1991; Davis et al., 2003). Contrasting with these findings is a study of cotton-top tamarins (*Saguinus oedipus*) which indicated that captive, naive individuals do not respond more strongly to a live *Boa constrictor* than they do to live but nonthreatening rats (Hayes & Snowdon, 1990); further, anecdotal comparisons indicated that the responses of captive individuals to the boa were weaker than are those of wild conspecifics. Studies of captive rhesus macaques (*Macaca mulatta*) have similarly shown that individuals must learn to fear snakes by observing the fear responses of conspecifics (Mineka & Cook, 1988). Interestingly, similar observations of conspecific fear behaviors conducted in association with innocuous stimuli (e.g., flowers) do not cause the subjects to fear these objects.

Other insights into the ontogeny of anti-predator behavior in primates have come from examinations of alarm calling behaviors of wild subjects (e.g., Seyfarth & Cheney, 1980, 1986; Fischer et al., 2000; Fichtel, 2008; see also Hollén & Manser, 2006; Hollén et al., 2008 for similar studies with non-primate mammals**)**, most of which indicate that recognition of predators and appropriate anti-predator reactions to alarm calls are relatively undeveloped in immature individuals. For example, adult vervet monkeys (*Chlorocebus aethiops*) regularly produce distinct alarm call types in response to different categories of predators and respond to each call type with distinct, predator-specific behaviors (Seyfarth et al., 1980a,b). In contrast, infants and juveniles less often employ the appropriate response, indicating that appropriate reactions to these calls develop over time and are likely learned through experience (Seyfarth & Cheney, 1980, 1986; see also Fichtel, 2008 for similar trends among redfronted lemurs, *Eulemur fulvus rufus*). Further, immature vervet monkeys more often alarm call in response to non-threatening stimuli than do adults, for example giving the “leopard” alarm call in response to innocuous terrestrial mammals (Seyfarth & Cheney, 1980, 1986). Interestingly, immatures were not observed to use “leopard” alarm calls in response to aerial stimuli or “eagle” alarm calls to terrestrial stimuli. It thus appears that, among vervet monkeys, appropriate reactions to alarm calls and the ability to distinguish between threatening and non-threatening stimuli must be individually learned over time, while the production of these specific calls for specific classes of stimuli is either innate or learned very early in life. In contrast to these trends observed in vervet monkeys, a study of bonnet macaques (*Macaca radiata*) indicated that juveniles possess adult-like abilities to recognize predators and to respond to alarm calls; juveniles did not react differently than adults to playbacks of adult alarm calls (Ramakrishnan & Coss, 2000), nor did they differ from adults in their reactions to either potentially deadly snakes or to snakes which posed no threat (Ramakrishnan et al., 2005).

While age differences among age classes in alarm call response have been examined in wild Old World monkeys and lemurs (Seyfarth & Cheney 1980, 1986; Ramakrishnan & Coss, 2000; Fichtel 2008), the only wild primates in which alarm call use has been studied to examine predator recognition are vervets and macaques (Seyfarth & Cheney, 1980, 1986; Ramakrishnan et al., 2005), both Old World monkeys. Among New World primates, studies of these aspects of anti-predator behavior have thus far been examined only in captivity (e.g., Herzog & Hopf, 1984; Barros et al., 2002). Furthermore, given that the anti-predator behaviors of captive individuals may be an artifact of laboratory conditions (see Burton, 1993) and the sometimes contradictory results of these previous studies (c.f., Hayes & Snowdon, 1990; Caine, 1998), additional research with wild New World primates is needed to understand the development of these anti-predatory behaviors.

This study examines age-related differences in alarm call use and perception in a South American primate, the tufted capuchin monkey (*Cebus apella nigritus*). Specifically, this study addresses three main questions. First, do the patterns of tufted capuchin alarm call use indicate that adult-like recognition of dangerous stimuli is present in immature individuals? Second, do immature individuals have adult-like abilities to distinguish dangerous stimuli from physically similar but innocuous stimuli? Third, do immature individuals demonstrate adult-like abilities to response to different alarm calls with predator-specific behaviors? To address the questions one and two, the vocal reactions of infants, juveniles, and adults to models of dangerous (i.e., venomous) and innocuous (i.e, nonvenomous snakes that do not prey upon capuchins), respectively, were examined to determine whether immature individuals use alarm calls in the same contexts as adults (see Chapters 2 and 4). The third question was addressed by examining the reactions of infants, juveniles, and adults to playbacks of audio recordings of hiccups and barks, two anti-predator vocalizations which are associated with terrestrial and aerial predators, respectively (see Chapter 2).

Methods

Study site and subjects

Data collection was conducted from July through September 2004 and from May 2005 through December 2006 in Iguazú National Park, Argentina (25°40'S, 54°30'W). The site is described in further detail in Chapter 1.

Tufted capuchins are small-bodied (2.5-3.6 kg; Smith & Jungers, 1997) diurnal primates that live in stable social groups (Di Bitetti, 1997). Species of the genus *Cebus* are characterized by relatively long periods of infancy and juvenility (Ross, 1991). In Iguazú, infants nurse regularly until they are approximately 1 year old, at which point rates of nursing drop sharply (Baldovino & Di Bitetti, 2008). Females reach sexual maturity later than most other primates their size, with a modal age at first birth at 7 years, and earliest age at first birth at approximately 5 years (Di Bitetti & Janson, 2001a; Janson, unpublished data). Given that gestation length is approximately 5 months (Hartwig, 1996), first conception can occur at approximately 4.5 years of age. For the purposes of this study, individuals up to 1 year old were considered infants, individuals 1 to 4.5 years of age were considered juveniles, and individuals over 4.5 years of age were considered either subadults or adults (hereafter, “adults”).

Data were collected on three fully habituated groups in which all individuals were of known age- and sex-class and were recognized based on facial characteristics and fur patterns. These included a large group of 23-28 individuals (“Macuco”: 4-6 adult/sub-adult males, 8 adult/sub-adult females, 7-13 juveniles; 0-6 infants), a medium-sized group of 13-16 individuals (“Gundolf”: 2 adult/sub-adult males, 4 adult females, 5 juveniles, 2-3 infants), and a small group (“Guenon”: 2 adult males, 3 adult/sub-adult females, 3 juveniles, 1 infant).

Capuchin monkeys at Iguazú face both aerial and terrestrial threats. Terrestrial predators include three felid species (jaguars, *Panthera onca*; pumas, *Felis concolor*; and ocelots, *Leopardus pardalis*), and tayras (*Eira barbara*). Aerial predators include two species of raptor (ornate hawk eagle: *Spizaetus ornatus*; black hawk eagle: *S. tyrannus*). In addition, three species of vipers (*Bothrops neuwiedi, B. jararaca,* and *Crotalus durissus*) are also found at the site (Martinez et al., 1992). While these venomous snakes pose a mortal threat to capuchins, there have been no reports of these species preying upon any species of *Cebus* and they seem unlikely to be predators of capuchins given their body size. It is possible, however, that the very largest individuals in these viper populations could prey upon infant capuchins. While there are reports of species of the boa family in the region, they appear to be absent from the study site, although it is unclear how long this has been the case.

Tufted capuchins produce three acoustically distinct call types in response to these potentially fatal terrestrial and aerial stimuli. Two of these (the "hiccup" and the "peep") are given in response to felids and snakes, but not raptors, while the third (the "bark") is given exclusively in response to raptors and other aerial stimuli (see Chapter 2 for additional details).

Experimental protocols

Data on alarm call responses to threatening and non-threatening stimuli were collected using decoys of snakes (Figure 3.1; see also Chapters 2 and 4) indigenous to the study area (Giraudo & Scrocchi, 2002). Threatening stimuli included models painted to resemble venomous snakes (*B. neuwiedi*; *C. durissus*), while models painted to resemble nonvenomous snakes which do not prey on capuchin monkeys (*Pseudablabes agassizzi*; *Erythrolamprus aesculapii venustissimus*; *Dipsas indica bucephala*; *Boiruna maculata*; *Sibynomorphus mikani*) were used to mimic non-threatening stimuli.

Snake model experiments were conducted using a similar methodology to that described in Wheeler (2008). Models were placed on the ground approximately 50m ahead of the group in the direction in which they were traveling and remained stationary

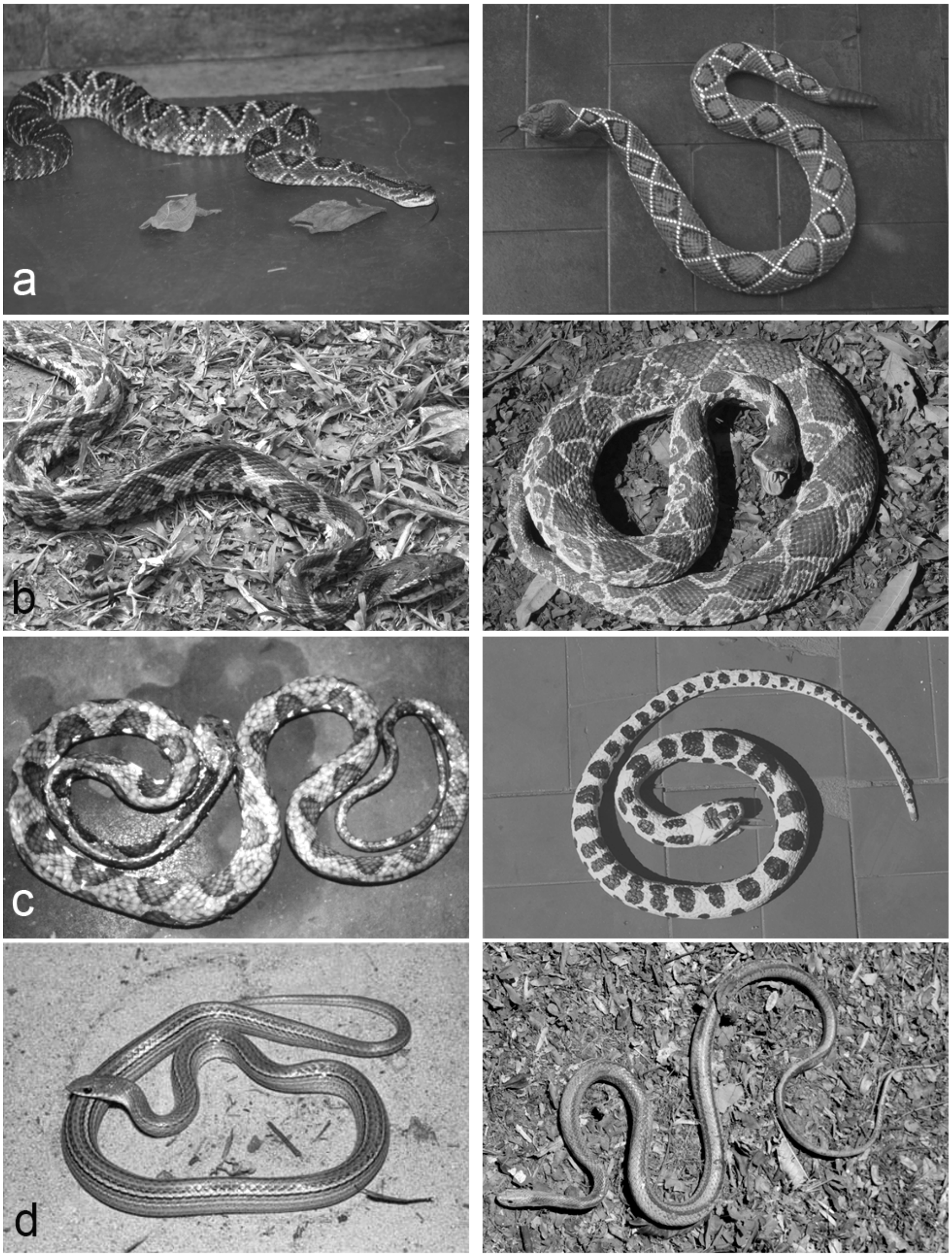

Figure 3.1. Photographs of actual snakes (left) and the decoys (right): a) *Crotalus durissus,* b) *Bothrops neuwiedi*, c) *Dipsas indica bucephala*, d) *Pseudablabes agassizzi*. Vipers include a and b, while non-venomous snakes include c and d. Photograph of the live *Bothrops neuwiedi* courtesy of Charles Janson. Photograph of the live *Dipsas indica bucephala* courtesy of Ariel López. Photograph of the live *Pseudablabes agassizzi* courtesy of Ricardo Sawaya.

throughout the experiment. Data were collected using a continuous focal sampling method (Martin & Bateson 2007) to record whether or not detecting individuals gave an alarm call upon detecting a snake decoy. Detections were defined as “instances in which the focal animal suddenly ceased the behavior in which it was engaged and began to stare attentively at the model” (Wheeler, 2008: 1468). Focal animals were chosen when they approached to within 15m and were followed until detecting the model or passing over it without detecting. If the focal animal detected the snake model, then the type of call it produced, if any, was noted. In addition, any conspicuous, non-vocal anti-predator behaviors performed by the focal (e.g., flee or display) were also noted. A call was considered to be in response to the model’s presence only if it occurred while the animal was looking towards the model or was performing additional anti-predator behaviors. In most cases, the models were placed uncovered so that any individual passing over could potentially detect the model. However, this protocol led to few detections by infants without older individuals first detecting and drawing attention to the models with alarm calls or mobbing displays. To facilitate detections by infants, the models were sometimes left covered until a subgroup of infants was certain to be the next to pass over the model. In these cases, the model was uncovered when the subjects were at least 20m away and were not attentive towards the observer to ensure that they did not witness the observer uncovering the model. An individual’s response to the snake models was included in the analysis if it was the first detector during that particular experiment or if previous detectors did not vocalize or perform any other conspicuous anti-predator behaviors which would allow subsequent detectors to cue in on the model’s presence. This reduces the possibility that an individual’s reaction was confounded by the behavior of previous detectors.

Data on alarm call perception were collected using playbacks of audio recordings of barks and hiccups given in response to models of ocelots, vipers, and hawk eagles (see Chapter 2). The experiments followed the same protocol described in Chapter 2 except that infants were also chosen as focal animals. Reactions of infants and juveniles were included in the analysis only if they were at least 5 m from any adult groupmates or if video analysis indicated that their anti-predator reactions occurred without first looking towards mature conspecifics neighbors, thus reducing the likelihood that their reactions were based on the reactions of mature neighbors. Definitions of anti-predator reactions are listed in Table 3.1. These include reactions specific to each of aerial predators and terrestrial predators as well as generalized reactions which would be appropriate in the context of either predator type.

Statistical methods

Differences between the age-classes in the type(s) of calls given in response to snakes was tested using a 2x3 Fisher's exact test. Infants and juveniles were each individually compared to adults to test if either or both of these two immature age classes differed from adults in the proportion of experiments which elicited hiccups, peeps, or a call series consisting of both call types. A 2x2 Fisher's exact test was used to test if either or both of the two immature age classes differed from adults in the propensity to produce any alarm call type to venomous snakes. The same type of test was used to test if adults differed from either infants or juveniles in the propensity to call to non-venomous snakes. For these tests, each individual was represented in the data set only once. For individuals whose detections met the criteria outlined above (i.e., detected without cues from previous detectors) on more than one occasion, the first such detection of a particular stimulus type was selected for inclusion in the analysis.

A Wilcoxon signed ranks test was conducted to test if immature individuals (infants plus juveniles) and/or adults alarm called more often in response to venomous snake than nonvenomous snake decoys, as would be expected if individuals of each age class could distinguish threatening from nonthreatening snakes. Infants and juveniles were considered together for this test due to sample size limitations which restricted the ability to examine them separately. All detections meeting the criteria outlined above were potentially included in this analysis; however, because most individuals were not sampled an equal number of times in both conditions, additional experiments of the oversampled condition were not included in the analysis. For example, if an individual was tested with venomous snakes five times but with nonvenomous snakes only 2 times, then the three last detections of the venomous snakes were not included in the analysis. Thus the possibility that differences exist due to oversampling in one of the conditions is eliminated.

Table 3.1. List of the behaviors falling into each of the three anti-predator behavioral categories and their definitions.

	behavior	definition
anti-aerial predator	look up	looking beyond immediate substrate, with head at least 45° above the horizontal
	run into cover	movement to an area with a vegetation density greater than that of the point of initiation
generalized anti-predator	run horizontal	quick horizontal movement of at least two meters
	approach speaker	movement within 45° of a straight line between the focal animal and the speaker
	scan	looking beyond immediate substrate in any direction other than up, down, or toward the speaker
	look to speaker	looking beyond immediate substrate, and within 45° of a straight line between the focal animal and the speaker
anti-terrestrial predator	look down	looking beyond immediate substrate, with head at least 45° below the horizontal
	run up	quick vertical movement of at least two meters

Differences between age-classes in responses to the playbacks were also tested using Fisher's exact tests. Again, the reactions of infants and juveniles were compared separately to those of adults to test if either of the two immature age class differed from adults. Responses to playbacks of barks and hiccups were each examined separately. For each playback stimulus type, it was determined if immature and mature individuals differed in the likelihood of employing either a predator-specific response (i.e., responses uniquely suited for only aerial or terrestrial predators) or any appropriate response (i.e., all predator-specific responses plus generalized anti-predator responses appropriate for either aerial or terrestrial threats).

Results

Call use

A total of 47 experiments with models of venomous snakes and 28 with nonvenomous snakes successfully lead to detections by one or more individuals. These experiments yielded data on reactions from 7 infants on 24 occasions (14 with venomous and 10 nonvenomous snake models), 12 juveniles on 69 occasions (41 with venomous and 28 nonvenomous snake models), and 22 adults on 67 occasions (43 with venomous and 24 nonvenomous snake models).

When examining only those snake model experiments that elicited calls from detectors, there were no significant differences among the three age-classes in the types of calls that were produced. The models elicited both hiccups and peeps, but not barks, from all three age classes, although call series consisting of both of these call types were given only by juveniles and adults (Figure 3.2). These results indicate that neither infants nor juveniles differed from adults in the types of calls they gave in response to snake models (Fisher's exact test: infants vs. adults: p=0.598; juveniles vs. adults: p=1.0).

When looking within threat categories, there were no significant differences between immature and mature individuals in the rates in which they responded with anti-predator vocalizations, although some observed trends were in the direction predicted if immature individuals do not yet have adult-like abilities to recognize dangerous stimuli.

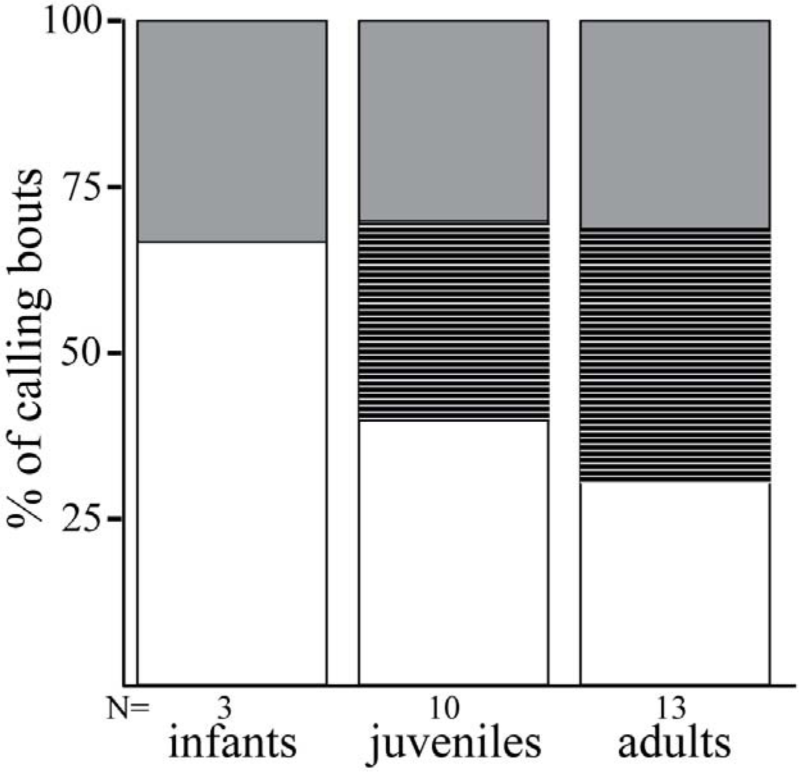

Figure 3.2. Stacked bar graph showing the types of calls that each age class produced in response to the snake models. Gray bars indicate hiccups only; hatched bars indicate a call series consisting of both hiccups and peeps; white bars indicate peeps only. Neither infants nor juveniles differed from adults in the call type(s) elicited by snakes.

While only 1 of 6 infants alarm called in response to venomous snakes models, 4 of 9 juveniles did so, as did 10 of 17 adults (Fisher's exact test: infants vs. adults: p=0.095; juveniles vs. adults: p=0.387; Figure 3.3). In response to nonvenomous snake models, 2 of 5 infants gave an anti-predator call, as did 6 of 11 juveniles and 3 of 11 adults (infants vs. adults: p=0.516; juveniles vs. adults: p=0.193; Figure 3.3).

When looking within age classes, there appear to be some differences between immature and mature individuals in their abilities to distinguish between venomous and nonvenomous snakes. Among infants and juveniles, 3 individuals alarm called more often to venomous than to nonvenomous snakes, 3 called more often in response to nonvenomous snakes, and 7 individuals alarm called at equal rates to the two stimulus categories, a non-significant difference (T+=9.5, T-=11.5; p>0.10; Figure 3.4). Adults, in contrast, alarm called significantly more often to venomous than nonvenomous snakes; 7 individuals responded with alarm calling behavior more often to venomous than non-venomous snakes, while one called more often in response to nonvenomous snakes, and 4 responded to the two stimulus categories with alarm calls at equal rates (T+=30.5, T-=5.5; p<0.05; Figure 3.4).

Call response

A total of 25 playbacks of aerial predator-associated calls (barks) were conducted: 6 with infants, 5 with juveniles, and 14 with adults. The number of experiments of each type which elicited particular reactions is listed in Table 3.2. The playbacks did not elicit appropriate anti-predator reactions less often in either infants or juveniles than in adults. Infants responded to these playbacks with generalized or aerial predator-specific reactions in 5 of 6 cases, compared to 5 of 5 cases for juveniles, and 11 of 14 cases for adults (Fisher's exact test: infants vs. adults, p=0.793; juveniles vs. adults, p=1.0; Figure 3.5a). When considering only aerial predator-specific behaviors, the playbacks of barks elicited such reactions in infants in 4 of 6 cases and in juveniles in 4 of 5 of cases, which was not, as predicted, less often than they did in adults (5 of 14 cases; infants vs. adults, p=0.962; juveniles vs. adults, p=0.989; Figure 3.5a).

Thirty-three playbacks of terrestrial predator-associated calls (hiccups) were conducted: 13 with infants, 8 with juveniles, and 12 with adults. The number of

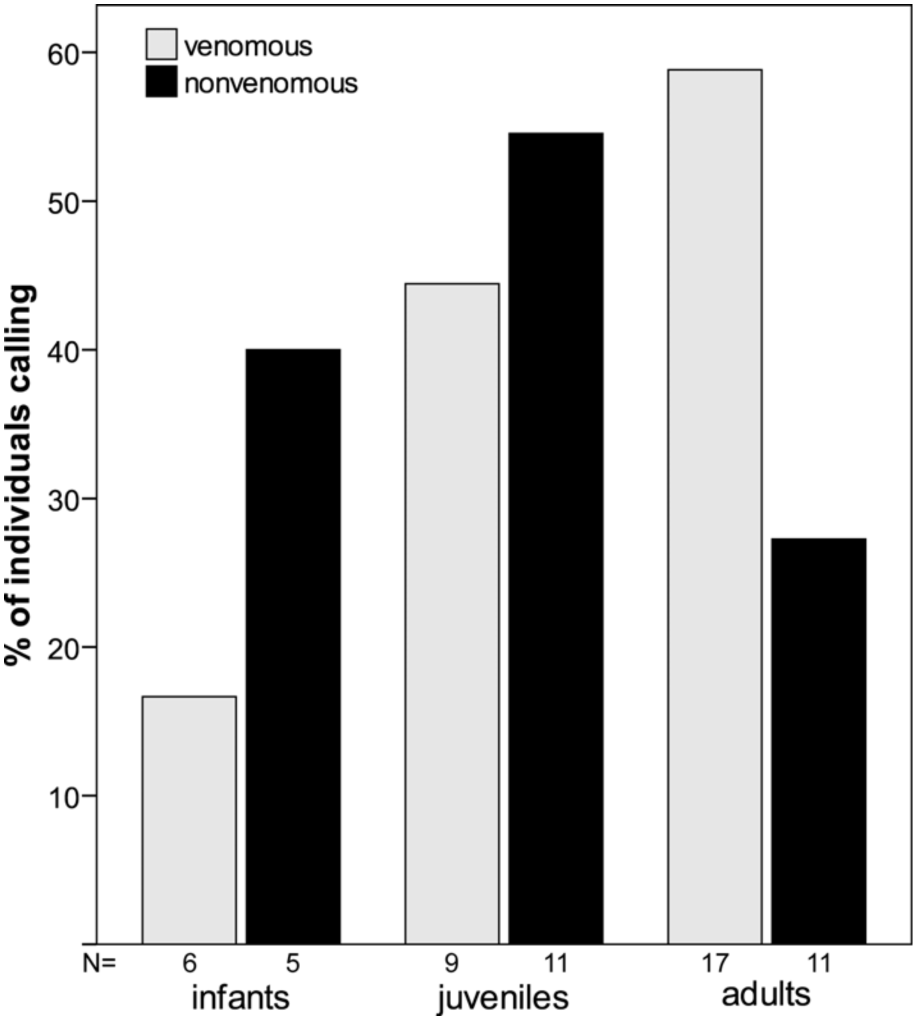

Figure 3.3. Percent of detectors from each age-class who alarm called in response to models of each of venomous and nonvenomous snakes. While there were no significant differences between either of the immature age classes and adults in propensity to alarm call in response to either stimulus type, the difference between infants and adults approached significance for responses to venomous snake models.

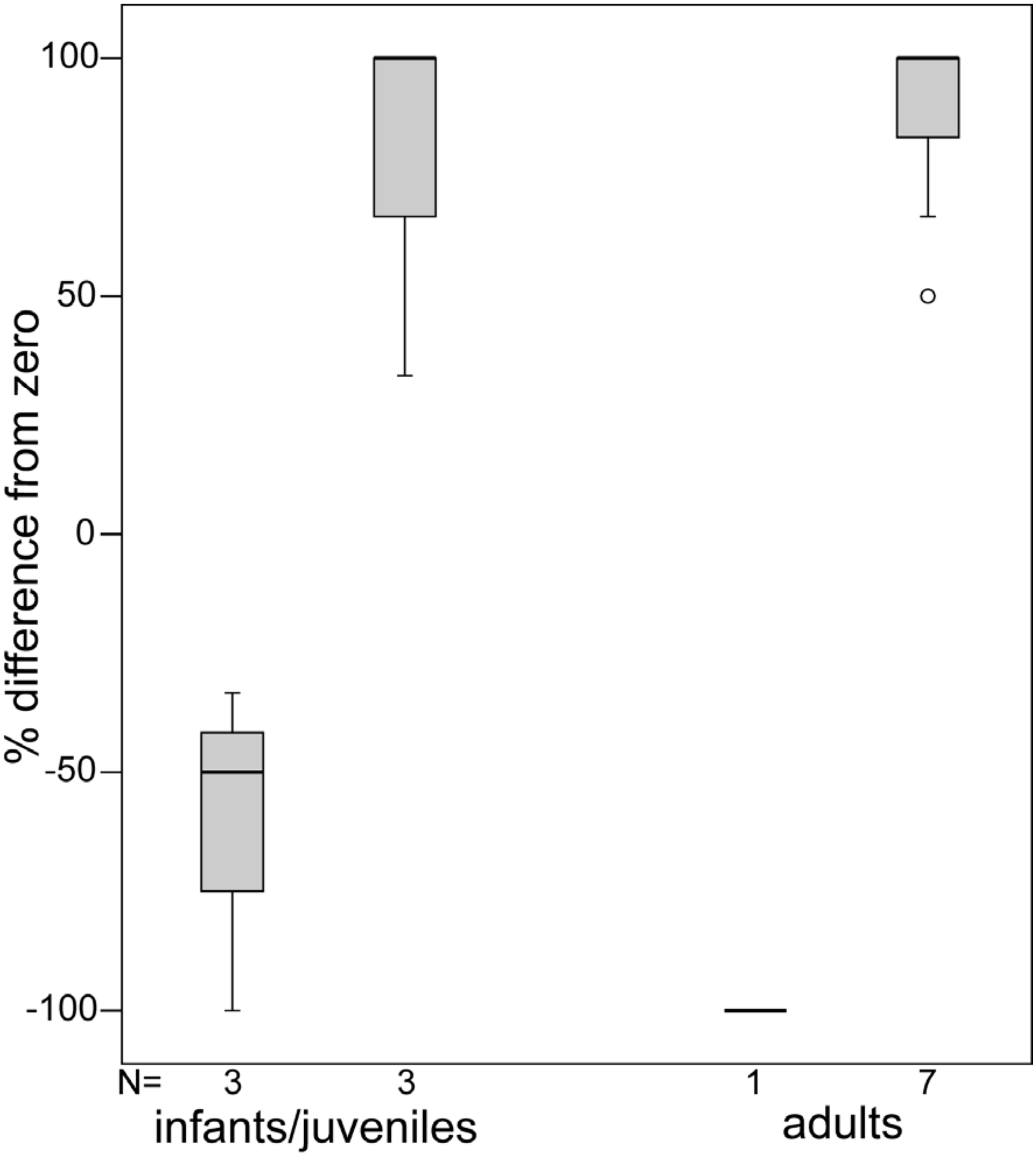

Figure 3.4. Boxplots showing the difference in response rates to venomous versus non-venomous snakes among immature (infants plus juveniles) and mature (adults) individuals. In the graph, each age class is divided into two categories: those individuals who alarm called more to non-venomous than to venomous snakes (negative values), and those who alarm called more to venomous than to non-venomous snakes (positive values). Boxplots show median (dark line), 1st and 3rd quartiles (box), range (whiskers), and extreme values (open circles). The propensity to alarm call more often to venomous than to non-venomous snakes was significant only for adults.

