Production and perception of situationally variable alarm calls in wild tufted capuchin monkeys (*Cebus apella nigritus*)

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Abstract

Many mammalian and avian species produce conspicuous vocalizations upon encountering a predator, but vary their calling based on risk-urgency and/or predator-type. Calls falling into the latter category are termed “functionally referential” if they also elicit predator-appropriate reactions in listeners. Functionally referential alarm calling has been well documented in a number of Old World monkeys and lemurs, but evidence among Neotropical primates is limited. This study investigates the alarm call system of tufted capuchin monkeys (*Cebus apella nigritus*) by examining responses to predator and snake decoys encountered at various distances (reflecting differences in risk-urgency). Observations in natural situations were conducted to determine if predator-associated calls were given in additional contexts. Results indicate the use of three call types. “Barks” are elicited exclusively by aerial threats but the call most commonly given to terrestrial threats (the “hiccup”) is given in non-predatory contexts. The rate in which this latter call is produced reflects risk-urgency. Playbacks of these two call types indicate that each elicits appropriate anti-predator behaviors. The third call type, the “peep”, seems to be specific to terrestrial threats, but it is unknown if the call elicits predator-specific responses. “Barks” are thus functionally referential aerial predator calls while “hiccups” are better seen as generalized disturbance calls which reflect risk-urgency. Further evidence is needed to draw conclusions regarding the “peep”. These results add to the evidence that functionally referential aerial predator alarm calls are ubiquitous in primates, but that non-catarrhine primates tend to use generalized disturbance calls in response to terrestrial threats.

Introduction

Many gregarious birds and mammals produce alarm calls upon encountering a predator. Such calls typically function to alert conspecifics to the presence of danger and/or communicate to the predator that it has been detected (Caro 2005). While some species have a generalized alarm call system, producing similar calls in different threatening situations, other species demonstrate "situationally variable" alarm calls (reviewed in Fichtel & Kappeler 2002; Caro 2005). 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 context 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. 1980; Blumstein 1999b). 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), although systems that combine both simultaneously are possible (Marler et al. 1992; Manser 2001).

Urgency-based alarm call systems are exemplified by yellow-bellied marmots (*Marmota flaviventris*), which vary their alarm calling based on a combination of the distance from the caller to the predator and the type of predator encountered, but not based on predator type alone (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 types of reactions (Blumstein & Armitage 1997; see also Leavesley & Magrath 2005). While urgency-based alarm call systems have long been recognized in the sciurid rodents (reviewed in Blumstein 2007), such alarm call systems have more recently been reported in birds (e.g., Baker & Becker 2002; Leavesley & Magrath 2005; Templeton et al. 2005), carnivores (Manser 2001; Furrer & Manser 2009), and some primates (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* (or *perception specificity*) in call response (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 predator; Blumstein 1999a). Stimulus independence of call reaction is shown if the call alone elicits an appropriate reaction (i.e., even if supposed referent is absent)

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 (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. 1980). 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 (*Suricata suricatta*), which simultaneously vary aspects of the calls with risk-urgency (Manser 2001; Manser et al. 2001), and several avian taxa (e.g., Seddon et al. 2002; Gill & Sealy 2004). Among primates, alarm calls that show both context and perception specificity have been documented only in lemurs (e.g., Macedonia & Evans 1993; Fichtel & Kappeler 2002) and Old World monkeys (e.g., Cheney & Seyfarth 1990; Zuberbühler 2000), but not New World monkeys or apes.

Several additional studies of alarm calls in primates and rodents have tested only one of the two criteria of functionally referential calling (see Blumstein 2007). 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), but the evidence of stimulus independent responses in these cases is limited because playback experiments were not conducted. 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 elicited by aerial and terrestrial stimuli respectively with predator-specific reactions, while only aerial predator alarm calls elicited such responses in *S. fuscicollis* (Kirchhof & Hammerschmidt 2006). However, data regarding the context of production of the alarm calls were not given for either of these tamarin species and it is thus unclear if their calls are indeed predator-specific. Examination of both call production and perception 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).

This study experimentally tests whether variation in alarm call production and response in a New World primate, the tufted capuchin monkey (*Cebus apella nigritus*), indicates an urgency-based and/or a functionally referential alarm call system in a species in which food-associated call have been shown to be functionally referential (Di Bitetti 2003). To address questions regarding alarm call production, the study subjects were observed in experimental contexts in which they detected models of raptors, felids, and snakes at varying distances to determine the call types and rates of calling elicited by these three stimulus types at difference levels of risk-urgency. These experiments were complemented with observations in natural contexts to determine if the call types produced in the experimental contexts are produced in any additional contexts. To test whether responses to the calls are stimulus independent, playbacks of the call types elicited by the predator models were conducted.