Table 3.2. Anti-predator behaviors elicited by the alarm call playbacks for each of the three age-classes. Note that the rows do not sum to 100% because some playbacks elicited more than one anti-predator behavior.

					anti-aerial predator			**generalized anti-predator**					**anti-terrestrial predator**		
		total # of pbs	no rxn	appr rxn	look up	run to cover	≥1 AAP	run horiz	appr spkr	scan	look spkr	≥1 GAP	run up	look down	≥1 ATP
barks	**inf**	6	1	5	1	4	4	0	0	1	0	2	1	0	1
	juv	5	0	5	2	2	4	0	0	2	1	3	0	0	0
	ad	14	3	11	5	0	5	1	0	4	7	11	0	0	0
hiccups	**inf**	13	5	8	1	0	1	0	1	1	5	6	3	0	3
	juv	8	3	5	1	1	2	0	2	0	4	4	1	1	2
	ad	12	1	11	1	0	1	0	3	0	10	10	2	4	5

PBs = playbacks; no rxn = no reaction; appr rxn = any appropriate anti-predator reaction; AAP = anti-aerial predator specific behavior; appr spkr = approach playback speaker; look spkr = look towards playback speaker; GAP = general anti-predator behavior; ATP = anti-terrestrial predator specific behavior.

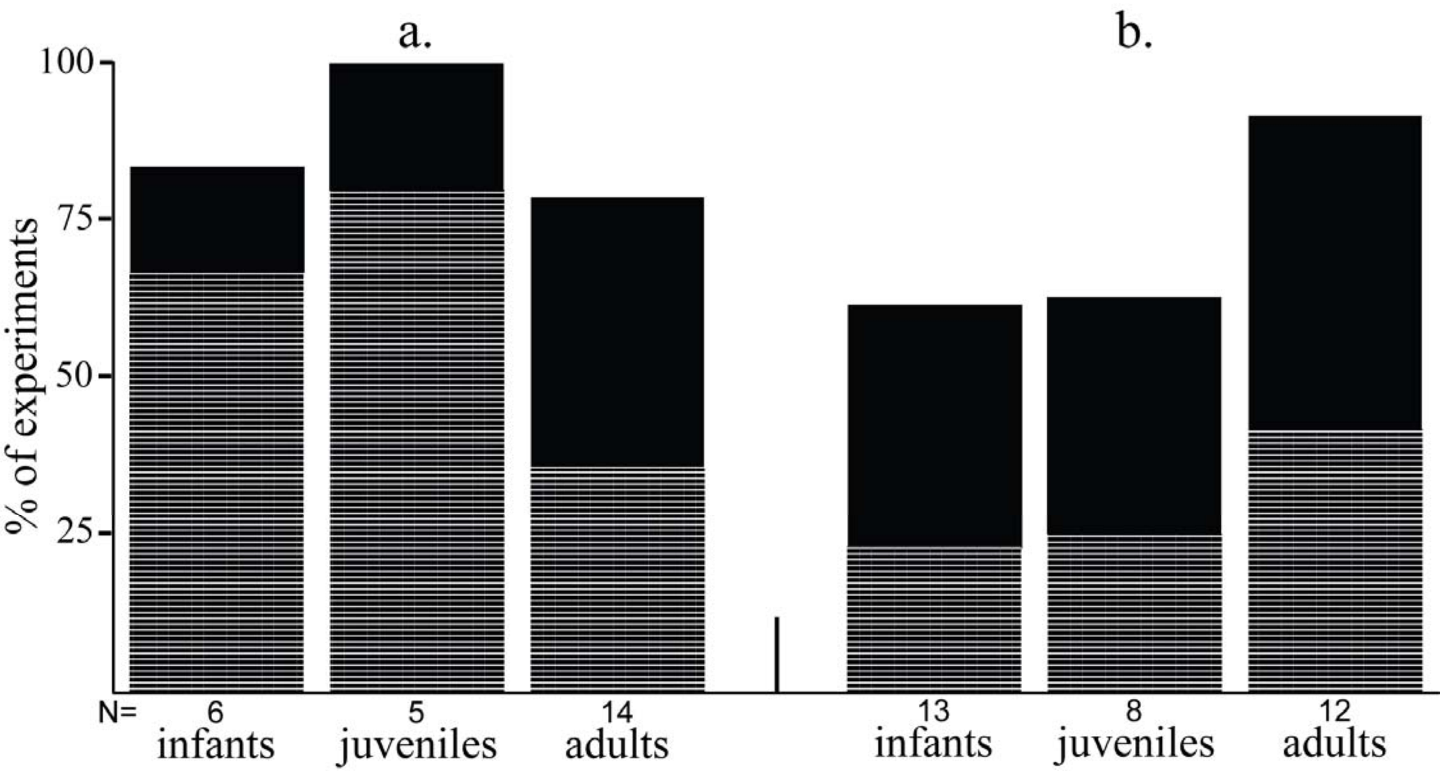

Figure 3.5. Stacked bar graphs showing the percent of playbacks of a) barks and b) hiccups which elicited predator-appropriate reactions in each age class. Black bars indicate the percent of experiments which elicited only generalized anti-predator reactions. Bars to not add up to 100% because some playbacks elicited no response. Hatched bars indicate the percent of experiments which elicited appropriate predator-specific reaction (either with or without generalized reactions). Neither infants nor juveniles differed from adults in the propensity to respond to alarm call playbacks with an appropriate anti-predator reaction. In the case of hiccups however, there was a non-significant trend for adults to respond with appropriate behaviors more often than infants.

experiments which elicited particular reactions can again be found in Table 2. As was the case with barks, the hiccup playbacks did not elicit predator-appropriate reactions less often in immature individuals than in adults, although the difference between infants and adults approached significance when considering together both generalized and terrestrial predator-specific reactions. Such anti-predator reactions were employed by infants following 8 of 13 playbacks, by juveniles following 5 of 8 playbacks, and by adults following 11 of 12 playbacks (infants vs. adults: p=0.097; juveniles vs. adults: 0.153; Figure 3.5b). When considering only terrestrial predator-specific reactions, infants responded with such behaviors following 3 of 13 playbacks, juveniles did so following 2 of 8 playbacks, as did adults following 5 of 12 playbacks (infants vs. adults: p=0.286; juveniles vs. adults: p=0.392; Figure 3.5b).

Discussion

The patterns of alarm call use and response indicate that some adult-like anti-predator behaviors appear early in the development of tufted capuchin individuals or may be innate, while others are less well developed in immature individuals and may be learned later. Specifically, neither infants nor juveniles differed from adults in either the types of calls given to snakes or in their reactions to aerial-predator associated alarm calls (barks). However, based on the currently available data it is impossible to determine if these anti-predator behaviors are indeed innate or simply learned during the first months when infants are completely dependent on their mothers for transportation. In contrast, the recognition of snakes as dangerous and the perception of terrestrial-predator associated calls (hiccups) as indicative of the presence of a dangerous stimulus seem underdeveloped in infants and seem to be learned later. Juveniles, though, do seem to recognize snakes as dangerous, but do not possess the skills of adults to differentiate between dangerous and non-dangerous snakes. In addition, the responses of juveniles to barks and hiccups did not differ from those of adults. Thus, while some of the observed trends are in the direction predicted if anti-predator behaviors must be learned, additional research is needed to draw firm conclusions.

Ontogeny of alarm call use

Infants, juveniles, and adults all produced the same call types (hiccups and peeps) in response to snake decoys. It thus seems that the production of these calls is either an innate response to this category of threats or is otherwise learned during the first months when infants are completely dependent on their mothers for transportation and experimentation was therefore impossible. In addition, although observations are limited (N=2), it appears that infants, like juveniles and adults, also produce these two call types in response to felid predators. Likewise, the only anecdotal observations of barks given by infants (N=2; one 10 months old, one 11.5 months) were in response to flying stimuli. Thus while further research is necessary, these initial observations indicate that immature capuchins, like vervets (Seyfarth & Cheney, 1980, 1986), do not use alarm calls “inappropriately” across categories (e.g., giving barks in response to snakes).

While infants and juveniles produced the same types of calls in response to snakes as did adults, infants (but not juveniles) called less often in response to vipers than did adults. These findings closely match trends observed in meerkats (*Suricata suricatta*) which indicate that infants and juveniles do not alarm call in response to predators as readily as adults (Hollén et al., 2008). While the difference between infants and adults in the current study only approached significance, it indicates that the recognition of venomous snakes as dangerous may not be innate. This contradicts the findings of a previous study of capuchins in captivity (Vitale et al., 1991). This latter study, however, showed only that juveniles and adults naive to the threat posed by snakes responded to snake decoys with fear behaviors; unfortunately it did not examine the behavior of infants (see also Smith, 1975, 1977). It is thus possible that the recognition of snakes as dangerous is indeed innate, but that it nevertheless develops slowly as the individual matures (see Hollén & Manser, 2006). However, studies of marsupials living in environments where predators were recently removed indicate that even adult individuals do not recognize visual or acoustic predator cues (Blumstein et al., 2004; see also Yorzinski & Ziegler, 2007; but see Coss, 1991, 1993). Furthermore, such developmental patterns would appear maladaptive when considering that infants are likely more vulnerable to predation attempts by snakes than are larger conspecifics, and thus might be expected to alarm call *more* often in response to these stimuli (see Galef, 1981; Owings

& Loughry, 1985; Coss, 1991). Indeed, among infant ground squirrels (*Spermophilus beecheyi*), who face a greater risk of predation from rattlesnakes than do adult conspecifics, there is evidence of innate recognition of the dangers posed by these vipers (Coss, 1991, 1993).

In addition to the differences between infants and adults in their propensity to alarm call in response to venomous snakes, there appear to be some differences among the age classes in their ability to distinguish venomous from nonvenomous snakes. While venomous snakes elicited alarm calls more often from adults that did nonvenomous snakes, there were no such differences in propensity to alarm call in response to these two stimulus categories among infants and juveniles. When considering this together with the fact that juveniles but not infants seem to have adult-like recognition of vipers as dangerous, it appears that: 1) infants do not readily recognize snakes as potentially dangerous stimuli, 2) juveniles do recognize snakes in general as dangerous, but they are unable to differentiate between those that pose a threat and those that do not, and 3) adults recognize some snakes as potentially dangerous and are able to differentiate between those that do and do not pose a threat.

Ontogeny of alarm call perception

The results indicate that the relationship between age and alarm call perception differs between the two alarm call types which were examined in this respect. Barks did not elicit appropriate anti-aerial predator behaviors more often in adults than in infants or juveniles. However, infants did respond to playbacks of hiccups with appropriate anti-predator behaviors less often than did adults (albeit not significantly less often), and the lack of a significant difference between juveniles and adults in this regard may be due to the relatively small number of playbacks conducted with juveniles. Such differences in the responses of immature individuals to aerial versus terrestrial predator-associated alarm calls have also been reported in squirrel monkeys (Herzog & Hopf, 1984), a species closely related to capuchin monkeys. It is thus possible that appropriate responses to aerial predator-associated calls are innate among cebids, while those appropriate for terrestrial predators must be learned. Alternatively, it is also possible that responses to both calls are learned, but that learning the appropriate responses to barks happens more quickly (i.e., during the months when infants are dependent on adults for transportation). Previous studies have indicated that the rate at which individuals learn to recognize alarm cues as indicative of the presence of danger is a function of the rate at which they are exposed to such cues (e.g., Hauser, 1988; Pollock & Chivers, 2004; see also Hollén et al., 2008). In the current study, though, it appears that infants more quickly learned to respond to barks than hiccups despite the fact the latter are produced more often (Chapter 2). This may be because barks are more reliably associated with potentially threatening stimuli, while hiccups are frequently associated with non-threats such as precarious foraging postures (Chapter 2) and aggression (see Chapter 6).

It is possible that immature individuals respond to each of these alarm call types not because they associate them with the presence of predators or the execution of anti-predator behaviors by groupmates, but because the acoustic features of the calls elicit attention and/or the initiation of movement (Owren & Rendall, 2001). This would seem not to be supported, at least in the case of the playbacks of barks, by the fact that these calls elicited aerial predator-specific responses (as opposed to generalized anti-predator behaviors) *more* often in infants and juveniles than in adults. A closer examination of the data indicates that this is largely because immature individuals more often employed escape reactions appropriate for aerial predators, whereas these calls more often elicited generalized vigilance behaviors in adults. Additional research is needed to determine if infants and juveniles react more strongly to these calls because they are more vulnerable to aerial predators than are adults (see Hanson & Coss, 2001), as indicated by the fact that juveniles in other tufted capuchin populations seem more likely than adults to choose spatial positions within the group that would best decrease predation risk (Janson, 1990b), or if the acoustic features of the calls simply elicit a stronger affective response in younger individuals than in adults. Indeed, these are not mutually exclusive; stronger affective responses to alarm calls in immatures than in adults may be adaptive if predation risk is higher in the former.

Conclusions and future directions

Most of the aspects of alarm call use and response examined in this study appear not to be fully formed in immature tufted capuchins, but instead develop into adult-like responses over time. Infants appear to differ from adults in their ability to recognize vipers as dangerous and in how to respond to terrestrial predator-associated calls, although larger sample sizes are needed to confirm this. Most behaviors were already adult-like in juveniles, but juveniles, together with infants, appear to be less adept than adults in distinguishing nonthreatening snakes from potentially deadly vipers. While these changes seem most likely to be due to learning through experience, further research is needed to determine if the changes are better explained as a result of developmental maturation. The only behaviors that were adult-like in infants were the call types of calls that were produced in response to snakes and the reactions of individuals upon hearing aerial predator-associated alarm calls. While these behaviors may well be innate, further research is needed to determine if they instead develop relatively quickly over the first few months of life when dependent on adults for locomotion. Additional research is needed on the use of alarm calls in response to aerial threats and to threatening terrestrial stimuli other than snakes (e.g., carnivores).

In the cases in which infants showed adult-like anti-predator behaviors, it remains unclear if these behaviors are innate or are learned during the very first several months of life. Resolving this question may require additional work with captive infants who are known to have never been exposed to alarm calls. This may require taking advantage of individuals raised in social isolation (see Herzog & Hopf, 1984) to test, for example, if such infants respond with appropriate anti-aerial predator behaviors upon hearing barks or give the same alarm call types as adults to different classes of predators. It also remains unclear how, as reviewed above, predator-naive adults in captivity are able to recognize predators (e.g., Caine & Weldon, 1989; Koenig, 1998). It is possible that predator recognition is indeed innate in many species, but that it appears only after reaching a certain level of maturation. Future studies of primates in captivity should therefore directly compare the anti-predator abilities of infants with adults, as this may reveal trends in the development of anti-predatory behaviors among predator-naive individuals that cannot be properly studied in the uncontrolled conditions of the wild.

Chapter 4

Selfish or Altruistic? The Adaptive Significance of Alarm Calling in Wild Tufted Capuchin Monkeys (*Cebus apella nigritus*)

Note: Please cite this chapter as:

Wheeler, B.C. (2008). Selfish or altruistic? An analysis of alarm call function in wild capuchin monkeys, *Cebus apella nigritus*. *Animal Behavior*: 76: 1465-1475.

Abstract

Alarm calls facilitate some anti-predatory benefits of group-living but also present what appears to be an evolutionary paradox. An individual who calls in the presence of a predator may endanger itself by attracting the predator's attention. The benefits afforded to an individual who gives an alarm call therefore need to be explained. The benefits afforded to an individual who gives an alarm call therefore need to be explained. A number of hypotheses invoking kin selection and individual selection have been proposed to explain how such behavior could evolve. This study tests eight hypotheses for alarm call evolution by examining the responses of tufted capuchin monkeys (*Cebus apella nigritus*) to models of felids, perched raptors, and vipers. Specifically, this study examines: 1) differences among individuals in their propensity to call in response to different threat types, 2) whether or not there is an audience effect for alarm calling, and 3) the response of conspecifics to alarms. Results indicate that the benefits likely afforded to the caller vary with stimulus type. Alarm calling in response to felids is most likely selfish, with calls apparently directed towards both the predator and potential conspecific mobbers. Alarm calling in response to vipers attracts additional mobbers as well, but also appears to be driven by kin selection in the case of males and parental care benefits in the

case of females. Alarm responses to perched raptors are rare, but seem to be selfish with callers benefiting by recruiting additional mobbers. Additional research that focuses on predators is needed in order to clarify why prey produce these conspicuous signals.

Introduction

Alarm calls, vocalizations given by prey species when predators or other threats are detected, are ubiquitous among birds and mammals and facilitate proposed anti-predatory benefits of group-living including the many-eyes effect (Lima, 1995) and cooperative defense (Curio, 1978a). However, the benefits afforded to the caller need to be explained because by warning conspecifics of the presence of a predator, an individual may decrease its own fitness by drawing the predator's attention to itself (e.g., Sherman, 1977; Ivins & Smith, 1983; Alatalo & Helle, 1990). Several hypotheses invoking both kin selection (Hamilton, 1964; Maynard Smith, 1965) and individual selection (*e.g.,* Charnov & Krebs, 1975; Woodland et al*.,* 1980) have been developed to explain how this apparently costly behavior can evolve and be maintained in a population (see Klump & Shalter, 1984; Hauser, 1996 for reviews). Many tests of these hypotheses have been conducted in avian and rodent taxa (e.g., Sherman, 1977, 1985; Smith, 1978; Schwagmeyer, 1980; Hoogland, 1983, 1996; Davis, 1984; Alatalo & Helle, 1990; Taylor et al., 1990; Cresswell, 1994a; Neudorf & Sealy, 2002; Shelly & Blumstein, 2005; Blumstein, 2007a,b) but only two studies have tested these hypotheses among primates (Cheney & Seyfarth, 1981, 1985; Zuberbühler et al., 1997, 1999). Few studies have differentiated between alarms given to different predator types, although this has been shown to be an important factor affecting selective pressures on alarm calling (Sherman, 1985; Zuberbühler et al., 1999). This study experimentally tests eight hypotheses (see Table 4.1) for the evolution of alarm calls in a group of wild tufted capuchin monkeys (*Cebus apella nigritus*) in Iguazú National Park, Argentina by examining reactions to models of predators (felids and raptors) as well as venomous snakes.

The earliest hypothesis developed to explain the evolution of alarm calling was based on kin selection. This hypothesis argues that such potentially costly behavior may be selected for if relatives of the caller benefit, increasing the caller's inclusive fitness

Table 4.1. Proposed hypotheses, associated predictions, and taxa in which they have been previously supported.

Hypothesis[a]	Prediction(s)[b]	Previous support in[c]:
Kin selection	Individuals with higher total *r* are more likely to call	rodents[1]
Parental care	Individuals with more offspring are more likely to call	primates[2], rodents[3], birds[4]
Mate protection	Mating males more likely to call than others	birds[5]
Selfish herd[d]	Neighbor density for caller is higher after an alarm call	birds[6]
Predator confusion[d]	Alarms cause a sudden burst of movement and/or vocalizations by conspecifics	rodents[7], birds[8]
Group maintenance	Dominants more likely to call than subordinates	primates[9]
Mobbing recruitment	Conspecifics more likely to mob predator following an alarm	birds[10,]
Pursuit deterrence[d]	No conspecific audience effect for calling	primates[11], rodents[12], birds[13]

a. Sources for each hypothesis are listed in the text.

b. Additional predictions may be applicable. Only those tested in this study are listed.

c. Not an exhaustive list of hypothesis support. See Caro (2005) for extensive review.

d. Hypotheses which assume a strict predator-prey relationship and are therefore not applicable to detections of vipers in the present study.

1. Sherman, 1977; Smith, 1978; Schwagmeyer, 1980; Hoogland 1983, 1996; 2. Cheney & Seyfarth, 1985; 3. Shields, 1980; Blumstein et al., 1997; 4. Griesser & Eckman, 2004; 5.Witkin & Ficken,1979; Gyger et al., 1986; Taylor et al., 1990; Hogstad, 1995; 6. Owens & Goss-Custard, 1976; 7. Sherman, 1985; 8. Cresswell, 1994b; 9. Cheney & Seyfarth, 1985; 10. Rohwer et al., 1976; 11. Zuberbühler et al., 1999; 12. Shelley & Blumstein, 2005; Clark, 2005; 13. Woodland et al., 1980; Murphy, 2006.

(Hamilton, 1964; Maynard Smith, 1965). This hypothesis predicts that individuals with more kin in the group should be more likely to give an alarm than those with fewer kin. Similarly, alarm calling may be a form of parental care wherein an individual increases its direct fitness by alerting offspring to the presence of a predator (Williams, 1966; Shields, 1980). This hypothesis predicts that individuals with more offspring will be more likely to call. Whether costly parental behavior (such as alarm calling) should be considered kin selection or individual selection is a matter of contention (c.f., Dawkins, 1976; Bertram, 1982). These are considered separately in this study since previous studies have indicated that alarm calling behavior may be based more on the presence of offspring than the presence of collateral kin (Shields, 1980; Blumstein et al., 1997; but see Sherman, 1980; Hauber & Sherman, 1998).

Several additional hypotheses also explain how alarm calling can increase a caller's direct fitness. First, the "mate protection" hypothesis states that an individual may increase its reproductive success by ensuring that potential mates survive (Witkin & Ficken, 1979). Under a polygamous mating system, this hypothesis predicts that adult males (i.e., potential sires) will call more often than will females or non-mating males (Hauser, 1996). Second, an alarm caller may benefit via a "selfish herd" effect (Hamilton, 1971). In this case, it is predicted that an alarm call results in an increase in group cohesion around the caller (see Owens & Goss-Custard, 1976). Third, it may be beneficial for an individual to call if protecting group members increases the caller's direct fitness ("group maintenance"; Smith, 1986b), for example through the dilution effect (Bertram, 1978) or as the result of between group feeding competition (e.g., Wrangham, 1980). Under this scenario, it is predicted that individuals who face greater costs from larger group sizes (subordinate individuals if there is within group contest competition for food or spatial position; Janson, 1985, Ron et al., 1996, Koenig et al., 1998) will be less likely to call than individuals who face fewer costs with increasing group size (Alatalo & Helle, 1990; see also Cheney & Seyfarth, 1985). Fourth, an alarm may benefit the caller by manipulating the behavior of conspecifics in a way that confuses the predator and allows the caller a chance to escape ("predator confusion"; Charnov & Krebs, 1975). This hypothesis predicts that alarms will generate sudden movement and/or vocalizations by conspecific receivers of the call. Fifth, alarm calls can be explained through individual selection if their production elicits mobbing of the predator by conspecifics ("mobbing recruitment"; see Curio, 1978b). Finally, callers would benefit if an alarm call communicates to the predator that it has been detected and a successful predation attempt is unlikely ("pursuit deterrence"; Woodland et al., 1980). Such communication between predator and prey could arise if the predator relies on surprise to capture prey and gives up once it knows that it's been detected. If alarms indeed do serve such a function, then it is predicted that individuals will call even in the absence of a conspecific audience. Of the eight hypotheses being tested, only the pursuit deterrence hypothesis predicts this lack of an audience effect; the presence of conspecifics is necessary for the caller to benefit under all other scenarios.

Among these eight hypotheses, the parental care and pursuit deterrence hypotheses have thus far found the most widespread support. Evidence in favor of these hypotheses has been found in all three taxonomic groups in which they have been examined, while other hypotheses have found support only within one of the three taxa (see Table 4.1). However, a lack of support for other hypotheses may be due to the fact that most previous studies did not test all possible hypotheses (e.g., Zuberbühler et al., 1999) and/or examined only overall differences in rates of calling among individuals rather than differences in rates in which individuals call upon detecting a predator (e.g., Cheney & Seyfarth, 1985).

This study tests each of the hypotheses listed in Table 4.1 by examining: 1) differences among individuals within tufted capuchin groups in their propensity to call upon detecting predator models, 2) whether or not there is an audience effect in the production of alarm calls, and 3) the response of conspecifics to alarm calls. Because the selective pressures acting on alarm calls have been shown to vary with predator type (e.g., Sherman, 1985), every hypothesis is evaluated separately for detections of each of the models used in this study: felids, vipers, and raptors. In addition, the selfish herd, predator confusion, and pursuit deterrence hypotheses are not considered for alarms given to vipers since these hypotheses assume a strict predator-prey relationship; venomous snakes are not known to prey on capuchins although they do pose a mortal threat to individuals that approach too closely.

Methods

Study site and subjects

The study was conducted from August - September 2003, July – September, 2004, and May 2005- December 2006 in Iguazú National Park, Argentina (25°40'S, 54°30'W). The site is part of the South American Atlantic Forest and is characterized by humid, semi-deciduous, sub-tropical forest (Crespo, 1982). The study area has been logged in the past and is in various stages of secondary growth (see Chapter 1; Di Bitetti et al., 2000; Di Bitetti, 2001a for further description of the study site).

Tufted capuchins are small (2.5-3.6 kg; Smith & Jungers, 1997), diurnal primates that feed primarily on fruits but spend a large proportion of time searching for insect prey by specialized destructive foraging (Terborgh, 1983; Brown & Zunino, 1990). The species is highly arboreal, inhabiting primarily the mid to lower canopy and the understory (Fleagle & Mittermier, 1980). Approximately 3% of their active time is spent on the ground, although this varies considerably by season (Wheeler, unpublished data). Groups are multimale-multifemale, typically consist of 7-30 individuals (Di Bitetti, 2001b), and are characterized by female philopatry and male dispersal (Di Bitetti, 1997). Dominance hierarchies are linear and dominant individuals benefit from contests over food and spatial position (Janson, 1985, 1990a,b; 1996; Di Bitetti & Janson, 2001b). In addition, although the dominant male likely sires the majority of offspring (Escobar-Páramo, 1999), subdominant adult males obtain some matings (Janson, 1994). All adult males but one were observed mating during the course of the current study, while only one copulation involving a natal (juvenile) male was observed. In addition, because all observed male takeovers at the study site have been the result of subdominant males within the group rising in rank (Janson, unpublished data), all adult males have the potential to sire offspring.

The species produces at least three distinct calls in association with predator encounters (Chapter 2). Two of these, the “hiccup” and “peep”, are given in response to both felids and vipers and are often produced together during a single predator encounter. The “hiccup” is also given in non-predatory contexts (including aggressive interactions and when foraging in a precarious position; Chapter 2; see also Di Bitetti, 2001a), has been shown to be an indicator of stress (Boinski et al., 1999), and may be best classified as a general "disturbance call" (Emmons et al., 1997). The third call, the "bark", is a functionally referential aerial predator alarm given only in response to flying stimuli or large perched birds (Chapter 2). A similar alarm call system has been described for white-faced capuchins (*C. capucinus*; Digweed et al., 2005).

Among the predators of capuchin monkeys at the site are three species of felids (jaguars, *Panthera onca*; pumas, *Felis concolor*; and ocelots, *Leopardus pardalis*), tayras (*Eira barbara*), and two species of raptors (hawk eagles: *Spizaetus ornatus* and *S. tyrannus*; see Chapter 1 for further descriptions of predators at the study site). In approximately 400 weeks of observation, one predation attempt by a felid has been recorded (Di Bitetti, 2001a); although several additional monkey-felid encounters have been observed, it is unclear if any of these were actual predation attempts. There have been two observed predation attempts by raptors at the study site, one of which was successful (Di Bitetti, 2001a). Capuchins in Iguazú also face threats from three species of vipers (*Bothrops neuwiedii, B. jararaca,* and *Crotalus durissus*; Martinez et al., 1992). While these snakes are not known to be capuchin predators, their presence nevertheless evokes a strong reaction in the capuchins, likely because of the mortal threat they pose to individuals who approach too closely.

Data were collected on three separate groups ("Macuco": 23-45 individuals; "Gundolf": 15 individuals; "Guenon": 9 individuals). The two latter groups split off from the former during the initial period of data collection to form new groups. For the majority of the study period, the Macuco group consisted of 23-28 individuals, with variation due to births. Maternal relationships for all individuals are known and all individuals were recognizable based on facial characteristics.

Observational and experimental protocols

Data were collected using models of ocelots, vipers, and hawk eagles (see Figure 2.1 in Chapter 2) and playbacks of puma vocalizations. Models were placed in front of the group while they were traveling or foraging. One observer went ahead of the group to place the model while one or more observers remained with the group to ensure that they did not approach too closely before the model was placed. Ocelot and snake models were placed at least 50m ahead and raptor models were placed 150m in front of the group. In all cases, the distance chosen was sufficient to prevent the study subjects from cueing in on the model placement. Viper models were always placed on the ground while ocelot models were placed on the ground or in trees at a height of 2 to 5m. Raptor models were suspended from tree branches at a height of 4 to 12m by a rope thrown over the branch. In most cases, the model remained stationary for the duration of the experiment. For a few experiments, snake (N=7) and ocelot (N=5) models were moved a short distance (less than 15cm) once every two minutes until a detection occurred. Although this movement sometimes caused individuals to detect the models when they otherwise would not have, there was no discernable difference in the way that they reacted to moving models relative to stationary ones. To avoid habituation, a given model type (e.g., felid, snake, raptor) was not used for seven days following a detection, while a specific model was not used for at least fifteen days; in most cases each model was used only once with each group in a thirty day period. Three exemplars of each of model type were used. The capuchins did not appear to habituate to the models, given that responses to the models remained consistent throughout the study period.

Continuous focal sampling (Martin & Bateson, 2007) was used simultaneously by three observers to record whether or not individuals gave an alarm upon detecting a model. A detection was defined as an instance in which a focal animal suddenly ceased the behavior in which it was engaged and began to stare attentively at the model. Individuals that approached to within 15m of the model were chosen as focal animals. A distance of 15m was chosen because detections of models are very unlikely from greater distances, even when visibility is relatively high (Janson, 2007b). Focal animals were followed until detecting or moving farther than 15m from the model.

Upon the detection, the focal animal's vocal behavior (or lack thereof) was noted, as was whether or not the detector performed any other conspicuous anti-predator behaviors (e.g., flee or display). If an alarm call was given by the detector, all-occurrence sampling (Martin & Bateson, 2007) was used to note if, immediately following the call, conspecifics reacted with: 1) a sudden burst of movement and/or vocalizations or ("pandemonium"; Sherman, 1977), 2) mobbing of the predator model (i.e., aggressive displays towards the model). In addition, a scan sample (Martin & Bateson, 2007) was conducted 30 seconds after the first alarm to record neighbor density (the number of conspecifics within 3m) for all individuals in the group, including the caller. These experimental scan samples were compared to scans conducted in non-experimental contexts at 30 minute intervals throughout the day. Only non-experimental scans which were taken when the group was traveling or foraging were included in the analysis since experiments were always conducted in this behavioral context.

Experiments were also conducted with individuals who had become separated from the group (hereafter "solitary") to test for audience effects on alarm calling. An individual was considered solitary if there were no conspecifics within 150m for at least 15 minutes. In most cases, the animal had been separated from conspecifics for at least several hours. These experiments used either an ocelot model or a playback of a puma vocalization and followed a protocol similar to that described for non-solitary individuals. Puma calls were deemed appropriate to use for solitary but not non-solitary individuals; non-solitary individuals may withhold alarms since all prey individuals simultaneously become aware of the predator's presence (see Arnold et al., 2008). Playbacks conducted with non-solitary individuals confirm that capuchins do typically call in response to this stimulus (Wheeler unpublished data). The calls used for playbacks were recorded at the study site during an encounter with a vocalizing puma. Recordings were made with a Marantz PMD-660 recorder and a Sennheiser ME67/K6 microphone at a sampling rate of 44.1 kHz. Recordings were played from a Saul Mineroff AFS speaker connected to a portable CD player at an intensity of 80-90 dB (measured by a Radio Shack 33-2055 digital sound level meter placed 1 meter from the speaker). The speaker was placed in dense vegetation at a height of 1m. Each playback consisted of a single vocalization played four times at 5 second intervals and began when the solitary individual approached to within 25m of the speaker. The individual was scored as alarm calling if it produced an alarm at any point from the initiation of the playback until 40 seconds after the last call was played.

All dyadic agonistic interactions (including aggression, submission, and spatial displacements) were noted ad libitum, entered into a dominance matrix, and analyzed using MatMan™ (Vers. 1.1.4; De Vries et al., 1993). Because the hierarchy of the

Macuco group was significantly linear, the ordering procedure within MatMan immediately provides an ordinal dominance rank for each individual with the "inconsistencies and strength of inconsistencies" (I&SI) method (De Vries, 1998). A sufficient number of interactions were recorded only for the Macuco group; the "group maintenance" hypothesis was therefore tested using only data from this group.

Data selection and statistical methods

An individual's response was included in the analysis only if it was the first detector during that particular experiment or if previous detectors did not call or perform any other conspicuous anti-predator behaviors which would allow subsequent detectors to cue in on the model's presence. It is thus unlikely that any individual's reaction was confounded by the behaviors of previous detectors. For individuals whose detections met these criteria on more than one occasion, the first such detection of a particular model type was selected for inclusion in the analysis. To ensure that all data points were independent, only a single detection from each experiment was used. Only detections by juveniles and adults were included in the analysis because, although juveniles readily recognize predators as dangerous, infants do not appear to have yet fully developed this recognition (Wheeler in prep.). The number of individuals of different age and sex categories which were included in the analysis is shown in Table 4.2.

Binary logistic regressions were used to determine if total maternal *r*, number of offspring, dominance rank, or "sire potential" predicts whether or not an individual produced a vocalization upon detecting a particular model type. "Total *r*" was calculated for each detector by summing the coefficient of relatedness (Wright, 1922) between the detector and all other individuals present at the time of detection. An individual was considered present if it had been seen in the group during the day of the experiment unless it was otherwise known to be absent from the group during the experiment; misclassification of an individual as present was unlikely given the rarity in which individuals separated from the group. Because paternity for many individuals is unknown, *r* values were based solely on maternal relationships (e.g., mother-offspring dyads = 0.50, maternal siblings = 0.25, aunt-nephew dyads = 0.13, etc.). Offspring (of

Table 4.2. Sample sizes by age and sex for each of the four experiment types.

	solitary (felid)	ocelot	viper	raptor
juvenile males	3	5	10	3
adult males	1	7	4	4
juvenile females	2	9	8	6
adult females	2	4	6	9

any age) were excluded when calculating an individual's total maternal *r* since this study examines the kin selection and parental care hypotheses separately. Due to the lack of paternity data, only females were included in tests of the parental care hypothesis. The sire potential variable divided individuals into two categories, adult males vs. all other individuals (i.e., adult females plus all juveniles). Logistic regressions were performed by examining each independent variable both alone and in a multivariate analysis including several independent variables simultaneously. In addition, because different selective pressures may act on male and female alarm calling (e.g., Alatalo & Helle, 1990), the interaction between sex and each predictor variable was examined in a univariate logistic regression. If the interaction variable was found to be significant, that variable was tested separately for males and females. Two multivariate logistic regressions were run for each predator model type. The first of these was based on all detections (i.e., by both males and females) and included the following predictor variables: total maternal *r*, dominance rank, sire potential, and the interaction between sex and each of these three independent variables. The second was based on detections by females only and included total maternal *r*, dominance rank, and number of offspring as predictor variables. Males were not included in this model because paternity is unknown in many cases.

Binomial tests were used to test whether mobbing of the model by conspecifics or "pandemonium" followed the production of alarm calls more often than expected. An expected value of 37.5% was chosen because this is the frequency in which conspecifics mobbed the models when no alarm call had been given by a previous detector (12 of 32 cases). Although this does not reflect the expected baseline values of "pandemonium" behavior, a value of 37.5% is conservative since such behaviors were rare. To determine if the sex of the caller predicted the reactions of conspecifics, a binary logistic regression was used. A Wilcoxon signed ranks test was used to determine whether or not individuals achieved a higher neighbor density subsequent to producing an alarm than those same individuals had in non-experimental contexts. To determine if overall group cohesion was greater in experimental than non-experimental contexts, the mean number of neighbors within 3m for all individuals was calculated for each scan in both contexts, was square root transformed, and compared using a one-tailed t-test. Finally, a Fisher's exact test was used to test for differences between solitary and non-solitary individuals in the probability of calling following a felid detection. Significance levels were set at $p<0.05$ for all tests; a result was considered to show a trend in the predicted direction if $p<0.10$. Regressions, signed ranks tests, and t-tests were conducted using SPSS 15.0 (SPSS Inc., Chicago, IL, USA). The binomial tests and Fisher's exact test were calculated by hand.

Results

Felid experiments

Twenty-three of the 25 individuals who detected an ocelot model gave an alarm call upon detecting the model (92.0%; Figure 4.1). The individuals who did not call included a low-ranking juvenile female and an alpha male. Whether or not an individual called upon detecting the ocelot model was not predicted by its total maternal *r*, number of offspring, dominance rank, or sire potential in the univariate analyses, and no variables showed a significant interaction with sex (see Table 4.3). Likewise, the multivariate logistic regressions were non-significant (whole group: $\chi^2_6=9.28$, N=16, p=0.158; females only: $\chi^2_3=6.03$, N=8, p=0.11). Pandemonium by conspecifics did not occur following any alarms (0 of 20 documented cases), but groupmates mobbed the model following an alarm call significantly more often than expected (15 of 20 documented cases; binomial test: $p<0.001$). The sex of the caller did not predict whether or not conspecifics mobbed the ocelot model (binary logistic regression: $\beta=-0.81$, N=20, p=0.44). Finally, callers did not achieve a greater number of neighbors within three meters in experimental contexts (mean ± SE = 0.67 ± 0.20 neighbors) than they averaged in non-experimental contexts (mean ± SE = 0.59 ± 0.04 neighbors; Wilcoxon signed ranks test: N=18; Z=-0.04, p=0. 97). However, when neighbor densities for all group members were averaged, there was a non-significant trend towards an increase in neighbor density in experimental contexts (mean ± SE = 1.05 ± 0.16 neighbors) relative to non-experimental contexts (mean ± SE = 0.72 ± 0.02 neighbors; one-tailed t-test on square root transformed data: $t_{28}=1.69$, $N_1=28$, $N_2=641$, p=0.10).

Four experiments with a model ocelot and four using a puma call playback were conducted with solitary individuals. Six of eight (75%) solitary detectors called,

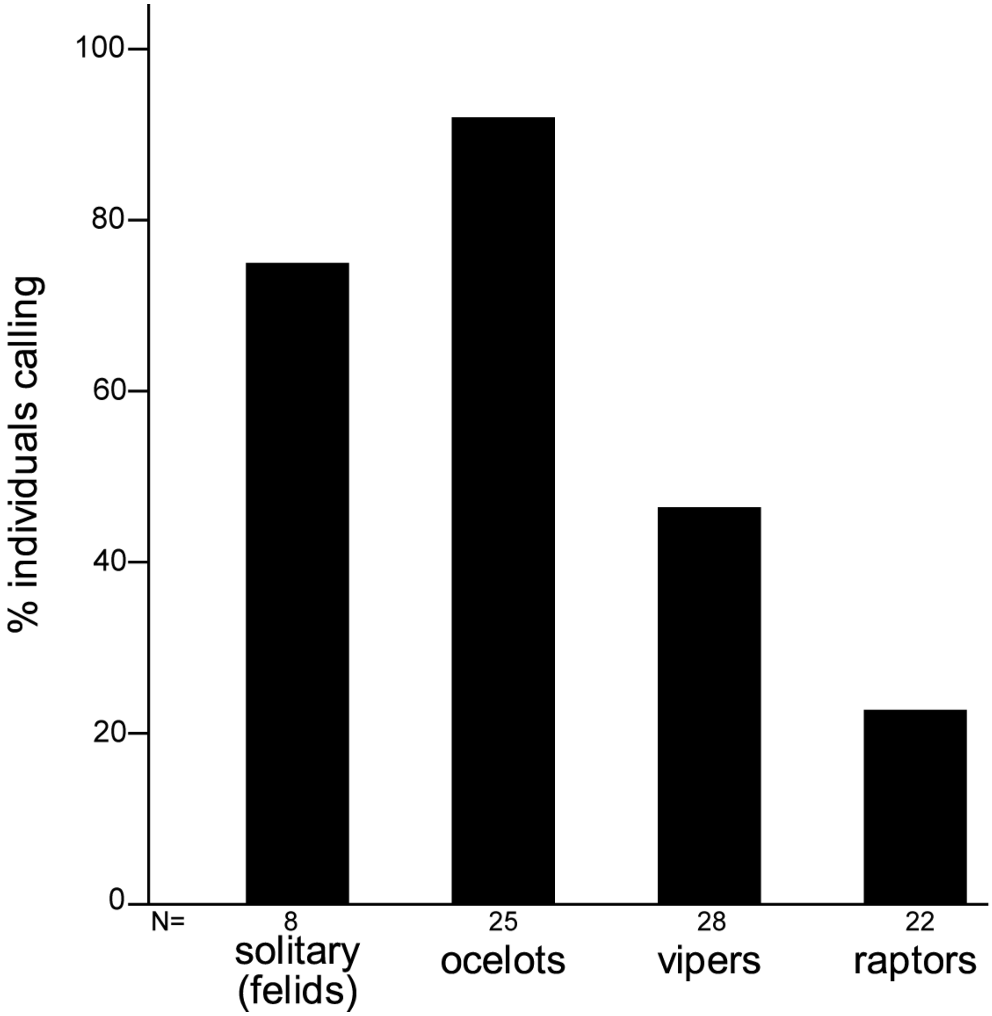

Figure 4.1. Percent of detectors alarm calling in relation to model type. The first column represents the percent of solitary individuals who called to felid models. While nearly all detectors alarm called in response to the ocelot models, fewer than half called in response to vipers, and less than a quarter called in response to raptors. The difference between solitary and non-solitary individuals in propensity to call to felids is not significant (Fisher's exact test: p=0.21).

Table 4.3. Results of univariate binary logistic regression analyses for detections of ocelot models

predictor variable	β	p	N
whole group			
maternal *r*	0.20	0.85	25
dominance rank	-0.08	0.44	16
sire potential	-0.29	0.83	25
sex*maternal *r*	112.18	0.99	25
sex*rank	0.48	0.40	16
sex*sire potential	19.47	0.99	25
females			
# of offspring	17.70	0.99	13

including all four detections of the ocelot model and following two of the four playbacks (Figure 4.1). This probability of calling per detection does not differ significantly from that of non-solitary individuals (Fisher's Exact test: $p=0.21$). In addition, three of the four detectors mobbed the ocelot model, while both individuals who called in response to the puma call approached the speaker.

Viper experiments

Thirteen of 28 (46.4%) individuals called upon detecting a viper model (Figure 4.1). Whether or not an individual called in this context was not predicted by its total maternal *r*, dominance rank, or its sire potential in the univariate analyses (see Table 4.4). Among females, there was a non-significant trend ($p=0.10$) for the number of offspring to predict the response to viper models (see Table 4.4, Figure 4.2). In addition, tests of the interaction between sex and each of the independent variables indicated a significant interaction between sex and total maternal *r* as well as sex and sire potential (see Table 4.4). Further analysis showed that kinship was a nearly significant predictor of whether or not males, but not females, gave an alarm upon detecting a viper model (see Table 4.4, Figure 4.3). The sire potential variable approached significance in the case of males, although with a trend for non-potential sires to be more likely to alarm (see Table 4.4). The latter variable was not tested for females because all females are assigned to the non-potential sire category. Neither the multivariate logistic regression for the whole group ($\chi^2_6=7.02$, $N=22$, $p=0.32$) or for females ($\chi^2_3=7.14$, $N=11$, $p=0.07$) was significant; although the latter model approached significance, none of the individual predictor variables was significant. Finally, additional conspecifics approached and mobbed the model in nine of 13 documented cases, significantly more often than expected (binomial test: $p=0.02$); the sex of the caller did not predict whether or not conspecifics mobbed the model viper (binary logistic regression: $\beta=-0.41$, $N=13$, $p=0.77$).

Perched eagle experiments

Five of 22 individuals (22.7%) alarm called following the detection of a raptor model (Figure 4.1). Callers included a subdominant adult male and four mid to low ranking adult and juvenile females. All five individuals who called as well as 7 of 17

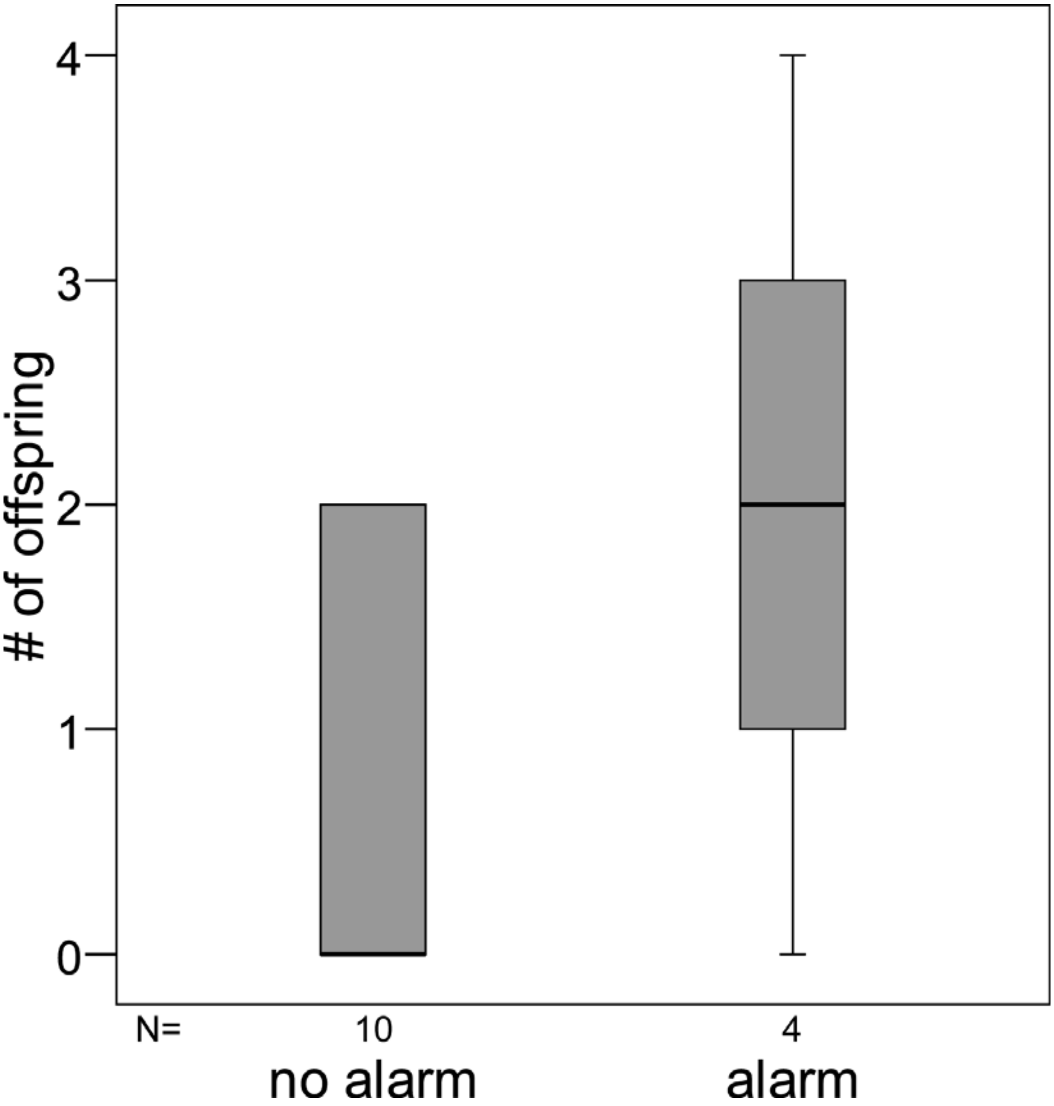

Figure 4.2. Boxplots representing the number of offspring present in the group for females who did and did not call upon detecting a model viper. Boxplots show median (dark line), 1st and 3rd quartiles (box), range (whiskers), and extreme values (open circles). Although non-significant, there is a trend for females with more offspring to be more likely to alarm call.

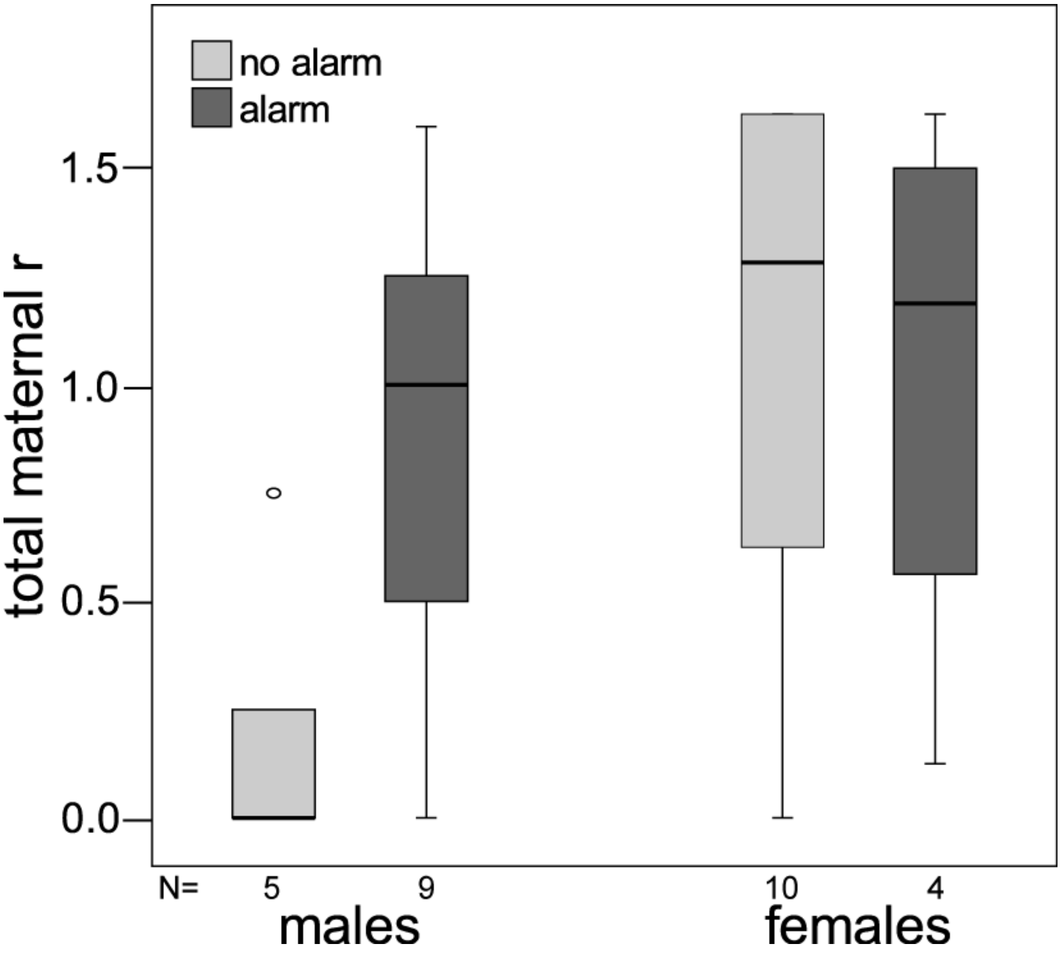

Figure 4.3. Maternal relatedness values for males and females and responses when detecting a model viper. Note that total maternal *r* values do not include an individual's offspring. Boxplots as in Figure 4.2. Total maternal *r* was a nearly significant predictor of whether or not a male alarm called to vipers, while this variable did not predict whether or females called.

Table 4.4. Results of univariate binary logistic regression analyses for detections of viper models

predictor variable	β	p	N
whole group			
maternal *r*	0.43	0.50	28
dominance rank	0.07	0.32	22
sire potential	1.10	0.37	28
sex*maternal *r*	3.21	0.03	28
sex*rank	0.13	0.09	22
sex*sire potential	2.34	0.02	28
females			
# of offspring	0.98	0.10	14
maternal *r*	-1.95	0.85	14
males			
maternal *r*	3.40	0.06	14
sire potential	2.49	0.08	14

Table 4.5. Results of univariate binary logistic regression analyses for detections of raptor models.

predictor variable	β	p	N
whole group			
maternal *r*	1.66	0.12	22
dominance rank	-0.01	0.90	16
sire potential	0.15	0.91	22
sex*maternal *r*	-69.94	0.99	22
sex*rank	-0.14	0.51	16
sex*sire potential	-20.17	0.99	22
females			
# of offspring	0.07	0.87	15

(41.2%) non-callers approached and mobbed the predator model. None of the independent variables or the interaction variables were significant in the univariate analyses (see Table 4.5). Likewise, the multivariate analyses were also nonsignificant (whole group: χ^2_6=3.63, N=16, p=0.73; females only: χ^2_3=2.08, N=10, p=0.55). Sudden "pandemonium" did not follow any of the alarms, while additional group members mobbed the model following all five alarm calls, a value significantly greater than expected (binomial test: p=0.01). Insufficient data were collected to test whether or not intragroup spacing decreased following the alarms.

Discussion

While alarm calls given to each of felids, vipers, and snakes can be explained by the mobbing recruitment hypothesis, no other single hypothesis for the evolution of alarm calling seems to apply to tufted capuchins across all contexts (Table 4.6). However, each of the kin selection, parental care, mobbing recruitment, and pursuit deterrence hypotheses received some support for at least one stimulus type. The selfish herd, group maintenance, conspecific manipulation, and mate protection hypotheses were not supported for any stimulus type. Because of the small percentage of perched hawk eagle detections which resulted in alarms, it is difficult to determine which hypothesis may best explain the evolution of alarms given in this context although the observed trends allow some hypotheses to be eliminated. While the low observed rate of calls given to perched raptors may be a result of insufficiently realistic models, this seems unlikely given that most detectors mobbed the models. Less intense reactions to perched relative to flying raptors have been noted in several previous studies of prey species (e.g., Marler, 1955; Ferrari & Lopes Ferrari, 1990; Macedonia & Evans, 1993; Digweed et al., 2005).

Kin selection

The kin selection hypothesis was not supported for alarms given for felids or raptors but found mixed support for those given in response to vipers (Table 4.6). Immigrant males, unlikely to have kin in the group, consistently alarmed in response to felids and were among the few individuals who called in reaction to the raptor models. In

Table 4.6. Summary of hypothesis support for each stimulus type.

	felids	vipers	perched raptors
Kin selection	-*	+	-
Parental care	-*	+	-
Mate protection	-*	-	-
Selfish herd	-	n/a	U
Predator confusion	-	n/a	-
Group maintenance	-*	-	-
Mobbing recruitment	+	+	+
Pursuit deterrence	+	n/a	-

+ = hypothesis supported
- = hypothesis not supported
* = hypothesis not supported but effects may be obscured by communication to predator
n/a = hypothesis not applicable for vipers
U = not tested, but unlikely to be supported

contrast, total *r* was a nearly significant predictor of whether or not males called in response to the viper models. The lack of significance in this case is likely due to the small number of males who were tested (N=14) In addition, the lack of data on paternity may obscure paternal kinship effects (but see Perry et al, 2008). Support for the kin selection hypothesis for alarm calling has been primarily limited to rodent taxa (see Table 4.1) with only weak support among primates (Tenaza & Tilson, 1977; Chapman et al., 1990).

Parental care

Similar to the kin selection hypothesis, the parental care hypothesis received some support only for alarms given in response to vipers (Table 4.6). In this case, there is a positive trend (albeit nonsignificant) for females with more offspring to be more likely to call in response to a viper than those females with fewer offspring. Again, the lack of significance in the regression model may be a result of a small sample size (N=14). This adds to the widespread support for this hypothesis found in previous studies (e.g., birds: Griesser & Eckman, 2004; primates: Cheney & Seyfarth, 1985; rodents: Shields, 1980; Blumstein et al., 1997; but see Sherman, 1980; Hauber & Sherman, 1998; see also Table 4.1). The fact that the current study gives some support to the parental care but not the kin selection hypothesis for alarm calling among females lends credence to the argument that these hypotheses should be considered separately in future analyses (see Shields, 1980; Blumstein et al., 1997).

Mate protection

The mate protection hypothesis was not supported for alarms given in any context (Table 4.6). In fact, among the viper detections by males, there was a nonsignificant trend for potential sires were to be less likely to alarm. This trend is likely due to the fact that, among males, only juveniles are not potential sires, and juvenile males are more likely than adult males to have kin in the group. While considerable support for this hypothesis has been found in several avian taxa (see Table 4.1), there is only weak evidence suggesting that such selective pressures act on mammalian prey; a study of captive vervets indicated that males alarm more often when in the presence of females than in the presence of other males, although the sample size in this study was extremely small (N=4; Cheney & Seyfarth, 1985).

Selfish herd

The selfish herd hypothesis was not supported (Table 4.6) because individuals who called upon detecting the ocelot model did not achieve a higher neighbor density than in non-experimental contexts. However, group cohesion did increase, albeit not significantly, following an alarm given to felids, probably as a result of individuals approaching and mobbing the predator model (see below). A lack of support for this hypothesis is not surprising given that the short distances in which the capuchins tend to detect predators (Janson, 2007b) provide a small amount of time to employ a proper anti-predator defense. The constraints of an arboreal environment make it unlikely that a caller could attract enough individuals quickly enough to protect itself from an immediate attack (see Terborgh, 1990). Indeed, the only support for a selfish herd benefit for alarm calling has been found among avian taxa in an open environment (Owens & Goss-Custard, 1976). Not only are such taxa more likely to detect predators from long distances, but they can also become a cohesive group much more quickly than can arboreal primates.

Predator confusion

The predator confusion hypothesis was not supported for alarms given in response to ocelots or perched eagles (Table 4.6) because alarm calls did not cause a response in conspecifics that would be predicted to confuse the predator (i.e., a sudden burst of movement or vocalizations). Given that predator detection distances are extremely short (Janson, 2007b), conspecifics likely do not put themselves at great risk by not responding immediately to an alarm call since the detector itself should be far more likely to be chosen by the predator. The predator confusion effect has been argued to benefit flocking redshanks (*Tringa totanus*; Cresswell, 1994a,b) and individuals in groups of Belding’s ground squirrels (*Spermophilus beldingi*; Sherman, 1985). However, there is no evidence indicating that arboreal mammals use the confusion effect to reduce predation risk (Terborgh, 1990).

Group maintenance

The group maintenance hypothesis was not supported (Table 4.6) because no significant relationship between dominance rank and call production was found for any model type. This hypothesis has found support in only one previous study of wild vervet monkeys (*Chlorocebus aethiops*; Cheney & Seyfarth, 1981, 1985). In this case, the authors hypothesized that dominant individuals in vervet groups may benefit by alerting subordinates to the presence of a predator because the loss of an individual often leads to instability in the dominance hierarchy (Cheney & Seyfarth, 1985). Thus the loss of a groupmate to a predator may be both costly to dominants and a beneficial to subordinates (Cheney & Seyfarth, 1985). Because such variation in costs and benefits between dominants and subordinates is also expected in capuchins (see Janson, 1985, 1990a,b), this may explain why dominant capuchins alarm in response to dangerous stimuli, but it does not explain why subordinates also do so.

Mobbing recruitment

Mobbing recruitment was supported for all three stimulus types (Table 4.6). Because alarm callers normally approached and mobbed the models, it is possible that conspecifics were reacting to this non-vocal cue rather than to the call; however, this seems unlikely given that forest density greatly limits the effectiveness of non-vocal communication. This is supported by the fact that playbacks of alarm calls often caused others to approach the speaker (Chapter 2; Wheeler, unpublished data). Mobbing is a common anti-predatory strategy among vertebrates including birds (e.g., Owings & Coss, 1977), fish (e.g., Ishihara, 1987), rodents (e.g., Kobayashi, 1996), and primates (e.g., Gautier-Hion & Tutin, 1988; Ross, 1993, Passamani, 1995; Gursky, 2005, Lloyd et al., 2006; Erbere & Kappeler, 2007) and is well-documented in capuchin monkeys (*C. apella*: van Schaik & van Noordwijk, 1989; *C. capucinus*: Chapman, 1986; Boinski, 1988; Perry et al., 2003a) and it has been suggested that their alarms may recruit conspecifics to mob (Digweed et al., 2005). Such behavior by conspecifics may be beneficial if it deters the predator and/or if it allows immatures to learn to identify dangerous stimuli ("cultural transmission" hypothesis: Curio, 1978b; Srivastava, 1991). The latter may increase the caller's inclusive fitness if it aids immature kin in predator recognition but can also directly benefit the caller if the younger individual later recognizes a predator and alarm calls, thereby warning the original caller (Curio, 1978a).

Pursuit deterrence

The pursuit deterrence hypothesis was supported for calls given to felids (Table 4.6). The lack of an audience effect in this context indicates that alarm calls may serve to communicate to the predator itself in addition to conspecifics (i.e., to recruit mobbers). Since most forest-dwelling felids depend largely on surprise in order to ambush their prey (see Terborgh, 1990; Treves and Palmqvist, 2007), capuchin monkeys should benefit by communicating to such a predator that it has been detected and that the chance of a successful hunt has therefore diminished. This hypothesis is further supported by two additional lines of evidence. First, nearly all detections of ocelots resulted in alarm calls, indicating that nearly all detectors likely benefit by calling. This may in fact obscure other benefits for the caller, including the decreased predation risk for mates and/or kin. Second, capuchin monkeys more often respond to playbacks of terrestrial predator-associated alarms by approaching the speaker than by fleeing to safety (Wheeler in prep.). The latter behavior suggests that an individual likely benefits by locating the potential predator even if it must move closer to do so. Previous studies have indicated mixed support for the pursuit deterrence hypothesis. Support has been found in a study of six sympatric Old World monkeys, wherein more alarm calls were given in response to the leopards (*Panthera pardus*), which rely on surprise to capture prey, than to those of chimpanzees (*Pan troglodytes*), which pursue primate prey through the trees even after being detected (Zuberbühler et al., 1999). Likewise, several studies of birds and ungulates have demonstrated a lack of a conspecific audience effect for the production of anti-predator signals (Woodland et al., 1980; Reby et al., 1999; Haftorn, 2000; Murphy, 2006; see also Ostreiher, 2003). The strongest evidence favoring this hypothesis comes from studies showing that ambush predators give up their hunt when prey produce anti-predator signals (e.g., Clark, 2005; Zuberbühler et al., 1999) . In contrast, the hypothesis is not supported by a number of studies among primates and birds which demonstrate a conspecific audience effect for alarm calling (Sullivan, 1985; Karakashian et al., 1988; Cheney & Seyfarth, 1990; Wich & Sterck, 2003; Krams et al., 2006). Such findings indicate that the lack of an audience effect in the current study is unlikely due to cognitive constraints.

Future directions

Future studies of alarm call function in capuchin monkeys should examine calls given in response to flying raptors. Several studies have indicated that alarm calling behavior in response to flying raptors differs considerably from that which occurs in response to perched raptors (e.g., Marler, 1955; Ferrari & Lopes Ferrari, 1990; Macedonia & Evans, 1993). The behavior of Neotropical felids that prey on capuchins should be examined to determine whether or not alarm calling affects their hunting behavior as has been in shown in forest leopards (Zuberbühler et al., 1999; Zuberbühler & Jenny, 2007; see also Chapter 5). Finally, possible within-species variation in alarm call function based on habitat type (e.g., open vs. closed) should be examined to determine if predator detection distances affect alarm calling behavior.

Conclusions

In summary, the fitness benefits that tufted capuchin monkeys receive by alarm calling in the presence of predators and vipers vary with the type of stimulus detected. Specifically:

1. The group maintenance, selfish herd, and mate protection hypotheses do not explain the benefits an individual receives by alarm calling in any context examined.
2. Alarms given in response to predatory felids are likely selfish, serving to communicate to the predator that it has been detected. This is supported by the fact that even solitary individuals with no conspecific audience alarm call in response to these predators. Individuals who alarm call following a felid detection may also directly benefit by recruiting conspecific mobbers since this may further deter the predator, drive it out of the area, and/or allow younger individuals to learn to identify the predator.
3. Alarms given to vipers, which are unlikely to be capuchin predators, demonstrated the only example of altruistic alarm calling in the study animals.

Alarms given by males in this context are best explained by kin selection. In contrast, alarm calls given by females in response to vipers appear to serve as a form of parental care. Individuals nay further benefit by calling in this context by recruiting individuals to mob the viper. Mobbing by conspecifics may benefit the caller by allowing young individuals to learn to recognize dangerous stimuli via cultural transmission.

4. Capuchins infrequently gave alarms to perched eagle models. In the few cases when detectors did call in this context, the call was followed by mobbing by additional conspecifics, indicating that alarm calling in this context is a selfish behavior. However, it is unclear why they do not give alarm calls more often; calling would be relatively low-cost given that non-calling detectors normally approached and mobbed the predator model.

Chapter 5

Are Tufted Capuchin Monkey Alarm Calls Pursuit Deterrent Signals? Insights from Hawk Eagle Behavior

Abstract

One proposed function of anti-predator signaling in animals is that they deter the predator from pursuing the caller. While a number of studies of alarm calling in vertebrates have lent support to the "pursuit deterrence" hypothesis, the majority of these studies examined only the behavior of the prey species. In this study, the effect of anti-predator calls of tufted capuchin moneys (*Cebus apella nigritus*) on the hunting behavior of a primate predator, the crowned hawk eagle (*Spizaetus* spp.), was examined at a wildlife rehabilitation center near Igauzú National Park, Argentina. Captive hawk eagles were presented with a choice of two identical prey items (house mice: *Mus musculus*) each accompanied by either a capuchin monkey alarm call, a capuchin food-associated call, or no acoustic stimulus. The intensity of the acoustic stimulus was varied such that in some experiments the alarm call was of higher amplitude or lower amplitude than the food-associated call. The hawk eagles did not prey less often on individuals associated with anti-predator calls, but they did prey less often on those associated with high amplitude calls. This suggests that while production of a specific type of call is not necessary for capuchins to deter predators, capuchins who vocalize intensely during predator encounters may benefit by discouraging the predator from engaging in pursuit.

Introduction

Individuals who produce conspicuous signals in the presence of a predator may benefit either indirectly, for example by alerting kin, or directly, for example by deterring the predator from launching an attack (reviewed in Hauser, 1996; Caro, 2005). This "pursuit deterrent" function of alarm calling may occur if predators rely on surprise to successfully capture prey and the chances of a successful hunt diminish considerably once the predator has been detected (Woodland et al., 1980). A number of studies of bird, rodent, and mammalian alarm calls have lent support to this hypothesis (e.g., Cresswell, 1994c; reviewed in Caro, 2005). However, many of these studies focused only on the behavior of the prey species and rely primarily on the elimination of alternative hypotheses (Caro, 1995). For studies that rely exclusively on the behavior of the prey species, the best evidence has been the lack of a conspecific audience effect for the production of anti-predator signals; if individuals produce the signals even when there are no potential conspecific receivers in the area, then it seems likely that the signaler is attempting to communicate with the predator (e.g., Woodland et al., 1980; Murphy, 2006; Wheeler, 2008). Stronger evidence in favor of the pursuit deterrent hypothesis has come from studies that show that predators do not attempt to prey on individuals who have produced anti-predator signals. For example, in a study of forest leopards (*Panthera pardus*), it was shown that these predators give up their hunt following the production of alarm calls by primate prey (Zuberbühler et al., 1999). Likewise, foraging timber rattlesnakes (*Crotalus horridus*) waiting in ambush leave the area and find a new location to sit and wait following the production of conspicuous visual signals by rodent prey (Clark, 2005).

Acoustic signals may deter predators for two distinct but non-mutually exclusive reasons. First, if prey that have detected a predator both regularly produce a particular call and are less likely to be captured than those that have not detected the predator, then predators may associate the production of that call with decreased hunting success and avoid individuals that produce it. Second, the acoustic features typical of alarm calls, such as high amplitudes (i.e., perceived as loud), are known to elicit arousal or annoyance in call receivers (reviewed in Owren & Rendall, 2001). If alarm calls have such an affective response on predators, then they may efficiently deter pursuit (see Masters, 1979; Kraus et al., 1997; Patek et al., 2001).

Among tufted capuchin monkeys (*Cebus apella nigritus*), the lack of a conspecific audience effect for the production of alarm calls in the presence of terrestrial predators has been argued to provide indirect support for the pursuit deterrence hypothesis for the production of these calls (Wheeler, 2008). It is unclear, however, if alarm calling by capuchins reduces the likelihood that predators will attempt to prey on the caller. This study tests whether or not the production of capuchin alarm calls specifically or high amplitude calls generally affects the prey choice of a capuchin predator (hawk eagles: *Spizaetus* spp.) in a captive setting. If the calls that capuchins produce upon encountering predators serve as pursuit deterrent signals, it is predicted that hawk eagles will avoid preying upon individuals associated with these calls. If predators are deterred not by specific call types but rather by call intensity, then it is predicted that prey individuals associated with higher amplitude calls will be selected less often by hawk eagles than individuals associated with lower amplitude calls, regardless of the context that typically characterizes the production of the particular call type. Finally, if neither call type nor call amplitude affects predator hunting decisions, then hawk eagles should show no prey preference based on either of these two criteria.

Methods

Study site and subjects

The study was conducted at Güirá Oga, a privately owned wildlife rehabilitation center that borders the Iguazú National Park in Puerto Iguazú, Argentina. The center houses several avian and mammalian species indigenous to the area, with the ultimate goal of reintroducing them to their natural habitat. During the period from May 2005 to December 2006, the center housed one adult male black hawk eagle (*Spizaetus tyrannus*) and one adult male and one adult female ornate hawk eagle (*S. ornatus*). Each of the three individuals was wild-born but all were trapped as juveniles and kept as pets until being confiscated and given to the rehabilitation center. As a part of the rehabilitation process, the individuals were taught to hunt small birds and rodents, including house mice (*Mus musculus*).

Both the black and the ornate hawk eagle are found throughout much of tropical Central and South America (Brown & Amadon, 1968). Adult black hawk eagles range in size from 0.9 to 1.1 kg while ornate hawk eagles are somewhat larger at 0.8 to 1.6 kg (data cited in Terborgh, 1983). Most observations indicate that Neotropical hawk eagles prey primarily on smaller-bodied vertebrates including birds, monkeys, rodents, and snakes (Robinson, 1994). The majority of reports of predation on primates by these species indicate a preference for smaller-bodied species including *Callicebus*, *Saguinus*, and *Saimiri* (Terborgh, 1983; Heymann, 1990), all of which weigh less than 1.5 kg (Smith & Jungers, 1997). However, black hawk eagles have been observed to hunt species as large as the brown howler monkey (*Alouatta guariba*; Miranda et al., 2006), which, at 4.4-6.7 kg, is among the larger of the New World monkeys (Smith & Jungers, 1997).

Tufted capuchin monkeys are diurnal and arboreal primates (Fleagle, 1999) that range in size from 2.5-3.5 kg (Smith & Jungers, 1997). In Iguazú National Park, these two species of hawk eagles are the only aerial predators present that are likely to pose a threat to capuchins (J. Anfuso, pers. comm.). Since observations on capuchins began at the site in 1991, hawk eagles have been observed to attack capuchin groups on only two occasions (Di Bitetti, 2001a; see also Chapter 1 for additional details). However, despite the paucity of observed predation attempts by raptors at the site, capuchins seem to recognize raptors as potentially dangerous because they regularly give alarm calls in response to even non-threatening flying stimuli which superficially resemble raptors (e.g., vultures and toucans; see Chapter 2). Capuchins at the site also face terrestrial threats from carnivores (tayra: *Eira barbara*; ocelot: *Leopardus pardalis*; puma: *Puma concolor*; jaguar: *Panthera onca*) and venomous snakes (rattlesnake: *Crotalus durissus*; lance-head viper: *Bothrops neuwiedi*, *B. jararaca*). Tufted capuchins produce three distinct call types in response to these aerial and terrestrial threats. Two of these (the “hiccup” and the “peep”) are given in response to potential terrestrial threats, but not aerial ones; the third call, the “bark”, is given only in response to aerial stimuli (see Chapter 2).

Experimental protocol

To test whether prey vocalizations affect predator hunting behavior, experiments were conducted in which a hawk eagle was simultaneously presented two choices of live prey (house mice) which differed in the accompanying acoustic stimulus. The mice used in these experiments were bred at the Güirá Oga rehabilitation center to be given to the raptors to hunt as a part of their rehabilitation training. The protocols were approved by Stony Brook IACUC (protocol numbers 2005-1448 and 2006-1448). The hawk eagle was placed on a perch approximately 0.5 meters above the ground. Each prey individual was placed 20 meters from the raptor in such a way that the angle from one rodent to the raptor to the second rodent was 60º (Figure 5.1). The two rodents were therefore also separated by 20 meters, which is a large enough distance that the raptor could easily determine which prey individual was associated with which acoustic stimulus, even if the calls were somewhat ventriloqual (Marler, 1955). The rodents were tethered to a small branch by a string approximately 15 centimeters in length in order to prevent them from escaping during the experiment. Speakers were placed behind a blind (a large leaf) approximately one meter behind each prey. Besides the speaker, speaker cable, and blind, a 5 m radius around each prey individual was cleared of all material to ensure that both were equally visible and capturable from the raptor's perspective. The prey individuals and speakers were set up while the hawk eagle was out of sight, and the playbacks began a few seconds after the raptor was placed on the perch. Playbacks were conducted with a compact-disc player or an Apple iPod connected to a RadioShack mini-amplified speaker (#277-1008) by a 30 m cable.

During most experiments, one speaker played a recording of an aerial predator-associated call (the "bark") while the second played a food associated whistle series (see Di Bitetti, 2001a, 2003) or no call. In several other experiments, a terrestrial predator-associated call (the "hiccup") was used instead of the bark. In three experiments one speaker played a whistle series while the second played no stimulus (see Table 5.1 for the number of experiments conducted with each stimulus pair). The playback of each of the barks and the hiccups consisted of two calls played two seconds apart and repeating every 30 seconds. Playbacks of food calls consisted of a single call series that lasted approximately three seconds and repeated every 30 seconds. The second playback was initiated 15 seconds following the first, such that one of the two playback stimuli would play every 15 seconds, without any temporal overlap between the two acoustic stimulus types. Sounds pressure levels were set at 65 to 85 dB, measured by a RadioShack 33-

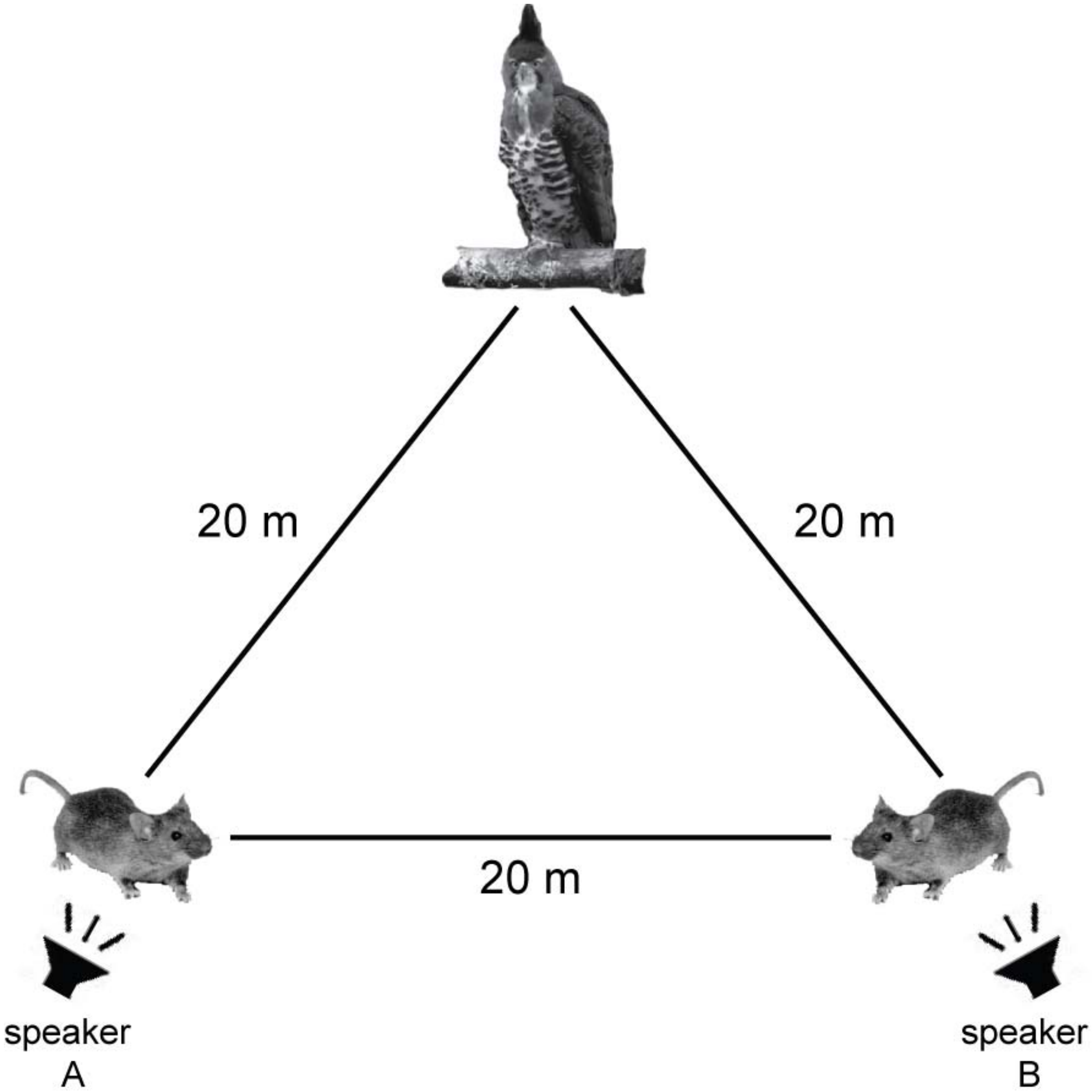

Figure 5.1. The experimental setup used to test the prey preference of hawk eagles based on the acoustic stimulus accompanying each prey individual. Photo of hawk eagle courtesy of Charles Janson. Photograph of mouse from public domain.

Table 5.1. The number of experiments conducted with each pair of acoustic stimuli.

		Stimulus 1			
		bark	hiccup	food call	none
Stimulus 2	bark	-	0	9	4
	hiccup	-	-	0	3
	food call	-	-	-	3

2055 digital sound level meter at a distance of 1 m. Which of the two stimulus types was of higher intensity varied between experiments, such that each of the alarm call and the food-associated call was sometimes the higher-intensity stimulus.

Statistical analyses

Each experiment was scored based on whether or not the raptor chose the prey associated with: 1) the alarm call or not, and 2) the higher intensity call or not. A binomial test was used to determine if the predators preferentially avoided prey individuals associated with certain acoustic stimuli. Three distinct tests were conducted to determine if hawk eagles preferentially avoided prey associated with: 1) barks, 2) either barks or hiccups, and 3) high intensity calls. While a combined model including call type and sound intensity would be ideal as independent variables would be ideal, the limited sample size precludes this possibility.

Results

A total of 19 experiments were conducted in which the hawk eagle chose one of the two prey individuals (see Table 5.1). While the raptor most often chose its prey five to ten minutes after the initiation of the experiment, on a few occasions it occurred as quickly as 45 seconds or as long as 20 minutes into the experiment.

The raptors did not preferentially avoid the prey individuals associated with capuchin aerial predator-associated alarm calls (barks), choosing the other prey individual in only 7 of 13 cases (binomial test: p=0.500; Figure 5.2). Likewise, they did not avoid prey associated with alarm calls generally, avoiding the prey individual associated with the alarm call in 10 of 16 cases (p=0.227; Figure 5.2). Finally, the raptors did show a preference for prey based on the intensity of the stimulus; predators avoided the prey individual associated with the higher intensity call in 14 of 18 trials (p=0.015; Figure 5.2).

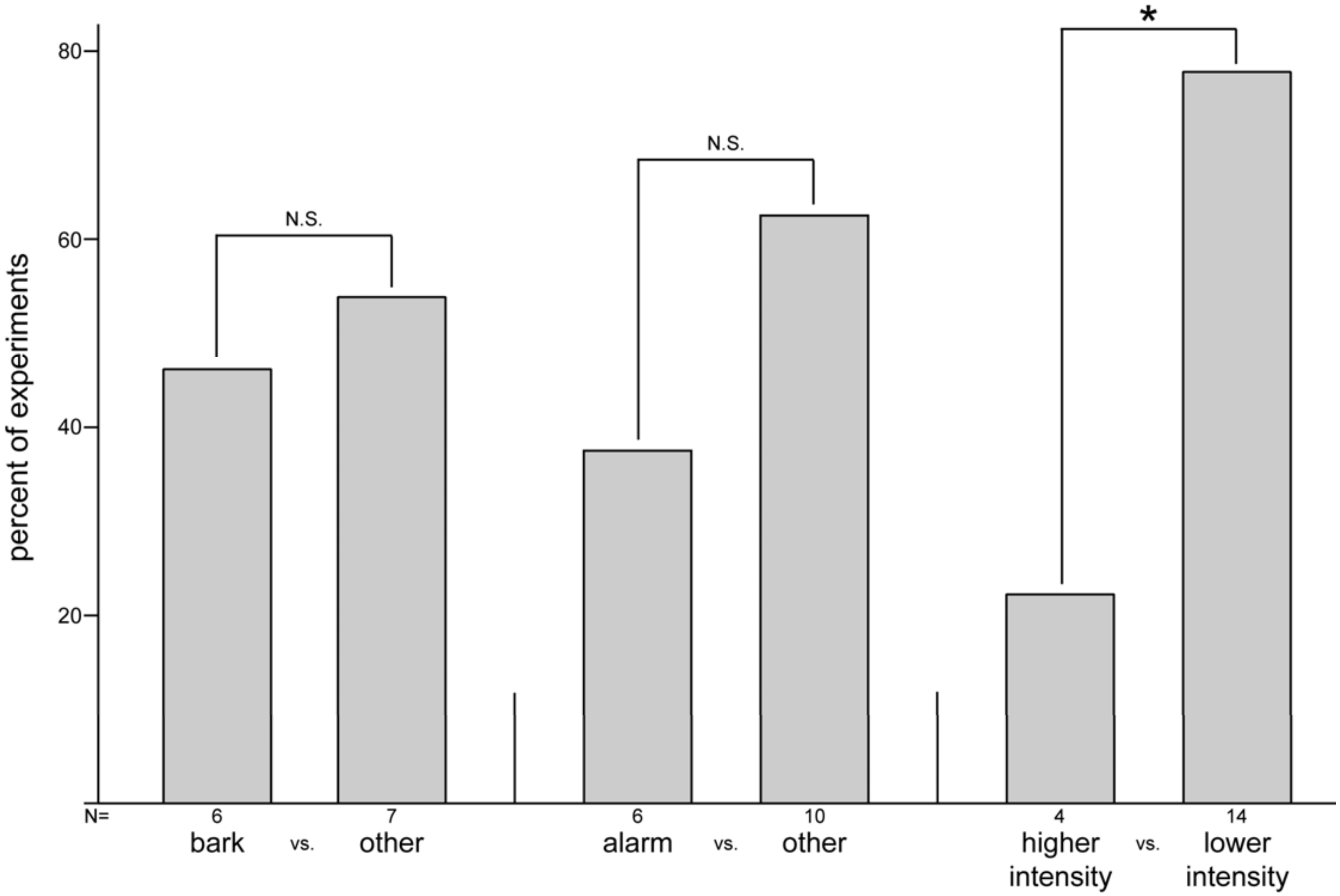

Figure 5.2. Prey preferences of the hawk eagles based on the acoustic stimulus that accompanied each of the two prey individuals. N.S.= nonsignificant; *p<0.05.

Discussion

The results of this study indicate that capuchin vocalizations can be effective at deterring predation by raptors, although aerial predator-specific calls are not uniquely suited to doing so. Indeed, when the hawk eagles had a choice between a prey individual associated with a relatively low intensity bark and another associated with a relatively high intensity non-alarm call, the predator showed a strong preference for the prey associated with the alarm call. It thus seems unlikely that the tamed hawk eagles used in this study associate production of these calls with a decrease in hunting success. However, because these individuals likely had only limited experience hunting under natural conditions (and perhaps no experience in hunting prey as large as capuchins), it is not clear if such patterns would characterize experienced capuchin-hunting raptors in the wild. Thus, although previous work has shown that in some avian taxa even inexperienced individuals recognize visual warning signals that communicate the unprofitability of potential prey (Smith, 1975, 1977), it seems unlikely that hawk eagles have innate recognition of the alarm calls of prey species.

Although the observed trends do not indicate that aerial predator-associated calls are better suited to deter pursuit by raptors than are other calls not typically produced in the context of predation, they do lend support to the hypothesis that conspicuous, high intensity sounds in general may distract predators (Masters, 1979; see also Owren & Rendall, 2001). Capuchin monkeys may therefore be able to effectively deter predation attempts by raptors by vocalizing conspicuously when detecting them, adding to the taxonomically-widespread evidence, both direct (e.g., Zuberbühler et al., 1999; Clarke, 2005) and indirect (e.g., Woodland et al., 1980; Caro et al., 1995; Murphy, 2006; Wheeler, 2008), for such a function of anti-predator signaling.

These results indicate that a primary benefit to capuchins who call upon detecting raptors may be a selfish one, with such behaviors decreasing the likelihood that the caller will be preyed upon. However, it is unlikely that communication with the predator is the sole function of such calling. Capuchin mokeys produce a specific call in response to raptors (barks), and this call is not produced in other contexts (see Chapter 2). Because other call types can efficiently deter pursuit by raptors, it would be unnecessary for capuchins to produce a predator-specific call if pursuit deterrence was the sole function. It thus seems likely that the context specificity of production of barks functions to alert conspecifics to the presence of an aerial predator. Alerting conspecifics to a raptor's presence seems to be a selfish act in tufted capuchins, because the calls regularly recruit other individuals to mob the predator (Wheeler, 2008). Further investigation, however, may reveal additional functions such as warning of kin (Maynard Smith, 1965), offspring (Williams, 1966), or mates (Witkin & Ficken, 1979).

Conclusions and future directions

The vocal behavior of prey individuals has an effect on the hunting behavior of hawk eagles. These raptors avoid preying on individuals that produce high intensity vocalizations, likely because such calls by prey cause an affective reaction of annoyance or disturbance in the predators. However, the data do not indicate that raptors preferentially avoid prey that produce alarm calls. This may be a result of the fact that the individuals tested had little experience hunting in the wild and therefore have not formed an association between specific call types by prey and detection of the predator by those prey. Future studies should examine the effect that alarm calls and call intensity have on the hunting behavior of wild, experience predators. Attention should also be paid to situational variation in intensity of alarm calls by prey. Although it seems that tufted capuchins produce higher intensity alarm calls in higher urgency situations (i.e., when the threat of an immediate attack is relatively high and pursuit deterrence is likely most beneficial), no quantitative data are available to demonstrate this convincingly (see Chapter 2).

Chapter 6

Monkeys Crying Wolf? Tufted Capuchin Monkeys Use Functionally Deceptive Anti-predator Calls to Usurp Resources from Conspecifics

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Abstract

The use of "tactical deception" is argued to have been important in the cognitive evolution of the Order Primates, but systematic studies of active deception in wild nonhuman primates are lacking. This study tests whether wild tufted capuchin monkeys (*Cebus apella nigritus*) use alarm calls in a functionally deceptive manner to usurp food resources. If capuchins use alarm calls "deceptively", it was predicted that false alarms should be: 1) given by subordinates more than by dominants, 2) more frequent when food is most contestable, 3) more frequent when less food is available, and 4) given when the caller is in a spatial position in which it could increase its feeding success if conspecifics react to the call. These predictions were tested by observing subjects in experimental contexts in which the amount and distribution of a high value resource (banana pieces) were manipulated using wooden platforms suspended from tree branches. While false alarms were more common when more food was available, the three remaining predictions were supported. These results generally support the hypothesis that alarm

calls are used by capuchins to reduce the effects of feeding competition. Whether this is intentional on the part of the caller requires further investigation.

Introduction

Animal signals are argued to function to manipulate the behaviour of signal receivers in a way that preferentially benefits the signaller (Dawkins & Krebs, 1978; Krebs & Dawkins, 1984). Anti-predator signals have long been challenging to explain because of the danger that the signaller imparts on itself in an apparent attempt to warn others of impending danger. While numerous hypotheses potentially explain how an individual who has detected a predator can benefit directly or indirectly by eliciting anti-predator behaviour in conspecifics (reviewed in Hauser, 1996; Wheeler, 2008), individuals could also use alarm calls in the absence of a predator to distract signal receivers and take advantage of the momentary diversion of attention. Cases such as this wherein individuals produce a signal outside its "normal" context in order to distract listeners is a form of what has been termed tactical or functional deception (Whiten & Byrne, 1988; Hauser, 1996, 1997).

Functionally deceptive behaviours are expected to be uncommon, especially in social animals where the need to cooperate with group members is common and the potential for targets to habituate to such behaviours is high (Cheney & Seyfarth, 1990). This prediction has been largely supported by the fact that observation of behaviours that can be interpreted as functionally deceptive are rare and largely anecdotal (Byrne & Whiten, 1990). However, functionally deceptive behaviours can in theory be relatively common if the cost of not responding with an "appropriate" reaction is high (Mitchell, 1988) or if targets are largely unable to determine whether or not the agent's behaviour was indeed deceptive or honest (Whiten & Byrne, 1988). Both of these criteria may apply to alarm calls, as the cost of not responding with an anti-predatory behaviour is potentially death, and because false alarms due to misclassification of innocuous stimuli may be common (e.g., Haftorn, 2000), especially in environments with poor visibility (see Evans, 1997).

Given these features of alarm calls, it is perhaps not surprising that nearly all systematic studies of functionally deceptive uses of vocalizations among vertebrates in natural conditions have involved the use of predator-associated vocalizations outside a predatory context. In one of these studies, it was found that the post-copulatory calls given by male Formosan squirrels (*Callosciurus erythraeus*) do not differ acoustically from the calls that are typically given in response to terrestrial predators, and that playbacks of post-copulatory calls cause receivers to employ anti-predator behaviours similar to those observed in reaction to calls that are given in response to predators (Tamura, 1995). Such anti-predator reactions in post-copulatory contexts likely benefit the caller because they reduce the likelihood of sperm competition and therefore increase the proportion of the female's litter being sired by the caller. Similarly, male barn swallows (*Hirundo rustica*) frequently give false alarm calls in apparent attempts to mate-guard (Møller, 1990). In a third study, two avian taxa, white-winged shrike tanagers (*Lanio versicolor*) and bluish-slate antshrikes (*Thamnomanes scistogynus*), were observed to use false alarms to distract foraging competitors in a way that potentially allowed the caller to arrive at the food source before it could be obtained by the competitor (Munn, 1986a,b).

An additional study conducted under experimental conditions similarly showed that great tits (*Parus major*) successfully used false alarms to distract competitors during feeding (Møller, 1988). Here it was found that individuals did not give false alarms if they were only in the presence of individuals whom they could easily displace with threat displays (i.e., subordinate individuals), but did when in the presence of those that could not be easily displaced (i.e., individuals of similar or higher rank). In addition, false alarms were more common when the food was more clumped, and therefore more easily monopolized by dominants, than when it was more dispersed. Similar uses of false alarms in feeding contexts have been observed anecdotally in a number of taxa including nuthatches (Tramer, 1994), foxes (Rüppell, 1986), and primates (Byrne & Whiten, 1990; Gouzoules et al., 1996).

To date, only a pair of studies have examined passive deception (i.e., the withholding of information) in free ranging primates by showing that some species selectively withhold food calls on some occasions (Hauser, 1992; Di Bitetti, 2005).

Passive deception is likely more common among animals than active deception (i.e., providing false information, such as producing food calls in the absence of food) due the difficulty in detecting the behaviour (Cheney & Seyfarth, 1990). However, the classification of instances in which individuals do not provide information to others as deceptive has been criticized on the basis that the withholding of an altruistic act is not necessarily "cheating" (see Owings & Morton, 1998). In contrast, actively providing false information is more widely accepted as a functionally deceptive behaviour (see Searcy & Nowicki, 2005). There is not yet systematic evidence that any primates actively use signals outside their "appropriate" context (but see Slocombe & Zuberbühler, 2007 for evidence of functionally deceptive exaggeration of signals in chimpanzees, *Pan troglodytes*), Systematic studies of such behaviour with wild primates are important given that the ability to use tactical deception is argued to have been an important factor in the cognitive evolution of primates (Whiten & Byrne, 1988).

This study examines the use of terrestrial predator-associated calls by tufted capuchin monkeys (*Cebus apella nigritus*) in experimental feeding contexts when no predators or other potentially threatening stimuli are present. This study was undertaken after initial *ad libitum* observations indicated that these calls were given far more often in these experimental contexts than in natural contexts, although it was not clear if this increased production of alarm calls reflected a strategy for usurping resources, as has been shown in the avian taxa discussed above. If anti-predator calls are indeed used during feeding to usurp resources from conspecifics, several testable predictions can be made. First, because dominants can easily usurp resources from subordinates through displacements (although the reverse is not true), false alarms should be given more often by subordinates than by dominants (see Møller, 1988). Second, false alarms should be more common when food is more clumped, and therefore more contestable, than when more dispersed. Third, false alarms are expected to be more common when less food is available. Fourth, false alarms should be given when the caller is close enough to the contested resource to take advantage of any conspecific reactions. Finally, the false alarms should elicit anti-predator reactions, just as alarm calls given in response to real threats do (Wheeler in preparation).

Methods

Study site and subjects

Data were collected between May 2005 and December 2006 in Iguazú National Park, Argentina (25°40'S, 54°30'W), a semi-deciduous and sub-tropical forest (see Di Bitetti et al., 2006 for additional details regarding the study site). Tufted capuchins are largely frugivorous primates, although a considerable portion of their diet consists of insect prey (Brown & Zunino, 1990). In Iguazú, capuchin groups typically range in size from 7-30 individuals (Di Bitetti, 2001), although groups of up to 45 individuals have been observed (C. Janson unpublished data). Dominance hierarchies are linear with dominant individuals winning contests over food and spatial position (Janson, 1985, 1990a,b, 1996; Di Bitetti & Janson, 2001b). The species is mostly arboreal, primarily inhabiting the mid to lower canopy (Fleagle & Mittermeier, 1980). All data for this study came from a single study group, the Macuco Group, which ranged in size from 23-28 individuals during the study period. All study subjects were readily recognizable based on facial characteristics.

The alarm call repertoire of tufted capuchins includes three acoustically distinct call types; one of these (the "bark") is given exclusively in response to aerial stimuli, while the other two (the "peep" and the "hiccup") are given in response to both felids and snakes (Wheeler, in preparation). The number of hiccups an individual produces seems to reflect the degree of risk facing the caller. Callers tend to give two or more hiccups in quick succession in high-risk situations (such bouts are hereafter referred to as "high-urgency hiccups"). In contrast, in non-urgent situations (i.e., when no predators are present) which are nevertheless stressful for the caller (primarily when the risk of falling is high), callers tend to produce only a single call (Wheeler, in preparation). Playbacks of both barks and high-urgency hiccups indicate that these calls elicit anti-predator reactions in call receivers, although "look" reactions are far more common than "escape" reactions (Wheeler, in preparation). In contrast, call bouts consisting of only a single hiccup rarely elicit anti-predator reactions in call receivers (Wheeler, unpublished data), indicating that conspecific listeners do not interpret such calls as indicative of a threat.

Experimental protocol

Data on false alarm call production during feeding were collected in experimental contexts wherein the quantity and distribution of a high-value resource (banana pieces measuring approximately 2.5 cm) were manipulated using 1m x 1m platforms suspended from tree branches by a system of ropes and pulleys at 3 to 10m above the ground (Figure 6.1; see also Janson, 1996; Di Bitetti & Janson, 2001b for additional descriptions of feeding platform experiments). Within a given experimental site, the fruit pieces were distributed across one to six platforms in order to vary the degree of monopolizability of the resource. The quantity of food available was manipulated by varying the number of bananas provided from two to 30. Within a site, individual platforms were spaced at least 15 m apart, but the site was spread over no more than 40 m. Different experimental sites were separated by at least 250 m and were placed at least 150 m from naturally occurring fruit patches. The spatial distribution of the platforms within and between sites, relative to group spread, allowed each site to mimic a single food patch, while different sites mimicked distinct patches. During most months, two experimental sites were used simultaneously; the sites were set up on the final day of the month and were provisioned once a day for thirteen consecutive days following their discovery by the study group. During the three months of the Argentine winter there were 8 sites used simultaneously and bananas were provided at each site everyday that the study group visited for the entire three month period.

The banana pieces were placed in the platforms as the group approached the experimental site, but before arriving. When the group arrived, one or two observers each chose a focal individual over six months in age (when they begin to spend most of their time away from their mothers), following it until all banana pieces had been eaten, and collected data on the its behaviour using both instantaneous and continuous sampling methods (Martin & Bateson, 2007). All data were spoken into an audio recorder. Every thirty seconds, observers noted the focal animal's location (within 2 m of a platform with food or greater than 2 m from a platform with food). All hiccups given by the focal animal were noted continuously, and the animal's location at the moment the call was given was recorded. All occurrences of anti-predator escape reactions employed by other

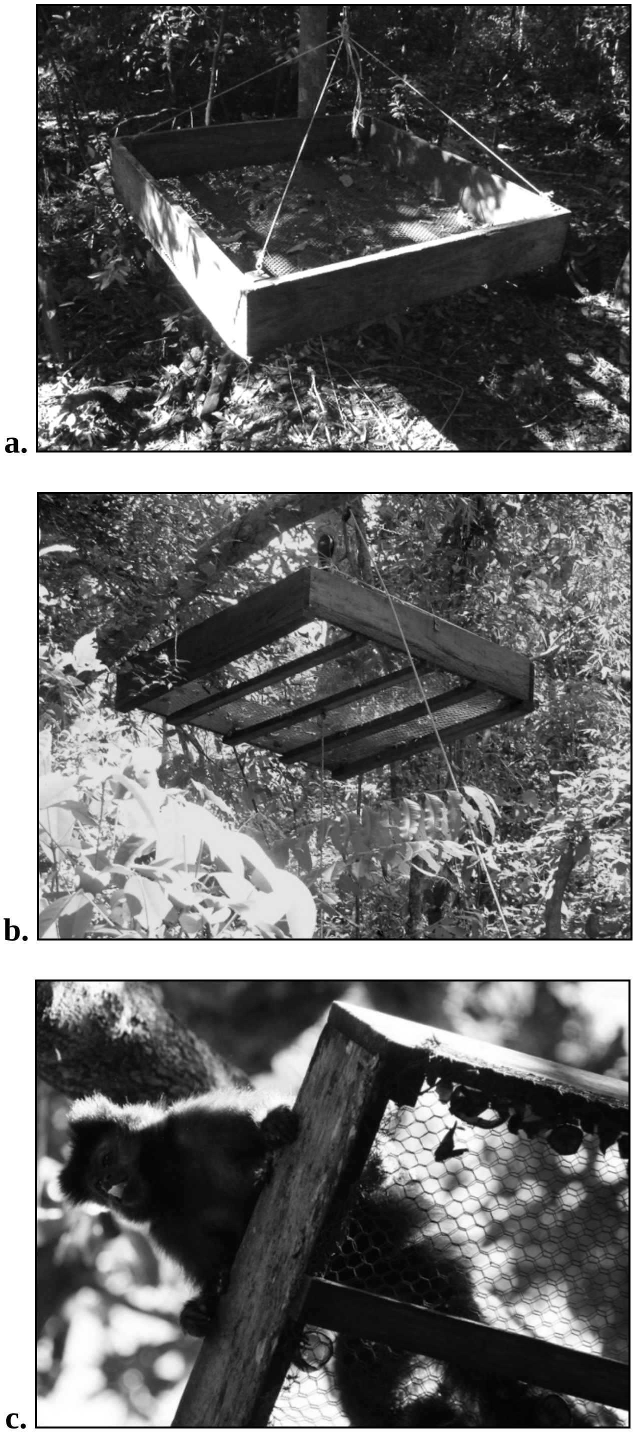

Figure 6.1. The feeding platforms used in this study: a) a lowered platform, b) a raised platform, c) the alpha female feeding in a raised platform.

group members within a 10 m radius of the focal animal following an alarm call by the focal were noted.

A hiccup produced in the experimental feeding contexts was considered a resource-related (functionally) deceptive alarm call (RRDA) if certain criteria were met which eliminated other likely explanations for call production. First, there must have been an absence of actual or potentially threatening terrestrial stimuli (i.e., felids, snakes, or any similar stimuli which could reasonably be misclassified by the caller to be one of these threats). Because the observer might not see all such stimuli, calls given in conjuction with additional anti-predatory behaviours (including escape reactions, threat displays, or sudden vigilance towards the ground) were considered to have been given in response to actual or potential threats. Likewise, the focal animal's alarm call had to be the first one given in the bout (i.e., no alarm calls were produced by other individuals in the one minute preceding the focal animal's alarm call), as calls given in response may reflect the caller's perception of danger. Second, because hiccups are frequently given by individuals receiving aggression (Di Bitetti, 2001a), calls given in this context were not considered RRDAs. While such calls may be functionally deceptive, as this often causes the aggressive bout to end suddenly, dismissing these calls is a conservative approach toward testing the resource usurpation hypothesis. Finally, the calling bout had to consist of at least two hiccups given over a period of 3 s or less; this rate is similar to the higher-urgency bouts typically associated with detections of vipers and felids. Audio recordings made during the experiments with a K6/ME67 Sennheiser microphone connected to a Marantz PMD-660 digital audio recorder were reviewed to determine if the call rate was sufficient to be considered high-urgency.

Data analysis

For each individual focal follow (of which there were one or two per individual experiment), it was noted simply whether or not the focal animal gave an RRDA at any point during the experiment. Unless otherwise stated, the tests described below are based on whether or not RRDAs were produced during an observation period, not the number of RRDAs given. A Fisher's exact test was used to test whether or not subordinate individuals were more likely to produce RRDAs than dominants. The six highest ranking individuals (as determined through analysis of dyadic agonistic interactions; see Wheeler, 2008 for additional details), including the group's four adult males and the two highest ranking adult females, were placed in the "dominant" category as these are the only individuals who were able to effectively exclude more subordinate individuals (18 of which were sampled) from accessing the platforms (pers. obs.). For this test, each individual was scored based on whether or not it was observed to give an RRDA at least once during any of the first 20 experiments in which it was a focal animal. Many animals were sampled more than 20 times, but additional experiments were not included in this analysis in order to avoid oversampling certain individuals. A few individuals from the study group were sampled less than 20 times (e.g., due to death or dispersal). Although some of these individuals were observed to produce RRDAs, all undersampled individuals were excluded from this analysis in order to prevent a bias towards calling. Wilcoxon signed ranks tests for small sample sizes (Siegel & Castellan, 1988) were used to test whether or not individuals produced RRDAs more often when food was more monopolizable (i.e., distributed across 1 to 3 platforms) than when less contestable (4 to 6 platforms). To be included in this analysis, each individual had to be sampled at least 5 times in each of the two conditions. Because most individuals were not sampled an equal number of time in both conditions, additional experiments of the oversampled condition were not included in the analysis. For example, if an individual was sampled 10 times with 1 to 3 platforms and 15 times with 4 to 6 platforms, then only the first 10 experiments with 4 to 6 platforms were included in the analysis; alarm calls given in any subsequent experiments were not counted. The percent of experiments which elicited RRDAs was then calculated for each individual in each of the two experimental conditions. This same methodology was used to test if false alarms were more common when less food was available. This was tested for both the total amount of food presented (10 bananas or less versus more than 10 bananas) and for the number of bananas per platform (5 bananas or less per platform versus more than 5 bananas per platform). A binomial test was used to determine if RRDAs were given more often than expected when an individual was within 2 m of a platform with food, as callers could easily take advantage of any escape reactions the calls elicited from this short distance. The expected values for this test were calculated as the mean of the percent time (based on the instantaneous focal samples) the callers spent within 2 m of a platform during each experiment in which an RRDA was produced. Although some individuals were observed to produce RRDAs during more than one experiment, only the first such observation by each individual was included in this analysis in order to avoid pseudoreplication. Fisher's exact tests were conducted using SPSS 15.0. Wilcoxon signed ranks tests for small sample sizes were calculated following Siegel and Castellan (1988).

Results

A total of 321 individual feeding platform experiments were successfully conducted during the study period. This resulted in a total of 499 focal follows and a total of 45 hours of focal animal observation. The total number of focal follows conducted with a given number of platforms and food quantity are provided in Table 6.1. Focal animals did not produce high-urgency hiccups in the vast majority of experiments; such bouts were observed during 60 focal follows, while bouts that met the criteria to be considered a resource-related deceptive alarm were given by focal animals in 25 experiments (5% of all focal follows; see Table 6.2).

Production of RRDAs was non-random in terms of which individuals called and in what contexts they did so. Twenty four of the 25 RRDAs were given by subordinate individuals. In total, subordinate individuals produced an RRDA during 24 of 366 experimental focal follows, while dominant individuals did so during only one of 133 focal follows; Figure 6.2). When considering only those individuals sampled at least 20 times, none of the four dominant individuals was observed to produce an RRDA during the first 20 experiments in which they were sampled, while 7 of 8 subordinate individuals did so, a significant difference (Fisher's exact test: N=12, p=0.010). The remaining subordinate individual did produce an RRDA during one experiment, but not until the 22nd experiment in which it was the focal. When undersampled individuals which were observed to produce RRDAs (and are therefore known to be "deceptive callers") are included in the analysis, this difference between dominants and subordinates is even stronger (1 of 5 dominants calling versus 12 of 13 subordinates; N=18, p=0.008). The rank-related difference remained significant even when the one dominant and five

Table 6.1. The total number of focal follows conducted with a given number of bananas distributed across a given number of platforms.

# of platforms	# of bananas				total
	2-4.9	5-9.9	10-19.9	20-30	
1	4	20	28	0	52
2	8	38	49	0	95
3	5	43	39	0	87
4	0	15	78	60	153
5	0	0	23	19	42
6	0	13	43	14	70
total	17	129	260	93	499

Table 6.2. The number of high-urgency hiccups produced by focal animals attributed to each eliciting stimulus.

context of call production	# of instances
reactions to potential terrestrial threats	4
reactions to other alarms	15
reactions to conspecific aggression	16
RRDA	25
total high-urgency hiccups	60

subordinate individuals who were undersampled (i.e., less than 20 experiments) and were never observed to produce RRDAs were included in the analysis as "non-callers" (N=24; p=0.048).

RRDAs were given more often when food was distributed across fewer platforms (one to two platforms:14 of 147 focal follows, 9.5%; three to four platforms: 9 of 240, 3.8%; five to six platforms: 2 of 112, 1.8%; Figure 6.3). Among those individuals who were observed to give one or more RRDAs, 8 gave the calls more when the banana pieces were distributed across 1 to 3 platforms, 2 did so more often when 4 to 6 platforms were used, and one individual showed no difference between the two treatments (one-tailed Wilcoxon signed ranks test: T^- = 6; N=10; p=0.014). Indeed, closer examination shows that the calls were most common when food was distributed across 1 or 2 platforms than across 3 or more platforms (Figure 6.3). However, the frequency of RRDAs did not vary based on food quantity. While 8 individuals called more when more than 10 bananas were presented and only 3 called more when 10 or fewer bananas were given, the difference was not significant (T^+= 19; N=11; p>0.10; Figure 6.4). Likewise, there was no significant effect of the number of bananas per platform. Seven individuals called more when there were 5 or more bananas per platform, while 2 individuals called more when there were less than 5 bananas per platform (T^+=8.5; N=9; N>0.10).

Of the 14 individuals observed to produce RRDAs, 12 (85.7%) were within 2 m of a feeding platform during the first observed calling bout, a significant deviation from the expected value of 5.9152 (based on an average of 42.252% of the experimental time spent in such locations for these 14 experimental observation periods; one-tailed exact binomial test: p=0.001; Figure 6.5). When considering all 25 RRDAs (therefore including multiple contributions from some individuals), 20 (80%) were given when the caller was within 2 m of a feeding platform, again a significant deviation from the expected value of 10.869 (based on an average of 43.476% of the experimental time spent in such locations for these 25 experimental observation periods; one-tailed exact binomial test p=0.0002; Figure 6.5).

The false alarm calls elicited anti-predator escape reactions in one or more neighboring conspecifics in 10 of 25 cases (40%). In seven of these 10 cases, the caller likely increased its feeding success as a result of the conspecific reactions. On four

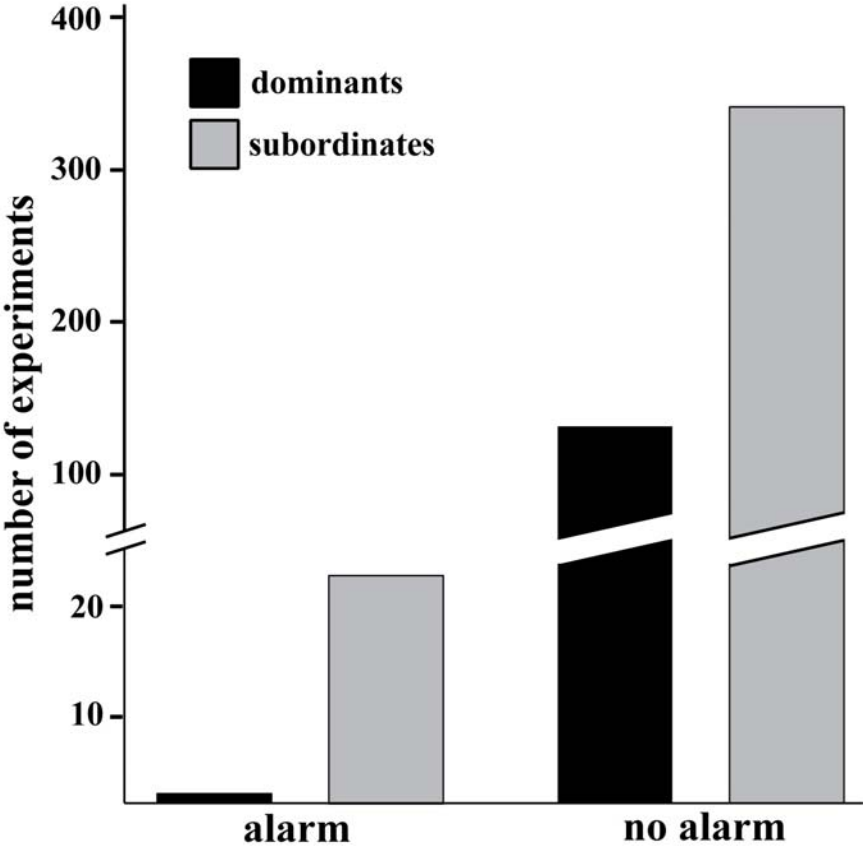

Figure 6.2. The number of experiments in which dominant and subordinate focal animals did and did not produce resource-related deceptive alarm calls. Subordinates were significantly more likely to produce deceptive alarm calls than were dominants.

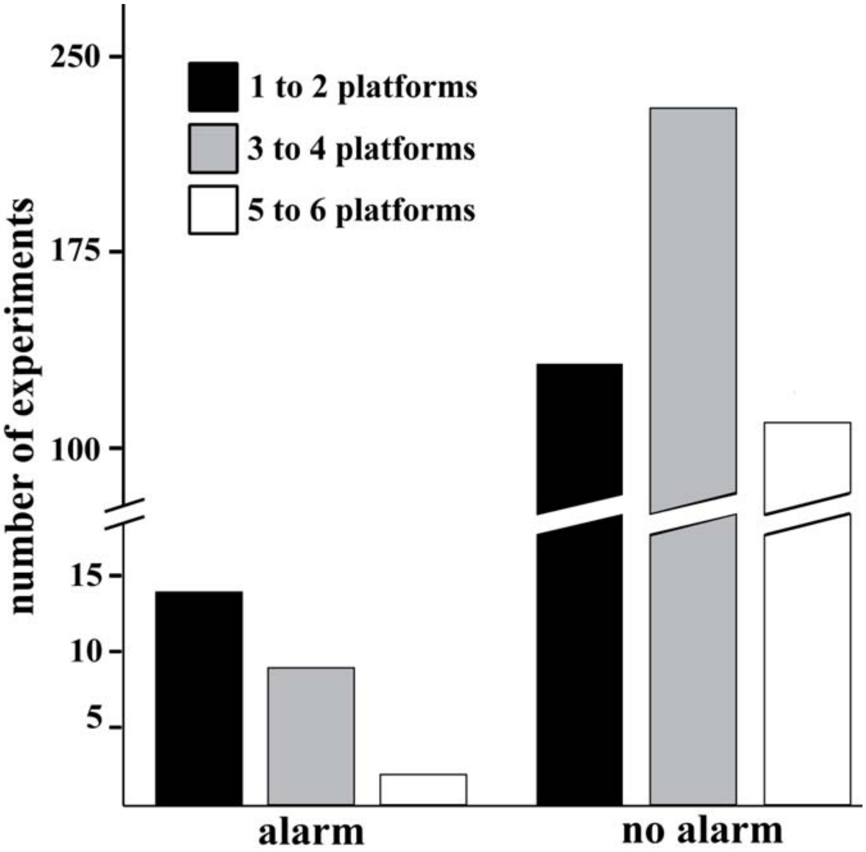

Figure 6.3. The number of experiments with a given number of platforms in which a focal animal did and did not produce resource-related deceptive alarm calls. Deceptive alarm calls were given significantly more often when food was distributed across fewer platforms.

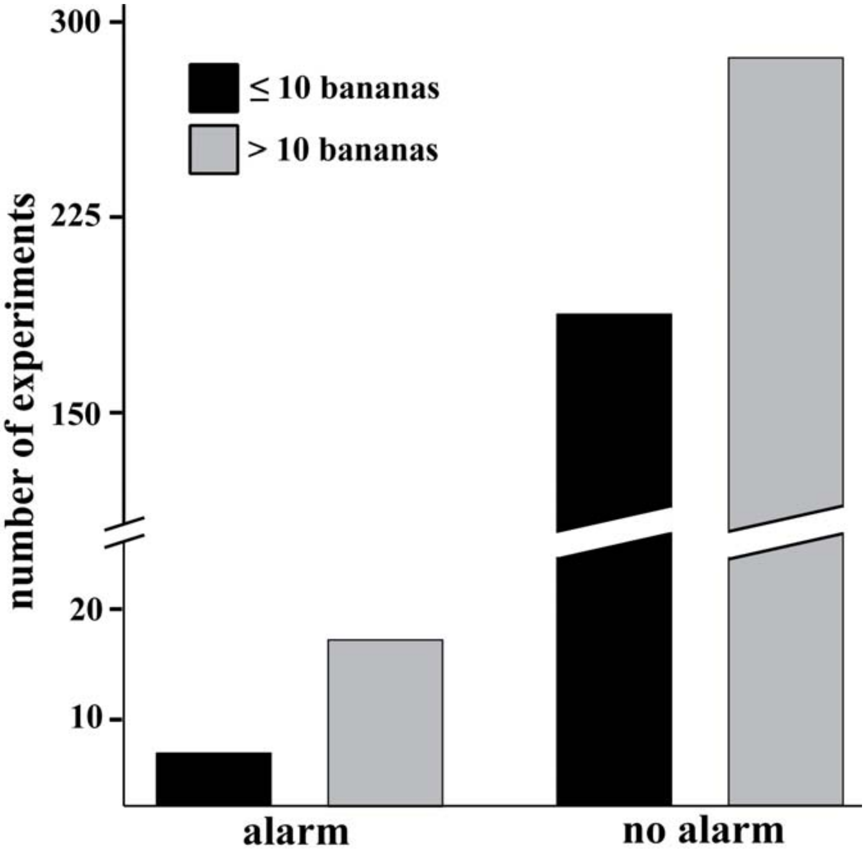

Figure 6.4. The number of experiments with a given amount of food in which a focal animal did or did not produce resource-related deceptive alarm calls. Deceptive alarm calls were given slightly, but non-significantly, more often when more food was available.

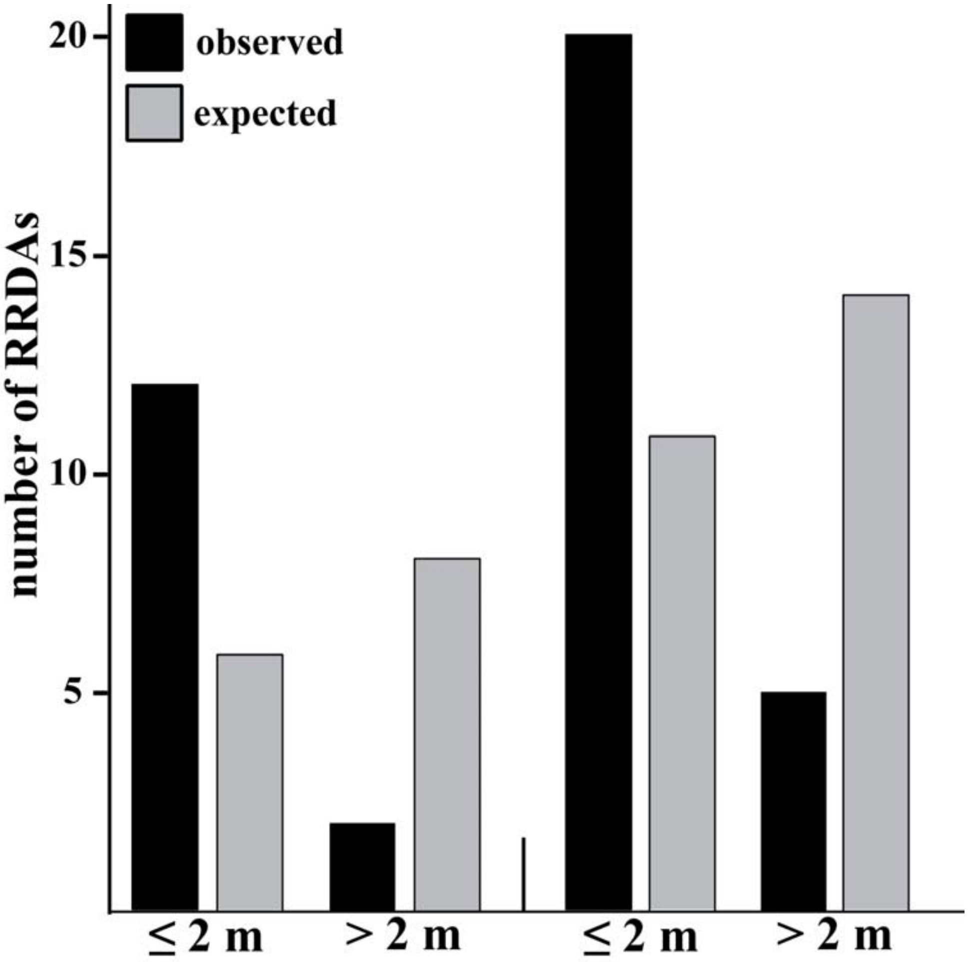

Figure 6.5. The number of resource-related deceptive alarm calls which were given when the caller was within 2 m and more than 2 m from a feeding platform versus the expected values that calls would be given when the caller was in such a location. Bars on the left side are based on the first observed RRDA from each calling individual. Bars on the right side are based on all 25 observed RRDAs. In both cases, deceptive alarm calls were given more often than expected when individuals were within 2 m of a platform.

occasions, the caller entered a feeding platform and obtained banana pieces immediately after others jumped out in response to the false alarm. On three occasions, the caller was already in a platform, but the false alarm caused others also in the platform to jump out, while the caller stayed and continued feeding. In the three remaining cases, the caller was unable to enter the platform because, although at least one neighboring individual reacted, one or more individuals did not and remained on the feeding platform.

Discussion

The resource usurpation hypothesis for false alarm call production was broadly supported, with four of the five predictions finding support in this study: subordinate individuals produced the calls far more often than dominants, the calls were given more often when the contested resources could most easily be monopolized by dominants, callers tended to be well positioned spatially to take advantage of any potential anti-predator reactions the calls elicited, and the RRDAs distracted conspecifics by eliciting anti-predator escape reactions (albeit less than half the time), with callers most often taking advantage of these reactions. The only prediction not supported was that RRDAs would be more common when less food was available. In fact, RRDAs were slightly, but non-significantly, more common when more food was available. Nevertheless, even without support for the latter prediction, a large proportion of the false alarms given while feeding appear to function to deceive competitors. Thus, as in some avian and rodent taxa (Munn, 1986a; Møller, 1988, 1990; Tamura, 1995), it seems that capuchin monkeys also use alarm calls to distract others during competitive situations, alleviating some of the costs associated with contest competition for food.

While only 40% of the RRDAs given by focal animals elicited escape reactions in one or more neighboring conspecifics, this is actually a high rate of such responses relative to the rate in which these behaviors were employed following playbacks of the same call type given in response to felid predator decoys (15% of which elicited such behaviors; Wheeler, unpublished data). The increase in escape responses to the false alarms relative to the “true” alarms are likely due to the fact that the individuals reacting were within 2m of the caller while the playback speaker was normally placed more than

5m from the nearest individuals. Individuals closer to the caller may be more likely to employ an escape reaction in response to these calls because a nearby conspecific who has detected a felid or snake likely represents a much greater threat than a caller at a greater distance, as average predator detection distances in this population are short (Janson, 2007b).

Functionally deceptive signaling is thought to have to necessarily be rare and/or have a low cost for the "deceived", otherwise the signal will simply be ignored and become ineffective (Fitch & Hauser, 2002; Searcy & Nowicki, 2005). In the current study, RRDAs were quite common, being given at a rate of 0.56 deceptive calls/individual/hr in the experimental feeding contexts. Previous studies have shown that false alarm call rates can exceed the rates in which alarm calls are given in response to real threats and still regularly elicit anti-predator reactions (Munn, 1986a; Møller, 1988). It seems likely that in these cases the cost of being deceived is indeed relatively low (loss of a small amount of food) compared to the cost to not responding to a real threat (potentially death). Call receivers may therefore employ a "better safe than sorry" approach in response to alarm calls (Haftorn, 2000) as the cost of being deceived, even on a regular basis, may be less costly than ignoring all calls given in competitive situations.

While these results support a *functionally* deceptive interpretation for the production of false alarms during feeding, it is difficult to prove that this behaviour is *intentionally* deceptive (see Hauser, 1997). A study of the proximate causes of call production would be needed to provide more insight in this regard (Fitch & Hauser, 2002). Intentionally deceptive calls would be driven proximately by the cognitive ability to understand that the "beliefs" of others (Hauser, 1997). Alternatively, false alarms may be common during feeding because, after having once produced an alarm call in this context, observed the reaction of neighboring conspecifics, and acquired food as a result, individuals associate call production with access to food. While such an explanation requires that individuals learn to associate false alarm production with a food reward, it does not require special cognitive abilities. It is also plausible that call production is driven proximately by physiological mechanisms. Previous work has shown that captive tufted capuchin monkeys who experience high cortisol levels due to chronic stress produce these calls more often than those under less stress (Boinski et al., 1999; see also Bercovitch et al., 1995; Blumstein et al., 2006). Subordinates may experience elevated stress (and increased cortisol levels) when the group is feeding on high quality food resources that are highly clumped in their distribution because dominant individuals can easily exclude subordinates from feeding (e.g., Janson, 1985, Koenig et al., 1998). Additional research is needed to confirm if stress is indeed a possible proximate explanation for call production.

Chapter 7

Alarm Calling Behavior of Tufted Capuchin Monkeys: A Summary and Synthesis

The goals of this dissertation were to: 1) identify the call types that are elicited in wild tufted capuchin monkeys (*Cebus apella nigritus*) by predators, 2) examine the contextual factors that explain variation in the production of these anti-predator calls (call "meaning"), 3) examine the ontogeny of call use and response, 4) test which of several hypotheses best explains the adaptive significance of this seemingly altruistic behavior (call function), and 5) determine whether the use of false alarm calls during feeding functions to "deceptively" distract conspecifics and usurp contestable food items. While most of these aspects of alarm calling behavior have been previously addressed in many species of birds, rodents, and ungulates (reviewed in Caro, 2005), previous studies of alarm calls in primates have focused primarily on call "meaning", that is, the contexts in which the calls are produced and the ways in which call receivers seem to perceive the calls (reviewed in Zuberbühler, 2003). While less well-studied, there have been a few attempts to investigate alarm call function (Cheney & Seyfarth 1981, 1985; Zuberbühler et al., 1997, 1999) and the ontogeny of alarm call use (Seyfarth & Cheney, 1980, 1986; Ramakrishnan et al., 2005) and response (Seyfarth & Cheney, 1980, 1986; Ramakrishnan & Coss, 2000; Fichtel, 2008), although these have been restricted to the Old World monkeys and Malagasy lemurs. The functionally deceptive use of alarm calls has not been previously addressed in primates. In fact, only one previous study has examined any type of active "deception" in a wild primate, an examination of the functionally deceptive exaggeration of agonistic screams in chimpanzees (*Pan troglodytes*; Slocombe & Zuberbühler, 2007). Thus, this is the first study to fully address alarm call meaning, ontogeny, and function in a New World primate, and the only study among primates to examine the functionally deceptive use of a behavior outside of its "normal" context.

Summary of the dissertation

In Chapter 2, I identified three distinct call types that are produced in response to aerial predators (raptors), terrestrial predators (felids), and snakes: barks, hiccups, and peeps. Of these, barks are produced exclusively in response to potential aerial threats (i.e., raptors and stimuli resembling raptors) and peeps appear to be given only in response to potential terrestrial threats (i.e., felids, snakes, and other stimuli which bear some physical resemblance to each of these), although additional research is needed to confirm this. Hiccups, like peeps, are given in response to potential terrestrial (but not aerial) threats, although they are also given in a range of additional contexts in which the caller is likely experiencing some degree of stress, most commonly when the caller is engaging in a precarious positional behavior, such as a suspensory feeding posture. The number of hiccups that an individual gives in the first seconds of a bout seems to vary with the urgency of the threat experienced, with less urgent stressful situations (such as suspensory behaviors) eliciting fewer calls than higher urgency threats (such as felid predators). Responses of listeners to each of barks and hiccups generally correspond to the predator types that elicit the calls: barks more often cause individuals to look up or run into more dense vegetation, while hiccups more often cause individuals to look down or run up. However, both of these call types most often elicit only generalized anti-predator reactions, including looking towards the caller, which may allow the individual to assess additional contextual cues regarding the nature of the current threat (Seyfarth et al., 1980a,b). An insufficient number of experimental playbacks of peeps were conducted to draw conclusions regarding how these calls are perceived by listeners; it cannot be assumed that the apparent specificity in the contexts in which these calls are produced will necessarily lead to perceptual specificity (Blumstein, 1995).

In Chapter 3, I tested whether the patterns of alarm call use and response among different age classes indicate that: 1) immature individuals use the same calls in response to the same threat categories as adults (as described above), 2) there are age-related differences in the ability to recognize dangerous stimuli and differentiate these from innocuous, but physically similar, stimuli, and 3) immature individuals show adult-like abilities to respond appropriately to each of barks and hiccups. The results indicate that:

1) there are no differences between the age classes in the types of calls that they produce in response to snakes, while anecdotal evidence indicates a similar pattern for calls given in response to both carnivores and raptors, 2) recognition of vipers as dangerous does not appear to be fully developed until the juvenile stage, although juveniles, along with infants, do not appear to have the adult-like ability to distinguish between vipers and those snakes that do not pose a threat, and 3) infants appear able to respond appropriately to barks, but not hiccups, while the responses of juveniles to both of these call types did not differ from those of adults. Some anti-predator behaviors therefore appear to be fully developed at a very young age, while others are refined through maturation. However, additional research is needed to determine the anti-predator abilities of very young infants (especially aged 6 months and less), as experimental protocols conducted with individuals younger than this were often difficult, if not impossible.

In Chapters 4 and 5, I investigated the ways that individuals could benefit by vocalizing in response to predators and snakes, an act that appears to be altruistic given the potential costs to callers resulting from drawing the predator's attention. One apparent benefit is that the behavior attracts other group members towards the caller (and therefore also towards the predator or snake, as these threats tend to be detected from no more than a few meters away; see Janson, 2007b), with most individuals then mobbing the predator once they detect it. The benefit of recruiting conspecifics to mob may benefit the caller if it drives away the predator, or if it allows younger individuals to learn to identify threatening stimuli as dangerous (see Curio, 1978a,b). This latter phenomenon can be beneficial to the caller if those younger individuals are kin, but the caller could also benefit if non-kin learn to recognize threats and then later give alarm calls that warn the original caller. This recruitment of mobbers does not appear to be the only benefit to calling in the cases of snakes and felids. In the former case, the patterns of giving and withholding of alarm calls indicate that the calls likely serve to warn others of the viper's presence: males call to warn collateral kin and females call to warn offspring.

In the case of felids, the lack of a conspecific audience effect for calling indicates that the calls may actually be directed toward the predator, which may be beneficial given that these predators likely rely on ambush to catch prey and give up the hunt if they have been detected (see Zuberbühler et al., 1999). It should be noted that although some weak support was found for both the kin selection and parental care hypotheses, it's not clear if the predictions tested are ideal for addressing these hypotheses. Should an individual with three offspring really be more likely to alarm call than an individual with only one? The latter stands to lose a greater proportion of its total reproductive effort if one offspring falls prey to a predator, and may therefore be more likely to incur the costs of alarm calling than will the individual with three offspring. However, the individual with three offspring may be at more risk of losing any one of those during a predator encounter than will an individual with only one, because the former's offspring constitute a greater proportion of the total prey individuals present. Those with fewer offspring face less risk that any one of theirs will be hunted than do those with more offspring, and so the potential benefits may therefore be higher. It is thus unclear if the *number* of kin or offspring is the best predictor variable for testing these hypotheses.

The "pursuit deterrence" hypothesis was further tested in Chapter 5 by examining whether capuchin alarm calls can effectively deter a tamed raptor from pursing a prey. The results indicate that capuchin calls can indeed deter these predators from initiating pursuit towards a particular individual, although alarm calls are not uniquely suited to doing so – capuchin food calls are also effective if produced loudly enough.

In Chapter 6, I investigated one additional way in which alarm callers may benefit: by eliciting anti-predator reactions in conspecifics in the absence of any predators. Previous studies have shown that such "deceptive" alarm calls can effectively allow callers to manipulate the behavior of competitors in the contexts of both mating and feeding (Munn, 1986a; Møller, 1988, 1990; Tamura, 1995). In this study, it appears that capuchins also do this, producing "high-urgency" hiccups in competitive feeding contexts. The patterns of call production in this case match what would be expected if these false alarms functioned to deceive conspecifics; spontaneous false alarms were given almost exclusively by subordinates (who are regularly denied access to food by more dominant individuals) most often when the food was distributed such that it could most easily be monopolized by dominant individuals, and when in close proximity to the resource. These calls regularly elicited anti-predator escape reactions in conspecifics, and the callers took advantage of these reactions whenever possible by quickly obtaining a few food items before the dominant individuals returned to the feeding location.

The ecology of capuchin monkey alarm calling

The alarm calling behavior of this population of tufted capuchin monkeys seems to be driven broadly by three main features of their ecology: the monkeys' exploitation of the arboreal niche, the dense forest habitat in which they live, and the behavior of the predators and snakes that threaten them. These factors, and the interactions between them, can largely explain the capuchin's alarm call repertoire, the reactions of listeners to the calls, the patterns of giving and withholding of alarm calls in response to threatening heterospecifics, the use of a generalized "disturbance" call (the hiccup) in response to both terrestrial threats and other stressors, and the ability to use this latter call in a functionally deceptive manner.

The alarm call repertoire of tufted capuchins (see Chapter 2) can be explained by a combination of the types of heterospecifics that pose a mortal threat to them and the monkeys' use of arboreal substrates. The main predatory threats of capuchins in Iguazú are raptors and felids, but the presence of vipers (which are unlikely to prey upon capuchins; see Chapter 1) also presents a deadly threat for individuals who, knowingly or unknowingly, approach too closely to one of these snakes. While these heterospecifics present three distinct types of threats, the arboreal environment exploited by the monkeys necessitates only two responses: the best way to evade an immediate attack from a raptor is to first locate it by scanning up and/or escape by running into dense vegetation (where these species are unable to fly effectively; Boinski et al., 2003), while the best way to evade an immediate attack from a felid or viper is to locate it by looking down and/or escape by running up. It thus makes sense that one call type would be given in response to aerial stimuli and another in response to the terrestrial stimuli. In addition, approaching the threatening stimulus is an appropriate strategy when facing felids or snakes, but it only makes sense to react in this way to a raptor if it is perched, as this would be an ineffective (if not impossible!) reaction to a raptor in flight (see also Ferrari & Lopes Ferrari, 1990). While such a strategy of approaching a threat seems counter-intuitive on the surface, it's effectiveness is largely explained by the arboreal environment; while each of raptors, felids, and snakes is able, to a degree, to move within the forest canopy, none are likely to be as well adapted to locomotion within this environment as are capuchins monkeys, and a successful attack on a capuchin aware of its presence therefore seems very unlikely. So long as the monkeys maintain a certain distance from these threats, they are likely better off knowing exactly where the threat is, and keeping their eye on it, than in simply knowing that a group member has spotted a threat somewhere in the vicinity.

One perhaps surprising result of this study was the low percentage of alarm calls that resulted in escape reactions from listeners. Attempts to locate the potential predator were far more common than attempts to escape from it (Chapter 2). This may be an effect of the dense vegetation that characterizes the study site, as this feature of the habitat leads to two phenomena which likely makes vigilance reactions a better strategy than escape reactions. First, because dense vegetation limits visibility, such habitats are expected to lead to high rates of misclassification of innocuous stimuli as threatening (Evans, 1997). Indeed, in the current study, alarm calls given in natural contexts were far more often a response to non-threatening than threatening stimuli (Chapter 2; see also Di Bitetti, 2001a). When false alarm calls such as these are common, employing an escape response as the default reaction can be costly; becoming vigilant or employing an escape response only in certain conditions (e.g., after a certain number of alarm calls have been given) can be a less costly strategy (Beauchamp & Ruxton, 2007). Second, the dense vegetation generally prevents the capuchins from detecting threats except from a very short distance (i.e., just a few meters; Janson, 2007b). Because of this, individuals hearing an alarm call from a conspecific that is 15 meters or more away (the distance separating the focal animal from the playback speaker in most experiments) are less likely to be facing an immediate threat than is the caller. In such situations, an immediate escape reaction may actually be costly; vigilance reactions may be less costly in terms of time and energy consumption and would allow the listener to take the proper precautions in case the threat becomes immediate.

The selective use and withholding of alarm calls, which provides insight into their adaptive function (Chapter 4), is also largely explained by the three factors of arboreality, dense forest, the behavior of eagles, raptors, and snakes, and the interactions between these. Specifically, the arboreal habits of the capuchins most certainly shape the hunting behavior of their predators. As outlined above, these predators are not as well adapted as are capuchins to moving quickly among the small and dense substrates that characterize the lower levels of the canopy, and it is therefore expected that they will depend largely on ambushing capuchins from a short distance in order to hunt them successfully. The dense forest environment provides ample cover for raptors and felids to "sit and wait" for capuchins to approach to within an appropriate distance for an effective ambush. Indeed, a study conducted by Charles Janson indicates that capuchins in Iguazú detect these predators from extremely short distances, so short in fact that the benefits of "many eyes" and early detection may be nearly absent (Janson, 2007b). It is thus not surprising that nearly all capuchins would alarm call whenever they detect a felid, even when they are without conspecifics – the calls are an efficient way for the monkeys to communicate with the predator that it has been detected and the necessary element of surprise has been lost. Communication with conspecifics may be only of secondary importance in these cases. The fact that vipers are not capuchin predators explains why capuchins wouldn't alarm call as often to these species: the snakes have no intent of pursuing capuchins as a prey and therefore alarm calls are not needed to deter them. Rather, production of the calls are best explained as a strategy to alert offspring and other kin to the snake's presence, reducing the likelihood that they will unknowingly stumble into its "personal space".

Given that the success of raptors also likely decreases once they've been detected, it is unclear why the capuchins did not alarm call more often in response to perched raptors (Chapter 4). This is especially puzzling when considering the fact that raptors can indeed be deterred by vocalizations from the prey (Chapter 5). One possibility is that raptors may prefer prey who have not detected them, but that surprise is not be an absolutely essential element in determining their success in hunting primates (see Boinski et al., 2000 for an anecdotal observation of a successful attack by a raptor on a primate group that had been mobbing it for several minutes). Another possible explanation for the withholding of alarm calls is the propensity for raptors, including *Spizaetus* spp., to regularly hunt in pairs (e.g., Hector, 1986; Yosef, 1991; Miranda et al., 2006; Shultz & Thomsett, 2007). Capuchins may withhold calling upon detecting a raptor in order to avoid drawing the attention of other nearby raptors that have not yet been detected. Instead, silent mobbing of the predator, which was far more common than vocal responses to perched raptors (Chapter 4), may serve as a pursuit deterrent (Curio, 1978a) without alerting other potentially present predators to the prey individual's location. Of course, it cannot be ruled out that the raptor models simply did not elicit the same reaction as would live, perched raptors, possibly due to the fact that the models remained motionless throughout the experiments (accept in cases when the monkeys pulled the rope from which they were suspended!).

The benefits of having a general disturbance call (the hiccup), elicited both by terrestrial threats and other apparent stressors, may also be attributable to the species' high degree of arboreality. The single most common context in which individuals produced this call was when engaged in some sort of precarious positional behavior, that is when the risk of falling was apparently high. This may be an artifact of the monkeys fear of the ground, which is apparent in their hesitancy to come down; individuals seem far more likely to come down if other conspecifics or coatis (*Nasua nasua*) are already on the ground (pers. obs.). While calls given in this context were never observed to elicit anti-predator escape reactions, they did, on some occasions, appear to elicit vigilance in conspecifics which were within a few meters of the caller (see also Hirsch, 2002). Such vigilance from neighboring individuals may be especially beneficial for an individual at risk of falling to the ground, where there is an increased risk of an attack by a felid or snake. If this is the case, then an argument can be made that hiccups given in these contexts, like those given during feeding, are a functionally deceptive way of increasing vigilance in listeners to the benefit of the caller. Indeed, in most of the additional non-predatory contexts in which use of these calls was observed anecdotally (e.g., mild aggression received by the caller, intense aggression related to an attempted male take-over or infanticidal events: Di Bitetti, 2001a; Barbara Tiddi, pers. comm.; pers. obs.) or systematically (e.g., during feeding on contestable resources; Chapter 6), there are clear benefits to the caller in invoking anti-predator reactions in listeners despite the absence of an actual predator.

Finally, the ability of the capuchins to use hiccups in a functionally deceptive manner during feeding (Chapter 6), and the fact that these calls caused anti-predator reactions more often than playbacks of "honest" alarms (Chapter 2), is largely explained by the dense vegetation and the associated limited ability to detect predators. As discussed above, the short distances in which predators are detected (Janson, 2007b) generally limits the danger that listeners are in when they hear alarm calls. One case when this would not be true for the listener, however, is when the caller itself is within a few meters. In such a situation, not employing an escape reaction can be extremely costly, as the predator, if actually present, is likely to be within just a few meters. While this limits the caller to "deceiving" only its immediate neighbors, it seems unlikely that a caller would be able to take advantage of reactions of more distant neighbors anyway; by the time the caller traversed the arboreal pathway to the contested resource, the "deceived" individual would have likely realizes that no threat is actually present and returned to feeding. An additional effect of dense vegetation, discussed above, may also make such functionally deceptive calling possible: the high rates of false alarm calling due to misclassification in such habitats may make it difficult to detect cheaters.

If these ecological features have indeed shaped the alarm calls of tufted capuchins as described above, then predictions can be made regarding the alarm calling behavior of tufted capuchins in other habitats or facing threats from different predator types. In areas of southeastern Brazil, tufted capuchins live in open, savannah-like environments (*cerrado*) and are considerably more terrestrial than are the populations of the Upper Paraná Atlantic Forest (see Janson, 2006; Ottoni & Izar, 2008). In such an environment, distinct call types for felids and snakes would be expected because such a call system would be beneficial for the same reasons it is beneficial for vervets (Seyfarth et al., 1980a): distinct behaviors are needed to respond to each of these threats. Escape reactions would more often be appropriate following felid detections, while the appropriate reaction to snakes (even constrictors which prey on capuchins) would simply be to locate the threat. This is due to the fact that the threat posed by a felid to highly terrestrial species in an open environment would be quite different from that faced by arboreal species in a dense forest. While arboreal capuchins in dense forest can safely approach both felids and snakes to within a given distance without facing an immediate threat, approaching a felid on the ground would be far more dangerous since the threat is far more immediate given the predator's ability to pursue prey in such a habitat. In contrast, the threat posed by a snake would differ little in the two contexts; snakes would be unable to pursue quickly-moving prey on either terrestrial or arboreal substrates. Hunting by humans certainly poses a threat to some tufted capuchin populations, and such predators are likely capable of successfully pursuing prey after detection. Such a threat may therefore select for the evolution of yet another alarm call type. However, humans elicit hiccups and mobbing behaviors in unhabituated tufted capuchins in Iguazú and neighboring protected areas (pers. obs.). Given that mobbing a human hunter would seem to be ineffective and maladaptive, these responses may be due to near absence of hunting by humans in these areas and individuals in hunted populations may well react differently. Among white-faced capuchins (*Cebus capucinus*), humans elicit the same type of alarm call as do raptors (Fichtel et al., 2005), possibly because, despite being terrestrial, humans hunt with projectile weapons (Fichtel, pers. comm.).

Variation in habitat density would also be expected to affect the rate of "false alarms" given in response to innocuous stimuli (Evans, 1997). For example, a habitat with a less dense understory or canopy cover should make it easier to differentiate actual terrestrial or aerial threats, respectively, from innocuous stimuli which bear some physical resemblance to real threats.

The costs and benefits of alarm calling should also differ between open and closed habitats and between populations that differ in their degree of arboreality. In a more open habitat, predators can presumably be detected at greater distances, thus increasing the potential anti-predator benefits of early detection of predators. Thus, the benefits may be more likely to come from alerting others to the predator's presence (including offspring, other kin, mates, etc.) as these other group members may well face a threat equal to or greater than that facing the original detector (in contrast to the higher threat facing the caller when detecting a extremely short distances; Janson, 2007b). Likewise, terrestrial detectors in an open environment should be less likely to direct their alarm calls towards the predator itself, as both felids and raptors (but not snakes) would seem to be more likely to be able to pursue prey in such an environment; the element of surprise would seem to be relatively less important for such predators hunting terrestrial prey in an open habitat than it is for hunting arboreal prey in a dense forest. One would also expect that alarm calls elicited by human hunters, in any habitat, would also be directed towards conspecifics, given that such predators are likely able to successfully pursue prey after being detected and pursuit deterrent signals would likely be ineffective.

Finally, while the ability to use alarm calls deceptively would likely, in some regards, be enhanced for a highly terrestrial population that exploited an open habitat, it would be more limited in others. Specifically, because escape reactions to alarm calls should be relatively common in such a population (see above), deceptive alarm calls could potentially be used more effectively than in a population in which such alarm call reactions are less common than simple vigilance reactions. Likewise, terrestrial individuals would be able to take advantage of reactions of conspecifics over a greater distance, given the absence of constraints associated with traversing an arboreal environment. However, the potential for deceptive alarm calling may also be limited in open habitats because the lack of obscuring vegetation may make it easier for signal receivers to quickly determine whether or not a real threat is present, allowing for more efficient detection of cheaters.

Alarm call meaning and function: How do capuchins fit in?

Alarm call "meaning"

The alarm calling behavior of tufted capuchins generally accords with that observed in previous studies of mammals generally and primates specifically. The use of different types of calls for different classes of predators (Chapter 2) is characteristic of most primates studied to date (reviewed in Fichtel & Kappeler, 2002), and contrasts with the more strictly urgency-based systems characteristic of sciurid rodents (reviewed in Fichtel & Kappeler, 2002; Blumstein, 2007a). Furthermore, while few studies have tested for differences in alarm calling between terrestrial carnivores and snakes, those that have indicate that the production of distinct call types for these two different threat categories occurs in terrestrial (Seyfarth et al., 1980; Range & Fischer, 2004) but not arboreal (Fichtel & Kappeler, 2002; Digweed et al., 2005; Fichtel et al., 2005) species. The use of terrestrial predator-associated calls in additional (non-predatory) contexts has also been reported for at least four additional arboreal primate taxa: redfronted lemurs (*Eulemur fulvus rufus*), white sifakas (*Propithecus verreauxi*; Fichtel & Kappeler, 2002), saddleback tamarins (*Saguinus fuscicollis*; Kirchhof & Hammerschmidt, 2006), and white-faced capuchins (*Cebus capucinus*; Fichtel et al., 2005). As in the current study, it was found that these species commonly produce their terrestrial-predator associated alarm call during aggressive interactions with conspecifics. Whether or not this represents additional examples of the functionally deceptive use of alarm calls has not yet been addressed. It is worth investigating if these species, like tufted capuchins, also produce these calls during intense within group contest competition for high value resources.

The demonstrated effect of risk-urgency on the rate of production of hiccups in the current study is among the first demonstrations of urgency signaling in primates, with only one previously published report of such signaling for bonnet macaques (*Macaca radiata*; Coss et al., 2007) and a pair of additional reports from recent conference abstracts (Price et al., 2008; Adams & Erhart, 2009). However, this accords well with trends observed among meerkats, who vary their alarm calling based on both predator type and urgency (Manser, 2001). This is likely far more common among primates than is currently reported, but most studies have not examined variation in call rate as a possible cue to the caller's risk-urgency.

While the findings of the current study fit well with the functionally referential paradigm, it is worth questioning whether other paradigms that do not evoke semanticity also offer plausible, or even better, explanations for the observed trends. For example, tufted capuchins may respond "appropriately" to alarm calls not because they elicit mental images of the supposed referent in listeners, but rather because the acoustic structure of the calls is such that they elicit an emotional response in listeners, and through previous experience the listeners have been conditioned to react in a particular way (Owren & Rendall, 1997, 2001; Owren et al., 2003). The alarm calling behavior of tufted capuchins in many ways accords with this "affect-conditioning" model. First, the acoustic structure of hiccups and barks seems to elicit attention, as demonstrated by the fact that alarm calls regularly elicit the attention of even infants (Chapter 3), a phenomenon predicted by the affect-conditioning model (Owren & Rendall, 1997). Second, generalized anti-predator behaviors were considerably more common than predator-specific behaviors for both of these call types (Chapter 2). Specifically, the most common response of listeners was to look towards the caller. Given this, it is quite plausible that listeners may employ addition, predator-specific reactions to the playbacks because they have formed an association between these calls and the caller's subsequent behaviors. For example, because barks often cause listeners to look toward the caller, and because the caller would often be looking up towards the eliciting stimulus in the moments following the call, a signal receiver would likely also begin to look up after having its attention diverted toward the caller by its vocalization. After this has occurred a few times, receivers may begin to spontaneously look up after hearing a bark. Thus the appropriate reactions to barks may not be due to conditioning which has led to an association between the call and the presence of an aerial threat, but conditioning which has led to an association between the call and the caller's subsequent behavior. Perhaps the only aspect of tufted capuchin alarm calling behavior which does not fit well with the "affect-conditioning" model is the fact that monkeys' peep calls, which are associated with both snakes and felids (Chapter 2), are a relatively soft, low intensity vocalization, not the type of acoustic structure that would be expected to elicit a strong emotional reaction in receivers. However, because playbacks of these calls are lacking, it is unclear if they do indeed elicit such reactions or not. In sum, while it is not necessary to evoke representational signaling to explain the observed behaviors regarding alarm call production and response, it remains unclear if one explanation or the other (i.e., referential versus affect-conditioning) is better supported.

Alarm call function

The function of tufted capuchin alarm calls also accords well with what is known regarding the potential benefits of alarm calling among mammals, with evidence that the calls are directed at both conspecifics and the potential predator. The evidence that alarm calls may warn offspring and other kin of a predator's presence adds to the taxonomically widespread support for the parental care and kin selection hypotheses (e.g., Sherman, 1977; Cheney & Seyfarth, 1985; Blumstein et al., 1997). The lack of support for the mate protection hypothesis indicates that, although this appears to be a common function of alarm calling in many bird species (e.g., Hogstad, 1995), alerting mates may be less important among mammalian taxa (but see below for further discussion on this topic). The absence of a conspecific audience effect for alarm calling in response to felids adds further evidence that these signals may be directed toward the predator, and anti-predator signaling may not be as costly as has long been presumed. Finally, while demonstration that alarm callers benefit by recruiting additional mobbers is absent among mammals (although limited evidence is available for birds; Rohwer et al., 1976), this is likely due to a lack of appropriate data to test the hypothesis rather than to the rarity of the phenomenon. Future studies of alarm call function should explicitly consider this hypothesis and collect the data necessary to test it.

Tests of the function of alarm calls in other primate populations or taxa that vary in aspects of their social organization and structure may reveal the benefits for alarm calling that are absent, or obscured, in tufted capuchins. For example, is alarm calling relatively less common in species, such as the mantled howler monkey (*Alouatta palliata*), in which neither sex is philopatric and individuals are therefore surrounded by fewer kin? Does the "group maintenance" hypothesis find greater support in species in which subordinates face greater costs and receive fewer benefits from with living in larger groups than they perhaps do in tufted capuchins? Likewise, within a species, how does group size affect alarm calling behavior; if living in large groups is costly, might individuals in larger groups be less likely to alarm call than those in smaller groups? Do predator densities affect alarm calling behaviors? Those living in areas with low predator densities may be less likely to call, because the anti-predator benefits of living in a group would be relatively low in such a habitat, and the loss of a group member due to predation may decrease within group feeding competition for the detector (see van Schaik, 1989). How does the mating system affect alarm calling in primates? While alarm calling to protect mates isn't predicted for females in species with polygamous mating systems, might this be a benefit for females in species with monogamous (e.g., gibbons), polyandrous (e.g., callitrichids), or polygynous (e.g., hamadryas baboons: *Papio hamadryas*) mating systems? In such species, the costs of alarm calling by females may be outweighed by the benefits of saving the male due to potential competition among females for mates (e.g., Ahsan, 1995; Garber, 1997) and/or the risk of infanticide if the mate dies (e.g., Swedell & Tesfaye, 2003).

The lack of support for the mate protection hypothesis in the current study is somewhat puzzling, given the obvious benefits that protecting mates has on an adult male capuchin's future reproductive success. It is quite possible that some of the benefits of alarm calling among adult male tufted capuchins do indeed come in the form of protecting mates, but that this is obscured given that callers simultaneously benefit in additional ways. This hypothesis could be better tested in another primate taxon in which additional benefits (such as warning kin, recruiting mobbers, and deterring pursuit) would not be expected. An ideal system to test this would be with any of the several cercopithecoid species of the Taï Forest, Ivory Coast which live in one-male groups (reviewed in McGraw & Zuberbühler, 2008). When males first take over a group, they are unlikely to be related to any of its groupmates and will not yet have sired any offspring; thus alarm calls would not serve to warn offspring or other kin. Furthermore, because chimpanzees (*Pan troglodytes*) hunt these monkeys through pursuit (Boesch & Boesch, 1989), alarm calls would not be effective as pursuit deterrent signals, and mobbing would also likely be quite dangerous. One could therefore examine the alarm calling behavior of such males following detections of chimpanzees; if they do indeed call regularly in these situations, this would provide strong evidence in favor of the mate protection hypothesis.

Future directions

Acoustic analysis

While acoustic analysis of the vocal repertoire of tufted capuchin monkeys has been described in detail (Di Bitetti, 2001a), including descriptions of both “hiccups” and “barks”, additional investigation into variation in the acoustic structure of these call types, as well as acoustic descriptions of peeps, may provide further insight into the meaning, ontogeny, function, and deceptive uses of alarm calls. For example, it is possible that the calls given to flying raptors differ slightly from those given to perched raptors, although they sound similar to the human ear. Likewise, there may be acoustic differences between the hiccups given to felids, those given to snakes, and those given in other contexts (e.g., aggression or suspensory behaviors). Do “deceptive” alarm calls given during feeding differ from “honest” ones? While the anti-predator reactions of listeners indicate that the false alarms are, at least sometimes, perceived similarly to honest alarm calls, it is possible that slight acoustic variation exists that the monkeys do not always attend to. Indeed, this may explain why the overall rate of anti-predator reactions (i.e., vigilance plus escape reactions) to hiccups given during the feeding platform experiments were lower than such rates in natural contexts (Wheeler, in preparation).

It also remains unclear if peeps are indeed distinct in acoustic structure from contact notes, or if they are simply contact notes given at a high rate. A comparison of the acoustic features of an individual's contact notes with calls within a sequence of that individual's peeps is needed to properly address this question.

Additional playback experiments

While the playback experiments presented in Chapter 2 give an indication of the ways in which capuchin monkeys perceive their barks and hiccups, it is unclear if peeps similarly elicit appropriate anti-predator reactions in listeners. Playbacks of this call type are needed to determine if individuals associate this call type with the presence of a terrestrial threat.

As mentioned above, alarm calls in the experimental feeding contexts (Chapter 6) elicited anti-predator reactions (all vigilance plus all escape reactions) less often than either those in natural contexts or the playbacks of "honest" alarm calls, despite the fact that escape reactions were overall more common during the feeding experiments (Wheeler, in preparation). While this may be due to acoustic differences between these calls, it may also be because listeners are "skeptical" of alarm calls given in competitive situations (Gouzoules et al., 1996). An understanding of the importance of skepticism and perception of acoustic differences could come from playbacks of "deceptive" alarm calls conducted in non-feeding contexts.

Demonstration of acoustic variation within or between call types indicates the *potential* for the monkeys to discriminate between different types of calls or between calls of the same type given in different contexts, but playback experiments are needed to understand the degree to which individuals actually attend to these differences. For example, while it is still unclear if peeps and contact notes differ in acoustic structure (see above), clues to understanding the ability of the capuchins to discriminate between these could be addressed by playing back artificial call sequences; an artificial series of contact notes in rapid succession could be played to determine if such sequences are differentiated from sequences of peeps. Likewise, a series of single hiccups (such as those given when engaged in precarious positional behaviors), could be played in rapid succession to determine if differences between high- and low-urgency hiccups in either call rate or acoustic structure are more important in eliciting reactions in call receivers.

Finally, while call intensity seems to be an important cue regarding risk urgency (in addition to being more effective at deterring pursuit by predators: Chapter 5), quantitative data to demonstrate this are not yet available (Chapter 2); additional playback experiments could be used to explore this possibility further. For example, one could conduct playback experiments wherein the volume in which a single recording is played back is systematically varied. If the higher intensity playbacks elicit reactions more quickly in individuals at a particular distance from the speaker, then it could be inferred that signal receivers do indeed perceive call intensity as important cue regarding the urgency of the threat facing the caller.

Reactions to flying vs. perched raptors

Additional experimentation is needed to address the function of calls given to flying raptors. While the current evidence indicates that mobbing recruitment is the best explanation for calls given to perched raptors, this does not seem a likely benefit to calling in response to raptors in flight. As discussed above, pursuit deterrence may not be particularly effective for a predator who has already initiated the final pursuit. The benefit to the caller in alerting conspecifics to an attacking raptor, however, remains unclear. A larger sample size of flying raptor detections may give some insight in this regard.

A greater number of vocal reactions to both perched and flying raptors is needed to address possible differences in rates of calling to each of these. While I strongly suspect that individuals tend to give a greater number of calls in response to perched than to flying raptors, the limited data available from the current study did not indicate a significant difference between these stimulus types. This, however, contradicts observations from populations which are regularly hunted by harpy eagles (*Harpia harpia*), which seem to produce *more* barks in higher urgency situations (C. Janson, pers. comm.). Additional experiments may reveal differences not borne out in the current study.

Proximate mechanisms underlying call production

Initial evidence indicates that stress, or the associated production of cortisol (see Sapolsky, 2002), may play a proximate role in the production of hiccups (Boinski et al., 1999; see also Bercovitch et al., 1995; Blumstein et al., 2006). The results of this study largely support this idea, as production of this call type was not specific to any particular context, but was seemingly produced in a range of contexts wherein the caller may be under some degree of stress. This ranged from situations as innocuous as the risk of falling (Chapter 2), to contest competition for a high value resource (Chapter 6), to situations as dangerous as infanticidal events (B. Tiddi, pers. comm.) or encounters with felid predators (Chapter 2). Further supporting the stress hypothesis is the fact that call rate varied with what is likely to be the degree of stress facing the caller (Chapter 2). However, the best support for this hypothesis will come from an endocrinological study in the wild, testing for an association between the production of these calls in different contexts and an associated increase in cortisol levels. Such support may indicate that, in contrast to the predictions of the "Machiavellian intelligence" hypothesis (Byrne & Whiten, 1988), cognitive mechanisms are not needed to explain the functionally deceptive uses of alarm calls observed in this study (Chapter 6).

If the production of hiccups is indeed driven proximately by stress, it would also be interesting to know the degree to which individuals are able suppress these calls when experiencing a stressful event. While anecdotal observations indicate that the individuals detecting predators will sometimes briefly withhold giving these calls until out of immediate attack range (pers. obs.; Di Bitetti, pers. comm.), additional data are needed to confirm that production of the calls is indeed subject to some voluntary control. Such a study may have implications for the pursuit deterrence hypothesis for alarm call function; individuals may produce the calls in the absence of a conspecific audience not because the calls function to communicate with predators, but because the detectors are unable to suppress the calls.

Interestingly, perhaps the only high-stress context in which hiccups were not regularly observed to be produced was encounters with raptors. While it is possible that the degree of stress elicited by this situation does not overlap that elicited by the situations in which hiccups are produced, this seems extremely unlikely. The lack of hiccup production in this context indicates that hiccup production may not simply be a result of stress and/or that individuals are indeed capable of suppressing the calls in some stressful situations. Further research is needed to determine if the production of barks, hiccups, and peeps has a physiological and/or a cognitive basis.

The hunting behavior of primate predators

Finally, the alarm calling behavior of a given species cannot be completely understood without some understanding of the hunting behaviors of the predators that elicit the calls. For example, if alarm calls are directed primarily towards conspecifics (i.e., to provide an "early warning"), then the prey must be able to detect the predators at a relatively long distance, as short detection distances limit the ability to employ the appropriate anti-predator response in time to prevent a successful attack. Recent work in Iguazú indicates that capuchins detect stationary predators from extremely short distances (usually only two to four meters), while moving predators are detected at a slightly longer distance (Janson, 2007b). Thus the ability for capuchins to provide an early warning likely depends on the predator's hunting behavior. If pure sit-and-wait strategies are adopted, then detection distances should be short and the detector itself is, at the point of detection, the most likely target of the predator, leaving early warnings ineffective. In contrast, if predators employ stealth to approach to within attack distances of prey, then they are more likely to be detected early and calls directed towards conspecifics could be effective in either warning others before they are attacked or in recruiting them to mob the predator before attacking the original detector. Under the first scenario, in which predators rely on ambush and detection distances are short, the most likely benefit of alarm calling would come from deterring the predator from initiating the final attack on the detector/caller. The current study found support for one prediction of the pursuit deterrence hypothesis for alarm calling in response to felids (i.e., a lack of a conspecific audience effect). Better support for this hypothesis would come from a study of the felids themselves: do these cats give up their hunt once the prey begin to alarm call? While study of the behavior of felids and raptors in the wild is difficult, especially in dense forest habitats, some evidence that these predator types are primarily ambush predators come from studies of radio-tracked animals (e.g., Shultz & Thommsett, 2007; Zuberbühler & Jenny, 2007). The behaviors of these predators could be recorded in even greater detail if equipment newly introduced to the field of animal tracking, such as accelerometers (e.g., Wilson et al., 2007, 2008; Preece et al., 2009), were employed alongside more traditional devices such as radio collars and GPS tracking devices. Additional insights could come from using experimental approaches with tracked predators, including conducting playbacks of prey vocalizations and measuring the movements these acoustic stimuli elicit.

References Cited

Adams D. B., Erhart E. M. (2009). Differential response to predators in the Gray's bald-faced saki monkey (*Pithecia irrorata*): a playback experiment. *American Journal of Physical Anthropology* S48:75.

Agostini I., Holzmann I., Di Bitetti M. S. (2008). Infant hybrids in a newly formed mixed-species group of howler monkeys (*Alouatta guariba clamitans* and *Alouatta caraya*) in northeastern Argentina. *Primates* 49:304-307.

Agostini I., Visalberghi E. (2005). Social influences on the acquisition of sex-typical foraging patterns by juveniles in a group of wild tufted capuchin monkeys (*Cebus nigritus*). *American Journal of Primatology* 65:335-351.

Ahsan F. (1995). Fighting between two females for a male in the Hoolock gibbon. *International Journal of Primatology* 16:731-737.

Alatalo R. V., Helle P. (1990). Alarm calling by individual willow tits, *Parus montanus*. *Animal Behaviour* 40:437-442.

Alexander R. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325-383.

Altmann S. A. (1967). The structure of primate social communication. In *Social Communication among Primates* (Altmann S. A., ed); pp 325-362. Chicago: University of Chicago Press.

Arnold K., Pohlner Y., Zuberbühler K. (2008). A forest monkey's alarm call series to predator models. *Behavioral Ecology and Sociobiology* 62:549-559.

Arnold K., Zuberbühler K. (2006). The alarm-calling system of adult male putty-nosed monkeys, *Cercopithecus nictitans martini*. *Animal Behaviour* 72:643-653.

Baker M., Becker A. (2002). Mobbing calls of black-capped chickadees: effects of urgency on call production. *Wilson Bulletin* 114:510-516.

Baldovino M. C., Di Bitetti M. S. (2008). Allonursing in tufted capuchin monkeys (*Cebus nigritus*): milk or pacifier? *Folia Primatologica* 79:79-92.

Barros M., Boere V., Eldon L. Mello J., Tomaz C. (2002). Reactions to potential predators in captive-born marmosets (*Callithrix penicillata*). *International Journal of Primatology* 23:443-454.

Bearder S. K., Nekaris K. A. I., Buzzell C. A. (2002). Dangers in the night: Are some nocturnal primates afraid of the dark? In *Eat or Be Eaten: Predator Sensitive Foraging among Primates*; pp 21-43. New York: Cambridge University Press.

Beauchamp G., Ruxton D. A. (2007). False alarms and the evolution of antipredator vigilance. *Animal Behaviour* 74:1199-1206.

Bercovitch F. B., Hauser M. D., Jones J. H. (1995). The endocrine stress response and alarm vocalizations in rhesus macaques. *Animal Behaviour* 49:1703-1706.

Bertram B. C. R. (1978). Living in groups: predators and prey. In *Behavioural Ecology: An Evolutionary Approach* (Krebs J. R., Davies N. B., eds); pp 64-96. Oxford: Blackwell Scientific Publications.

Bertram B. C. R. (1982). Problems with altruism. In *Current Problems in Sociobiology* (Group K. s. C. S., ed); pp 251–267. Cambridge, U.K.: Cambridge University Press.

Blumstein D. T. (1999b). Alarm calling in three species of marmots. *Behaviour* 136:731-757.

Blumstein D. T. (2007a). The evolution of alarm communication in rodents: structure, function, and the puzzle of apparently altruistic calling in rodents. In *Rodent Societies* (Wolff J. O., Sherman P. W., eds); pp 317-327. Chicago: University of Chicago Press.

Blumstein D. T. (1999a). The evolution of functionally referential alarm communication: multiple adaptations, multiple constraints. *Evolution of Communication* 3:135-147.

Blumstein D. T. (2007b). The evolution, function, and meaning of marmot alarm communication. *Advances in the Study of Behavior* 37:371-401.

Blumstein D. T. (1995). Golden marmot alarm calls. II. Asymmetrical production and perception of situationally specific vocalizations? *Ethology* 101:25-32.

Blumstein D. T., Armitage K. B. (1997). Alarm calling in yellow-bellied marmots: I. The meaning of situationally variable alarm calls. *Animal Behaviour* 53:143–171.

Blumstein D. T., Daniel J. C., Springettà B. P. (2004). A test of the multi-predator hypothesis: rapid loss of antipredator behavior after 130 years of isolation. *Ethology* 110:919-934.

Blumstein D. T., Patton M. L., Saltzman W. (2006). Faecal glucocorticoid metabolites and alarm calling in free-living yellow-bellied marmots. *Biology Letters* 2:29-32.

Blumstein D. T., Steinmetz J., Armitage K. B., Daniel J. C. (1997). Alarm calling in yellow-bellied marmots: II. The importance of direct fitness. *Animal Behaviour* 53:173-184.

Boesch C., Boesch H. (1989). Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology* 78:547-573.

Boinski S. (1988). Use of a club by a wild white-faced capuchin (*Cebus capucinus*) to attack a venomous snake (*Bothrops asper*). *American Journal of Primatology* 14:177-179.

Boinski S., Gross T. S., Davis J. K. (1999). Terrestrial predator alarm vocalizations are a valid monitor of stress in captive brown capuchins (*Cebus apella*). *Zoo Biology* 18:295-312.

Boinski S., Kauffman L., Westoll A., Stickler C., Cropp S., Ehmke E. (2003). Are vigilance, risk from avian predators and group size consequences of habitat structure? A comparison of three species of squirrel monkey (*Saimiri oerstedii, S. boliviensis* and *S. sciureus*). *Behaviour* 140:1421-1467.

Boinski S., Treves A., Chapman C. A. (2000). A critical evaluation of the influence of predators on primates: effects on group travel. In *On the Move: How and Why Animals Travel in Groups* (Boinski S., Garber P. A., eds); pp 43-72. Chicago: Univ Chicago Press.

Brown A. D., Zunino G. E. (1990). Dietary variability in *Cebus apella* in extreme habitats: evidence for adaptability. *Folia Primatologica* 54:187-195.

Brown L. H., Amadon D. (1968). *Eagles, Hawks and Falcons of the World*. Middlesex: Country Life Books.

Burton G. (1993). Behavioral relics and animal-environment mutualism: commentary on Coss (1991). *Ecological Psychology* 5:153-169.

Byrne R., Whiten A. (1990). Tactical deception in primates: the 1990 database. *Primate Report* 27:1-101.

Byrne R. W., Whiten A. (eds) (1988). *Machiavellian Intelligence*. Oxford: Oxford University Press.

Caine N. G. (1998). Cutting costs in response to predatory threat by Geoffroy's marmosets (*Callithrix geoffroyi*). *American Journal of Primatology* 46:187-196.

Caine N. G., Weldon P. J. (1989). Responses by red-bellied tamarins (*Saguinus labiatus*) to fecal scents of predatory and non-predatory Neotropical mammals. *Biotropica* 21:186-189.

Caro T. (1995). Pursuit deterrence revisited. *Trends in Ecology and Evolution* 10:500-503.

Caro T. M. (2005). *Antipredator Defenses in Birds and Mammals*. London: University Of Chicago Press.

Caro T. M., Lombardo L., Goldizen A. W., Kelly M. (1995). Tail-flagging and other antipredator signals in white-tailed deer: new data and synthesis. *Behavioral Ecology* 6:442-450.

Chapman C., Chapman L., Lefebvre L. (1990). Spider monkey alarm calls: honest advertisement or warning kin? *Animal Behaviour* 39:197-198.

Chapman C. A. (1986). *Boa constrictor* predation and group response in white-faced cebus monkeys. *Biotropica* 18:171-172.

Charnov E. L., Krebs J. R. (1975). The evolution of alarm calls: altruism or manipulation? *American Naturalist* 109:197-212.

Cheney D., Seyfarth R. (2007). *Baboon Metaphysics: The Evolution of a Social Mind*. Chicago: University of Chicago Press.

Cheney D. L., Seyfarth R. M. (1981). Selective forces affecting the predator alarm calls of vervet monkeys. *Behaviour* 76:25-61.

Cheney D. L., Seyfarth R. M. (1985). Vervet monkey alarm calls: manipulation through shared information? *Behaviour* 94:150-166.

Cheney D. L., Seyfarth R. M. (1990). *How Monkeys See the World: Inside the Mind of Another Species*. Chicago: University of Chicago Press.

Clark R. W. (2005). Pursuit-deterrent communication between prey animals and timber rattlesnakes (*Crotalus horridus*): the response of snakes to harassment displays. *Behavioral Ecology and Sociobiology* 59:258-261.

Clarke E., Reichard U. H., Zuberbühler K. (2006). The syntax and meaning of wild gibbon songs. *PLoS ONE* 1:e73.

Coss R. G. (1991). Context and animal behavior III: The relationship between early development and evolutionary persistence of ground squirrel antisnake behavior. *Ecological Psychology* 3:277-315.

Coss R. G. (1993). Evolutionary persistence of ground squirrel antisnake behavior: Reflections on Burton's commentary. *Ecological Psychology* 5:171-194.

Coss R. G., McCowan B., Ramakrishnan U. (2007). Threat-related acoustical differences in alarm calls by wild bonnet macaques (*Macaca radiata*) elicited by python and leopard models. *Ethology* 113:352-367.

Crespo J. A. (1982). Ecología de la comunidad de mamíferos del Parque Nacional Iguazú, Misiones. *Revista del Museo Argentino de Ciencias Naturales: Ecología* 3:1-172.

Cresswell W. (1994a). The function of alarm calls in redshanks, *Tringa totanus*. *Animal Behaviour* 47:736-738.

Cresswell W. (1994b). Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. *Animal Behaviour* 47:433-442.

Cresswell W. (1994c). Song as a pursuit-deterrent signal, and its occurrence relative to other anti-predation behaviors of skylark (*Alauda arvensis*) on attack by merlins (*Falco columbarius*). *Behavioral Ecology and Sociobiology* 34:217-223.

Crockett C. M. (1998). Conservation biology of the genus *Alouatta*. *International Journal of Primatology* 19:549-578.

Crockford C., Boesch C. (2003). Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: analysis of barks. *Animal Behaviour* 66:115-125.

Curio E. (1978a). The adaptive significance of avian mobbing: I. telenomic hypotheses and predictions. *Zeitschrift für Tierpsychologie* 48:175-183.

Curio E. (1978b). The adaptive signifcance of avian mobbing: II. Cultural transmission of enemy recognition in blackbirds: effectiveness and some constraints. *Zeitschrift für Tierpsychologie* 48:184-202.

Custance D., Whiten A., Fredman T. (1999). Social learning of an artificial fruit task in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology* 113:13-23.

da Costa Pinto C., de Lema T. (2002). Comportamento alimentar e dieta de serpentes, generos Boiruna e Clelia (Serpentes, colubridae). *Iheringia. Série Zoologia* 92:9-19.

Davis J. E., Parr L., Gouzoules H. (2003). Response to naturalistic fear stimuli in captive Old World monkeys. *Annals of the New York Academy of Sciences* 1000:91-93.

Davis L. S. (1984). Alarm calling in Richardson's ground squirrels (*Spermophilus richardsonii*). *Zeitschrift für Tierpsychologie* 66:152-164.

Davis R. O. (1991). Semantical communication in anti-predator alarm calls. In *Natural History of Eastern California and High-altitude Research* (Hall C. A. J., Doyle-Jones V., Widawsaki B., eds); pp 275—312. Los Angeles: University of California, White Mountain Research Station.

Dawkins R. (1976). *The Selfish Gene*. New York: Oxford University Press.

Dawkins R., Krebs J. (1978). Animal signals: information or manipulation?. In *Behavioural Ecology: An Evolutionary Approach* (Krebs J., Davies N., eds); pp 282-309. Oxford: Blackwell Scientific Publications.

De Vries H., Netto W. J., Hanegraaf P. L. H. (1993). Matman: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour* 125:157-175.

De Vries H. A. N. (1998). Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Animal Behaviour* 55:827-843.

de Waal F. (1986). Deception in the natural communication of chimpanzees. In *Deception: Perspectives on Human and Nonhuman Deceit* (Mitchell R., Thompson N., eds); pp 221-244. Albany: State University of New York Press.

Di Bitetti M. S. (1997). Evidence for an important social role of allogrooming in a platyrrhine primate. *Animal Behaviour* 54:199-211.

Di Bitetti M. S. (2001a). Food associated calls in the tufted capuchin monkey (*Cebus apella*). Ph.D. thesis: SUNY Stony Brook.

Di Bitetti M. S. (2001b). Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. *Journal of Zoology, London* 253:33-45.

Di Bitetti M. S. (2003). Food associated calls of tufted capuchin monkeys (*Cebus apella*) are functionally referential signals. *Behaviour* 140:565-592.

Di Bitetti M. S. (2005). Food-associated calls and audience effects in tufted capuchin monkeys, *Cebus apella nigritus*. *Animal Behaviour* 69:911-919.

Di Bitetti M. S., Janson C. H. (2001a). Reproductive socioecology of tufted capuchins (*Cebus apella nigritus*) in Northeastern Argentina. *International Journal of Primatology* 22:127-142.

Di Bitetti M. S., Janson C. H. (2001b). Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. *Animal Behaviour* 62:47-56.

Di Bitetti M. S., Paviolo A., De Angelo C. (2006). Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. *Journal of Zoology* 270:153-163.

Di Bitetti M. S., Placci G., Dietz L. A. (2003). Biodiversity vision for the Upper Parana Atlantic Forest Ecoregion: designing a biodiversity conservation landscape and setting priorities for conservation action. *World Wildlife Fund* 104.

Di Bitetti M. S., Vidal E. M. L., Baldovino M. C., Benesovsky V. (2000). Sleeping site preference in tufted capuchin monkeys (*Cebus apella nigritus*). *American Journal of Primatology* 50:257-274.

Digweed S. M., Fedigan L. M., Rendall D. (2005). Variable specificity in the anti-predator vocalizations and behaviour of the white-faced capuchin, *Cebus capucinus*. *Behaviour* 142:997-1021.

Doolan S. P., Macdonald D. W. (1997). Breeding and juvenile survival among slender-tailed meerkats (*Suricata suricatta*) in the south-western Kalahari: ecological and social influences. *Journal of Zoology* 242:309-327.

Dunford C. (1977). Kin selection for ground squirrel alarm calls. *American Naturalist* 111:782-285.

Emmons L. H., Whitney B. M., Ross D. L. (1997). *Sounds of Neotropical Rainforest Mammals: An Audio Field Guide*. Ithaca, NY: Cornell Laboratory of Ornithology.

Erberle M., Kappeler P. M. (2008). Mutualism, reciprocity, or kin selection? Cooperative rescue of a conspecific from a boa in a nocturnal solitary forager the gray mouse lemur. *American Journal of Primatology* 70:410-414.

Escobar-Páramo P. (1999). Inbreeding avoidance and the evolution of male mating strategies. Ph.D. thesis: SUNY Stony Brook.

Evans C. (1997). Referential signals. In *Perspectives in Ethology* (Owens D. H., Beecher M. D., Thompson N. S., eds); pp 99-143. New York: Plenum Press.

Evans C., Marler P. (1995). Language and animal communication: parallels and contrasts. In *Comparative Approaches to Cognitive Science* (Roitblat H., Meyer J., eds); pp 341-382. Cambridge, Mass: MIT Press.

Evans C. S., Evans L., Marler P. (1993). On the meaning of alarm calls: functional reference in an avian vocal system. *Animal Behaviour* 46:23-38.

Ferrari S. F., Lopes Ferrari M. A. (1990). Predator avoidance-behavior in the buffy-headed marmoset, *Callithrix flaviceps*. *Primates* 31:323-338.

Fichtel C. (2008). Ontogeny of conspecific and heterospecific alarm call recognition in wild Verreaux's sifakas (*Propithecus verreauxi verreauxi*). *American Journal of Primatology* 70:127-135.

Fichtel C., Kappeler P. (2002). Anti-predator behavior of group-living Malagasy primates: mixed evidence for a referential alarm call. *Behavioral Ecology and Sociobiology* 51:262-275.

Fichtel C., Perry S., Gros-Louis J. (2005). Alarm calls of white-faced capuchin monkeys: an acoustic analysis. *Animal Behaviour* 70:165-176.

Fischer J. (1998). Barbary macaques categorize shrill barks into two call types. *Animal Behaviour* 55:799-807.

Fischer J., Cheney D., Seyfarth R. (2000). Development of infant baboons' responses to graded bark variants. *Proceedings of the Royal Society of London Series B-Biological Sciences* 267:2317-2321.

Fischer J., Hammerschmidt K. (2001). Functional referents and acoustic similarity revisited: the case of Barbary macaque alarm calls. *Animal Cognition* 4:29-35.

Fischer J., Hammerschmidt K., Todt D. (1995). Factors affecting acoustic variation in Barbary-macaque (*Macaca sylvanus*) disturbance calls. *Ethology* 101:51-66.

Fischer J., Metz M., Cheney D. L., Seyfarth R. M. (2001). Baboon responses to graded bark variants. *Animal Behaviour* 61:925-931.

Fitch W. T., Hauser M. D. (2002). Unpacking "honesty": vertebrate vocal production and the evolution of acoustic signals. In *Acoustic Communication* (Simmons A., Fay R. R., Popper A. N., eds); pp. New York: Springer.

Fleagle J. G. (1999). *Primate Adaptation and Evolution*. San Diego: Academic Press.

Fleagle J. G., Mittermeier R. A. (1980). Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. *American Journal of Physical Anthropology* 52:301-314.

Fleagle J. G., Mittermeier R. A., Skopec A. L. (1981). Differential habitat use by *Cebus apella* and *Saimiri sciureus* in central Suriname. *Primates* 22:361-367.

Fujita K., Kuroshima H., Masuda T. (2002). Do tufted capuchin monkeys (*Cebus apella*) spontaneously deceive opponents? A preliminary analysis of an experimental food-competition contest between monkeys. *Animal Cognition* 5:19-25.

Galef B. G. (1981). The ecology of weaning: parasitism and the achievement of independence by altricial mammals. *Parental care in mammals*:211–241.

Garber P. A. (1997). One for all and breeding for one: cooperation and competition as a tamarin reproductive strategy. *Evolutionary Anthropology* 5.

Gautier-Hion A., Tutin C. E. G. (1988). Simultaneous attack by adult males of a polyspecific troop of monkeys against a crowned hawk eagle. *Folia Primatologica* 51:149-151.

Gentry E., Foltz J., Roeder J. J. (2008). Can brown lemurs (*Eulemur fulvus*) learn to deceive a human competitor? *Animal Cognition* 11:255-266.

Gill S. A., Sealy S. G. (2004). Functional reference in an alarm signal given during nest defence: seet calls of yellow warblers denote brood-parasitic brown-headed cowbirds. *Behavioral Ecology and Sociobiology* 56:71-80.

Giraudo A. R., Scrocchi G. J. (2002). Argentinian snakes: an annotated checklist. *Smithsonian Herpetological Information Service* 132:1-53.

Goodall J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, MA: Harvard University Press.

Gouzoules H., Gouzoules S., Miller K. (1996). Skeptical responding in rhesus monkeys (*Macaca mulatta*). *International Journal of Primatology* 17:549-568.

Griesser M., Ekman J. (2004). Nepotistic alarm calling in the Siberian jay, *Perisoreus infaustus*. *Animal Behaviour* 67:933-939.

Gunst N., Boinski S., Fragaszy D. M. (2008). Acquisition of foraging competence in wild brown capuchins (*Cebus apella*), with special reference to conspecifics' foraging artefacts as an indirect social influence. *Behaviour* 145:195-229.

Gursky S. (2005). Predator mobbing in *Tarsius spectrum*. *International Journal of Primatology* 26:207-221.

Gyger M. (1990). Audience effects on alarm calling. *Ethology Ecology & Evolution* 2:227-232.

Gyger M., Karakashian S. J., Dufty Jr A. M., Marler P. (1988). Alarm signals in birds: the role of testosterone. *Hormones and Behavior* 22:305-314.

Gyger M., Karakashian S. J., Marler P. (1986). Avian alarm calling: is there an audience effect? *Animal Behaviour* 34:1570-1572.

Haftorn S. (2000). Contexts and possible functions of alarm calling in the willow tit, *Parus montanus*: the principle of 'better safe than sorry'. *Behaviour* 137:437-449.

Hamilton W. (1964). The genetic evolution of social behavior. I. *Journal of Theoretical Biology* 7:1-16.

Hamilton W. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology* 7:1-52.

Hanson M., Coss R. (2001). Age differences in the response of California ground squirrels (*Spermophilus beecheyi*) to conspecific alarm calls. *Ethology* 107:259-275.

Hare B., Call J., Tomasello M. (2006). Chimpanzees deceive a human competitor by hiding. *Cognition* 101:495-514.

Hartwig W. C. (1996). Perinatal life history traits in New World monkeys. *American Journal of Primatology* 40:99-130.

Hauber M. E., Sherman P. W. (1998). Nepotism and marmot alarm calling. *Animal Behaviour* 56:1049-1052.

Hauser M. (1988). How infant vervet monkeys learn to recognize starling alarm calls: the role of experience. *Behaviour* 105:187-201.

Hauser M. (1992). Costs of deception: cheaters are punished in rhesus monkeys (*Macaca mulatta*). *Proceedings of the National Academy of Sciences* 89:12137-12139.

Hauser M. D. (1996). *The Evolution of Communication*. Cambridge, Mass.: MIT Press.

Hauser M. D. (1997). Minding the behaviour of deception. In *Machiavellian Intelligence II: Extensions and Evaluations* (Whiten A., Byrne R., eds); pp 112-143. Oxford: Oxford University Press.

Hayes S. L., Snowdon C. T. (1990). Predator recognition in cotton-top tamarins (*Saguinus oedipus*). *American Journal of Primatology* 20:283-291.

Hector D. P. (1986). Cooperative hunting and its relationship to foraging success and prey size in an avian predator. *Ethology* 73:247-257.

Herzog M., Hopf S. (1984). Behavioral responses to species-specific warning calls in infant squirrel monkeys reared in social isolation. *American Journal of Primatology* 7:99-106.

Heymann E. (1990). Reactions of wild tamarins, *Saguinus mystax* and *Saguinus fuscicollis* to avian predators. *International Journal of Primatology* 11:327-337.

Hirsch B. T. (2002). Social monitoring and vigilance behavior in brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology* 52:458-464.

Hogstad O. (1995). Alarm calling by willow tits, *Parus montanus*, as mate investment. *Animal Behaviour* 49:221-225.

Hollén L. I., Clutton-Brock T., Manser M. B. (2008). Ontogenetic changes in alarm-call production and usage in meerkats (*Suricata suricatta*): adaptations or constraints? *Behavioral Ecology and Sociobiology* 62:821-829.

Hollén L. I., Manser M. B. (2006). Ontogeny of alarm call responses in meerkats, *Suricata suricatta*: the roles of age, sex and nearby conspecifics. *Animal Behaviour* 72:1345-1353.

Hollén L. I., Manser M. B. (2007). Persistence of alarm-call behaviour in the absence of predators: a comparison between wild and captive-born meerkats (Suricata suricatta). *Ethology* 113:1038-1047.

Hoogland J. L. (1983). Nepotism and alarm calling in the black-tailed prairie dog (*Cynomys ludovicianus*). *Animal Behaviour* 31:472-479.

Hoogland J. L. (1996). Why do Gunnison's prairie dogs give anti-predator calls? *Animal Behaviour* 51:871-880.

Hoogland J. L., Cannon K. E., DeBarbieri L. M., Manno T. G. (2006). Selective predation on Utah prairie dogs. *American Naturalist* 168:546-552.

Ishihara M. (1987). Effect of mobbing toward predators by the damselfish *Pomacentrus coelestis* (Pisces: Pomacentridae). *Journal of Ethology* 5:43-52.

Ivins B. L., Smith A. T. (1983). Responses of pikas (*Ochotona princeps*, Lagomorpha) to naturally occurring terrestrial predators. *Behavioral Ecology and Sociobiology* 13:277-285.

Janson C. H. (1985). Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology* 18:125-138.

Janson C. H. (1990a). Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, Cebus apella. *Animal Behaviour* 40:910-921.

Janson C. H. (1990b). Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour* 40:922-934.

Janson C. H. (1994). Comparison of mating system across two populations of brown capuchin monkeys. *American Journal of Primatology* 33:217.

Janson C. H. (1996). Toward an experimental socioecology of primates. In *Adaptive Radiations of Neotropical Primates* (Norconk M., Rosenberger A., Garber P., eds); pp 309-325. New York: Plenum Press.

Janson C. H. (1998). Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. *Animal Behaviour* 55:1229-1243.

Janson C. H. (2006). Everything you ever wanted to know about capuchins. *American Journal of Primatology* 68:419-424.

Janson C. H. (2007a). Experimental evidence for route integration and strategic planning in wild capuchin monkeys. *Animal Cognition* 10:341-356.

Janson C. H. (2007b). Predator detection and the evolution of primate sociality: insights from experiments on a rain forest primate. *American Journal of Physical Anthropology* Suppl 44:136.

Janson C. H., Di Bitetti M. S. (1997). Experimental analysis of food detection in capuchin monkeys: effects of distance, travel speed, and resource size. *Behavioral Ecology and Sociobiology* 41:17-24.

Janson C. H., Karpanty S. M., Wheeler B. C. (2008). Experimental approaches to studying primate-predator interactions: from risk to alarm. *Primate Eye* 96:Abst #293.

Janson C. H., van Schaik C. P. (1993). Ecological risk aversion in juvenile primates: slow and steady wins the race. In *Juvenile Primates: Life History, Development, And Behavior*; pp 57-74. New York: Oxford University Press.

Karakashian S. J., Gyger M., Marler P. (1988). Audience effects on alarm calling in chickens (*Gallus gallus*). *Journal of Comparative Psychology* 102:129-135.

Kelly M. J., Noss A. J., Di Bitetti M. S., Maffei L., Arispe R. L., Paviolo A., De Angelo C. D., Di Blanco Y. E. (2008). Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. *Journal of Mammalogy* 89:408-418.

Kirchhof J., Hammerschmidt K. (2006). Functionally referential alarm calls in tamarins (*Saguinus fuscicollis* and *Saguinus mystax*) - evidence from playback experiments. *Ethology* 112:346-354.

Kiriazis J., Slobodchikoff C. N. (2006). Perceptual specificity in the alarm calls of Gunnison's prairie dogs. *Behavioural Processes* 73:29-35.

Klump G. M., Shalter M. D. (1984). Acoustic behaviour of birds and mammals in the predator context. *Zeitschrift für Tierpsychologie* 66:189-226.

Kobayashi T. (1994). The biological function of snake mobbing by Siberian chipmunks: I. Does it function as a signal to other conspecifics? *Journal of Ethology* 12:89-95.

Koenig A. (1998). Visual scanning by common marmosets (*Callithrix jacchus*): functional aspects and the special role of adult males. *Primates* 39:85-90.

Koenig A., Beise J., Chalise M. K., Ganzhorn J. U. (1998). When females should contest for food - testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). *Behavioral Ecology and Sociobiology* 42:225-237.

Krams I., Krama T., Igaune K. (2006). Alarm calls of wintering great tits *Parus major*: warning of mate, reciprocal altruism or a message to the predator? *Journal of Avian Biology* 37:131-136.

Kraus S., Read A., Anderson E., Baldwin K., Solow A., Spradlin T., Williamson J. (1997). A field test of the use of acoustic alarms to reduce incidental mortality of harbor porpoise in gill nets. *Nature* 388:341.

Krebs J., Dawkins R. (1984). Animal signals: mind-reading and manipulation. In *Behavioural Ecology: An Evolutionary Approach* (Krebs J., Davies N., eds); pp 380-402. Sunderland, MA: Sinauer.

Leavesley A. J., Magrath R. D. (2005). Communicating about danger: urgency alarm calling in a bird. *Animal Behaviour* 70:365-373.

Leger D. W., Nelson J. L. (1982). Effects of contextual information on behavior of calidris sandpipers following alarm calls. *Wilson Bulletin* 94:322-328.

Lima S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour* 49:11-20.

Lloyd E., Kreeltiyutanont K., Prabnasuk J., Grassman L. I., Borries C. (2006). Observation of Phayre's leaf monkeys mobbing a clouded leopard at Phu Khieo Wildlife Sanctuary (Thailand). *Mammalia* 70:158-159.

Macedonia J. M., Evans C. S. (1993). Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology* 93:177-197.

Manser M., Bell M., Fletcher L. (2001). The information that receivers extract from alarm calls in suricates. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268:2485-2491.

Manser M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268:2315-2324.

Marler P. (1955). Characteristics of some animal calls. *Nature* 176:6-8.

Marler P. (1977). Primate vocalization: affective or symbolic. In *Progress in ape research.* (Bourne G. H., ed); pp 85–96. New York: Academic Press.

Marler P. (1992). Functions of arousal and emotion in primate communications: a semiotic approach. In *Human Origins* (Nishida T., McGrew W., Marler P., Pickford M., de Waal F., eds); pp 225-233. Tokyo: University of Tokyo Press.

Marler P., Evans C., Hauser M. (1992). Animal signals: motivational, referential, or both? In *Nonverbal Vocal Communication: Comparative and Developmental Approaches* (Papousek H., Jurgens U., Papousek M., eds); pp 66-86. Cambridge: Cambridge University Press.

Marshall J. C. (1970). The biology of communication in man and animals. In *New Horizons in Linguistics.* (Lyons J., ed); pp 229–241. Harmondsworth: Penguin.

Martin P., Bateson P. (2007). *Measuring Behaviour: An Introductory Guide*. New York: Cambridge University Press

Martinez A. M., Martinez R. A., Montanelli S. B. (1992). Actualización de la distribución de los ofidios venenosos (Crotalidae y Elapidae) de la Provincia de Misiones (Argentina) y su relación con la distribución de suero antiofídico. *Acta Zoologica Lilloana* 41:307-310.

Masataka N. (1983). Psycholinguistic analyses of alarm calls of Japanese monkeys (*Macaca fuscata fuscata*). *American Journal of Primatology* 5:111-125.

Masters W. M. (1979). Insect disturbance stridulation: its defensive role. *Behavioral Ecology and Sociobiology* 5:187-200.

Maynard Smith J. (1965). The evolution of alarm calls. *American Naturalist* 99:59-63.

McCowan B., Franceschini N., Vicino G. (2001). Age differences and developmental trends in alarm peep responses by squirrel monkeys (*Saimiri sciureus*). *American Journal of Primatology* 53:19-31.

McGraw W. S., Zuberbühler K. (2008). Socioecology, predation, and cognition in a community of West African monkeys. *Evolutionary Anthropology* 17.

Mineka S., Cook M. (1988). Social learning and the acquisition of snake fear in monkeys. *Social learning: Psychological and biological perspectives*:51–73.

Miranda J. M. D., Bernardi I. P., Moro-Rios R. F., Passos F. C. (2006). Antipredator behavior of brown howlers attacked by black hawk-eagle in southern Brazil. *International Journal of Primatology* 27:1097-1101.

Mitchell R., Anderson J. (1997). Pointing, witholding information, and deception in capuchin monkeys (*Cebus apella). Journal of Comparative Psychology* 111:351-361.

Mitchell R. W. (1988). Ontogeny, biography, and evidence for tactical deception. *Behavioral and Brain Sciences* 11:259-260.

Møller A. (1988). False alarm calls as a means of resource usurpation in the great tit *Parus major*. *Ethology* 79:25-30.

Møller A. (1990). Deceptive use of alarm calls by male swallows, *Hirundo rustica*: a new paternity guard. *Behavioral Ecology* 1:1-6.

Munn C. (1986a). Birds that 'cry wolf'. *Nature* 319:143-145.

Munn C. (1986b). The deceptive use of alarm calls by sentinel species in mixed-species flocks of neotropical birds. In *Deception: Perspectives on Human and Nonhuman Deceit* (Mitchell R., Thompson N., eds); pp 169-175. Albany: State University of New York Press.

Murphy T. G. (2006). Predator-elicited visual signal: why the turquoise-browed motmot wag-displays its racketed tail. *Behavioral Ecology* 17:547-553.

Neudorf D., Sealy S. (2002). Distress calls of birds in a Neotropical cloud forest. *Biotropica* 34:118–126.

Notman H., Rendall D. (2005). Contextual variation in chimpanzee pant hoots and its implications for referential communication. *Animal Behaviour* 70:177-190.

Ostreiher R. (2003). Is mobbing altruistic or selfish behaviour? *Animal Behaviour* 66:145-149.

Ottoni E. B., Izar P. (2008). Capuchin monkey tool use: overview and implications. *Evolutionary Anthropology* 17:171-178.

Owens N. W., Goss-Custard J. D. (1976). The adaptive significance of alarm calls given by shorebirds on their winter feeding grounds. *Evolution* 30:397-398.

Owings D. H., Coss R. G. (1977). Snake mobbing by California ground squirrels: adaptive variation and ontogeny. *Behaviour* 62:50-69.

Owings D.H., Loughry W.J. (1985). Variation in snake-elicited jump-yipping by black-tailed prairie dogs: ontogeny and snake-specificity. *Zeitschrift für Tierpsychologie* 70:177-200.

Owings D. H., Morton E. S. (1998). *Animal Vocal Communication: A New Approach*: Cambridge University Press.

Owren M. J., Rendall D. (1997). An affect-conditioning model of nonhuman primate vocal signaling. In *Perspectives in ethology: communication* (Owens D. H., Beecher M. D., Thompson N. S., eds); pp 299-346. New York: Plenum Press

Owren M.J., Rendall D. (2001). Sound on the rebound: bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology* 10:58-71.

Owren M. J., Rendall D., Bachorowski J. A. (2003). Nonlinguistic vocal communication. In *Primate Psychology* (Maestripieri D., ed); pp 359-394. Cambridge, MA: Harvard University Press.

Owren M. J., Patel E. R. (2008). A little of this, a lot of that: specificity and variability in nonhuman primate vocal repertoires. *Primate Eye* 96:Abst #742.

Passamani M. (1995). Field observation of a group of Geoffroy's marmosets mobbing a margay cat. *Folia Primatologica* 64:163-166.

Patek S. N. (2001). Spiny lobsters stick and slip to make sound. *Nature* 411:153-154.

Paviolo A., de Angelo C. D., Di Blanco Y. E., Di Bitetti M. S. (2008). Jaguar *Panthera onca* population decline in the Upper Parana Atlantic Forest of Argentina and Brazil. *Oryx* 42:554-561.

Perry S., Baker M., Fedigan L., Gros-Louis J., Jack K., MacKinnon K. C., Manson J., Panger M., Pyle K., Rose L. (2003b). Social conventions in wild white-faced capuchin monkeys: evidence for traditions in a Neotropical primate. *Current Anthropology* 44:241-268.

Perry S., Manson J. H., Dower G., Wikberg E. (2003a). White-faced capuchins cooperate to rescue a groupmate from a *Boa constrictor*. *Folia Primatologica* 74:109-111.

Perry S. E., Manson J. H., Muniz L., Gros-Louis J., Vigilant L. (2008). Kin biased social behavior in wild white-faced capuchins, *Cebus capucinus*. *Animal Behaviour* 76:187-199.

Placci L. G., Arditi S. I., Cioteck L. E. (1994). Productividad de hojas, flores y frutos en el Parque Nacional Iguazú , Misiones. *Yviraretá* 5:49-56.

Pollock M. S., Chivers D. P. (2004). The effects of density on the learned recognition of heterospecific alarm cues. *Ethology* 110:341-349.

Preacher K. J., Briggs N. E. (2001). Calculation for Fisher's exact test: an interactive calculation tool for Fisher's exact probability test for 2 x 2 tables [Computer software available from http://www.quantpsy.org].

Preece S. J., Goulermas J. Y., Kenney L. P. J., Howard D., Meijer K., Crompton R., Beck T. W., DeFreitas J. M., Cramer J. T., Stout J. R. (2009). Activity identification using body-mounted sensors—a review of classification techniques. *Physiological Measurement* 30:R1.

Premack D. (1975). On the origins of language. In *Handbook of Psychobiology* (Gazzaniga M. S., Blakemore C. B., eds); pp 591–605. New York: Academic Press.

Price T. K., Arnold K., Zuberbühler K., Semple S. (2008). Vocal responses of male putty-nosed monkeys reflect a response-urgency rather than a referential calling system. *Primate Eye* 96:Abst #341.

Pulliam H. (1973). On the advantages of flocking. *Journal of Theoretical Biology* 38:419-422.

Rainey H. J., Zuberbühler K., Slater P. J. B. (2004). The responses of black-casqued hornbills to predator vocalisations and primate alarm calls. *Behaviour* 141:1263-1277.

Ramakrishnan U., Coss R. (2000). Age differences in the responses to adult and juvenile alarm calls by bonnet macaques (*Macaca radiata)*. *Ethology* 106:131-144.

Ramakrishnan U., Coss R. G., Schank J., Dharawat A., Kim S. (2005). Snake species discrimination by wild bonnet macaques (*Macaca radiata*). *Ethology* 111:337-356.

Ramirez-Llorens P., Di Bitetti M. S., Baldovino M. C., Janson C. H. (2008). Infanticide in black capuchin monkeys (*Cebus apella nigritus*) in Iguazú National Park, Argentina. *American Journal of Primatology* 70.

Range F., Fischer J. (2004). Vocal repertoire of sooty mangabeys (*Cercocebus torquatus atys*) in the Taï National Park. *Ethology* 110:301-321.

Reby D., Cargnelutti B., Hewison A. J. M. (1999). Contexts and possible functions of barking in roe deer. *Animal Behaviour* 57:1121-1128.

Robinson S. K. (1994). Habitat selection and foraging ecology of raptors in Amazonian Peru. *Biotropica* 26:443-458.

Rohwer S., Fretwell S. D., Tuckfield R. C. (1976). Distress screams as a measure of kinship in birds. *American Midland Naturalist* 96:418-430.

Ron T., Henzi S. P., Motro U. (1996). Do female chacma baboons compete for a safe spatial position in a southern woodland habitat? *Behaviour* 133:475-490.

Ross C. (1991). Life history patterns of New World monkeys. *International Journal of Primatology* 12:481-502.

Ross C. (1993). Predator mobbing by an all-male band of Hanuman langurs (*Presbytis entellus*). *Primates* 34:105-107.

Rüppell V. (1986). A "lie" as a directed message of the arctic fox (*Alopex lagopus* L.). In *Deception: Perspectives on Human and Nonhuman Deceit* (Mitchell R., Thompson N., eds); pp 177-181. Albany: State University of New York Press.

Sapolsky R. M. (2002). Endocrinology of the stress-response. In *Behavioral Endocrinology* (Becker J., Breedlove S., Crews D., McCarthy M., eds); pp 409-450. Cambridge, MA: MIT Press.

Schwagmeyer P. L. (1980). Alarm calling behavior of the thirteen-lined ground squirrel, *Spermophilus tridecemlineatus*. *Behavioral Ecology and Sociobiology* 7:195-200.

Searcy W. A., Nowicki S. (2005). *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*: Princeton University Press Princeton, NJ:.

Seddon N., Tobias J., Alvarez A. (2002). Vocal communication in the pale-winged trumpeter (*Psophia leucoptera)*: repertoire, context, and functional reference. *Behaviour* 139:1331-1359.

Seyfarth R., Cheney D. (1980). The ontogeny of vervet monkey alarm calling behavior: a preliminary report. *Zeitschrift für Tierpsychologie* 54:37-56.

Seyfarth R., Cheney D. (1986). Vocal development in vervet monkeys. *Animal Behaviour* 34:1640-1658.

Seyfarth R., Cheney D. (2003). Signalers and receivers in animal communication. *Annual Review of Psychology* 54:145-173.

Seyfarth R. M., Cheney D. L., Marler P. (1980a). Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science* 210:801-803.

Seyfarth R. M., Cheney D. L., Marler P. (1980b). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour* 28:1070-1094.

Shelley E. L., Blumstein D. T. (2005). The evolution of vocal alarm communication in rodents. *Behavioral Ecology* 16:169-177.

Sherman P.W. (1980). The meaning of nepotism. *American Naturalist* 116:604-606.

Sherman P. W. (1977). Nepotism and the evolution of alarm calls. *Science* 197.

Sherman P. W. (1985). Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? *Behavioral Ecology and Sociobiology* 17:313-323.

Shields W. M. (1980). Ground squirrel alarm calls: nepotism or parental care? *American Naturalist* 116:599-603.

Shultz S., Thomsett S. (2007). Interactions between African crowned eagles and their prey community. In *Monkeys of the Taï Forest: An African Primate Community*; pp 171-193. New York: Cambridge University Press.

Siegel S., Castellan N. J. (1988). *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.

Slocombe K. E., Zuberbühler K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences* 104:17228-17233.

Smith R. J., Jungers W. L. (1997). Body mass in comparative primatology. *Journal of Human Evolution* 32:523-559.

Smith R. J. F. (1986b). Evolution of alarm signals: role of benefits of retaining group members or territorial neighbors. *American Naturalist* 128:604-610.

Smith S. M. (1975). Innate recognition of coral snake pattern by a possible avian predator. *Science* 187:759-760.

Smith S. M. (1977). Coral-snake pattern recognition and stimulus generalization by naive great kiskadees (Aves: Tyrannidae). *Nature* 265:535-536.

Smith S. S. (1978). Alarm calls, their origin and use in *Eutamias sonomae*. *Journal of Mammalogy* 59:888-893.

Smith W. (1986a). An "informational" persepective on manipulation. In *Deception: Perspectives on Human and Nonhuman Deceit* (Mitchell R. W., Thompson N. S., eds); pp 71-86. Albany, NY: SUNY Press.

Sokal R. R., Rohlf F. J. (1995). *Biometry: The Principles and Practice of Statistics in Biological Research*. New York: W. H. Freeman and Co.

Srivastava A. (1991). Cultural transmission of snake-mobbing in free-ranging Hanuman langurs. *Folia Primatologica* 56:117-120.

Struhsaker T. (1967). Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In *Social Communication Among Primates* (Altmann S., ed); pp 281-324. Chicago: University of Chicago Press.

Sullivan K. (1985). Selective alarm calling by downy woodpeckers in mixed-species flocks. *Auk* 102:184-187.

Swedell L., Tesfaye T. (2003). Infant mortality after takeovers in wild Ethiopian hamadryas baboons. *American Journal of Primatology* 60.

Tabachnick B. G., Fidell L. S. (2001). *Using Multivariate Statistics*. Boston: Pearson.

Tamura N. (1995). Postcopulatory mate guarding by vocalization in the Formosan squirrel. *Behavioral Ecology and Sociobiology* 36:377-386.

Taylor R. J., Balph D. F., Balph M. H. (1990). The evolution of alarm calling: a cost-benefit analysis. *Animal Behaviour* 39:860-868.

Templeton C. N., Greene E., Davis K. (2005). Allometry of alarm calls: black-capped chickadees encode information about predator size. *Science* 308:1934-1937.

Tenaza R. R., Tilson R. L. (1977). Evolution of long-distance alarm calls in Kloss's gibbon. *Nature* 268:233-235.

Terborgh J. (1983). *Five New World Primates: A Study in Comparative Ecology*. Princeton: Princeton University Press.

Terborgh J. (1990). Mixed flocks and polyspecific associations: costs and benefits of mixed groups to birds and monkeys. *American Journal of Primatology* 21:87-100.

Tramer E. J. (1994). Feeder access: deceptive use of alarm calls by a white-breasted nuthatch. *Wilson Bulletin* 106:573.

Treves A., Palmqvist P. (2007). Reconstructing hominin interactions with mammalian carnivores (6.0-1.8 Ma). In *Primate Anti-Predator Strategies*; pp 355-381. New York: Springer.

van Schaik C. P. (1983). Why are diurnal primates living in groups? *Behaviour* 87:120-143.

van Schaik C. P. (1989). The ecology of social relationships amongst female primates. In *Comparative Socioecology* (Standen V., Foley R. A., eds); pp 195-218. Oxford: Blackwell.

van Schaik C. P., van Noordwijk M. A. (1988). Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). *Behaviour* 105:77-98.

van Schaik C. P., van Noordwijk M. A. (1989). The special role of male *Cebus* monkeys in predation avoidance and its effect on group composition. *Behavioral Ecology and Sociobiology* 24:265-276.

Vasquez M. R. O., Heymann E. W. (2001). Crested eagle (*Morphnus guianensis*) predation on infant tamarins (*Saguinus mystax* and *Saguinus fuscicollis*, Callitrichinae). *Folia Primatologica* 72:301-303.

Vine I. (1971). Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *Journal of Theoretical Biology* 30:405-422.

Vitale A., Visalberghi E., De Lillo C. (1991). Responses to a snake model in captive crab-eating macaques (*Macaca fascicularis*) and captive tufted capuchins (*Cebus apella*). *International Journal of Primatology* 12:277-286.

Warkentin K. J., Keeley A. T. H., Hare J. F. (2001). Repetitive calls of juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) communicate response urgency. *Canadian Journal of Zoology* 79:569-573.

Weary D. M., Kramer D. L. (1995). Response of eastern chipmunks to conspecific alarm calls. *Animal Behaviour* 49:81-93.

Wheeler B. C. (2008). Selfish or altruistic? An analysis of alarm call function in wild capuchin monkeys, *Cebus apella nigritus*. *Animal Behaviour* 76:1465-1475.

Whiten A., Byrne R. (1988). Tactical deception in primates. *Behavioral and Brain Sciences* 11:233-273.

Wich S. A., Sterck E. H. M. (2003). Possible audience effect in Thomas langurs (Primates; *Presbytis thomasi*): an experimental study on male loud calls in response to a tiger model. *American Journal of Primatology* 60:155-159.

Williams G. C. (1966). *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton, NJ: Princeton University Press.

Wilson R. P., Liebsch N., Davies I. M., Quintana F., Weimerskirch H., Storch S., Lucke K., Siebert U., Zankl S., Müller G. (2007). All at sea with animal tracks: methodological and analytical solutions for the resolution of movement. *Deep-Sea Research Part II* 54:193-210.

Wilson R. P., Shepard E. L. C., Liebsch N. (2008). Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* 4:123-137.

Witkin S. R., Ficken M. S. (1979). Chikadee alarm calls: does mate investment pay dividends? *Animal Behaviour* 27:1275-1276.

Woodland D. J., Jafaar Z., Knight M. L. (1980). The "pursuit deterrent" function of alarm signals. *American Naturalist* 115:748-753.

Wrangham R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour* 75:262-300.

Wright S. (1922). Coefficients of inbreeding and relationship. *American Naturalist* 56:330-338.

Yorzinski J. L., Ziegler T. (2007). Do naive primates recognize the vocalizations of felid predators? *Ethology* 113:1219-1227.

Yosef R. (1991). Foraging habits, hunting, and breeding success of lanner falcons (*Falco biarmicus*) in Israel. *Journal of Raptor Research* 25:77-81.

Zuberbühler K. (2000). Referential labelling in Diana monkeys. *Animal Behaviour* 59:917-927.

Zuberbühler K. (2001). Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli. Behavioral Ecology and Sociobiology* 50:414-422.

Zuberbühler K. (2003). Referential signaling in non-human primates: cognitive precursors and limitations for the evolution of language. *Advances in the Study of Behavior* 33:265-307.

Zuberbühler K., Byrne R. W. (2006). Social cognition. *Current Biology* 16:R786-R790.

Zuberbühler K., Jenny D. (2007). Interaction between leopard and monkeys. In *Monkeys of the Taï Forest: An African Primate Community*; pp 133-154. New York: Cambridge University Press.

Zuberbühler K., Jenny D., Bshary R. (1999). The predator deterrence function of primate alarm calls. *Ethology* 105:477-490.

Zuberbühler K., Noë R., Seyfarth R. (1997). Diana monkey long-distance calls: messages for conspecifics and predators. *Animal Behaviour* 53:589-604.