Methods

Study Site and Subjects

Data were collected from July - September 2004 and May 2005 - December 2006 in Iguazú National Park, Argentina (25°40'S, 54°30'W; see Di Bitetti et al. 2000 for a detailed description of the study site). Initial predator model experiments were conducted during the first period while all experimental protocols and natural observations were implemented during the second study period. Tufted capuchins are medium-sized (~ 3 kg), diurnal, and omnivorous primates that typically live in groups of 7-30 individuals characterized by female philopatry and male dispersal (Di Bitetti 2001). The population is highly arboreal with individuals spending the majority of time at 3 to 10 m above the ground and less than 3% of daytime activity occurring terrestrially (Wheeler unpublished data). Data were collected on three fully habituated multimale-multifemale 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. While all protocols were conducted with all three study groups, most experiments and observations were conducted with the Macuco group because this group allowed for a greater number of individuals to be sampled.

Likely predators of capuchins in Iguazú include carnivores (jaguars, *Panthera onca*; pumas, *Puma concolor*; ocelots, *Leopardus pardalis*; and tayras, *Eira barbara*), and two species of raptors (hawk eagles: *Spizaetus ornatus* and *S. tyrannus*; Di Bitetti 2001). Three species of vipers (*Bothrops neuwiedii, B. jararaca,* and *Crotalus durissus*) are also found at the site; while these snakes certainly pose a mortal threat to capuchins that approach too closely, the monkeys are likely too large to be preyed upon by these species (see Wheeler 2008).

Tufted capuchins produce at least three acoustically distinct call types in response to predators and snakes (Fig. 1), each of which is easily distinguishable by ear in humans. Two of these, the “bark” (Fig. 1a) and the “hiccup” (Fig. 1b), were described by Di Bitetti (2001) and labeled the “aerial predator alarm call” (APAC) and the “ground predator alarm call” (GPAC) respectively. *Ad libitum* observations by Di Bitetti (2001) indicated that APACs were elicited exclusively by flying stimuli while GPACs were elicited by terrestrial stimuli including felids and, possibly, venomous snakes as well as in response to conspecific aggression (Di Bitetti 2001). Di Bitetti (2001) also noted the use of “hiku” calls, which were not acoustically distinguishable from GPACs, by animals foraging in suspensory positions. Because of the lack of acoustic variation between the GPAC and the hiku, they are here considered a single call type (i.e., the hiccup). In addition to these two alarm call types identified by Di Bitetti (2001), a third call type, the “peep” (Fig. 1c), was identified during the course of the current study. While this call sounds and appears (spectrographically) to be similar to the species’ contact note (CN; Fig. 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 s per individual; Di Bitetti 2001). None of the three alarm call types were age or sex specific, being produced by all age-sex classes with the exception of very young infants (Di Bitetti 2001, pers. obs.). 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 types of calls and the rates in which they were given 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 Fig. 1 in Wheeler 2008). 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).

Models were placed 50-150 m in front of the group in the direction of movement. Perched raptor models were hung from tree branches by a rope thrown over the branch (normally at a height of 10 to 12 m, but on a few occasions lower if canopy height was especially low). 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 10-15 m down to 1.5 m 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 or fallen tree trunks. The placement of the models in terms of the surrounding vegetation was varied in order to ensure that the distance in which they were detected was varied. To avoid habituation, 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 15 day period. In total, 50 experiments were conducted with the ocelot models, 30 with perched raptor models, 8 with flying raptor models, 47 with venomous snake models, and 28 with non-venomous snake models. Of these, 97 were conducted with the Macuco Group, 30 with the Gundolf Group, and 36 with the Guenon Group

Data on vocal behavior during the experiments was collected using an all-occurrence sampling method (Martin & Bateson 2007). Three observers (the author and two assistants) standing within a 15 m radius of the model noted the identity of the first individual to vocalize upon detecting a model, the type(s) of call given, as well as the caller's height and distance to the model at the moment the vocalizations commenced. All age and sex classes were observed to react vocally to all model types and, with the exception of infants, were included in the analyses. A call was considered to be in response to the model if the caller was looking directly towards the model or simultaneously employing an appropriate escape reaction. Only the first caller from each experiment was included in the analysis, as subsequent detectors' perceived risk could be affected by the behavior of previous detectors. The first caller's risk-urgency was classified as high, medium, or low depending on the type of predator encountered and the distance to the model. Predators which could likely successfully attack the caller from their current position (i.e., low probability of escape for the caller) were considered a high urgency threat; these included stationary predators at a distance of less than 5 m and flying stimuli at a distance of less than 25 m. Encounters at greater distances were considered medium (stationary predators at 5 to 25 m; flying raptors at 25 to 100 m) or low urgency threats (stationary predators at more than 25 m; flying raptors at more than 100 m). Venomous snakes were always considered a low urgency threat because these species seem to be extremely unlikely prey on capuchins (see above) and in no case did a capuchin detect a venomous snake within a likely striking distance (i.e., less than 1 m).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 using either a Sennheiser ME-67/K6 or MKH-60 directional microphone. In nearly all cases, vocalizing animals were within 10 m of the microphone. 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 examined 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 begin to call once they have detected the predator model, calls given after this initial period could not always be easily assigned to a particular individual. 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 over the first 10 seconds. This, together with equipment failure on seven occasions, led to a larger number of experimental observations of call types given (N=82) than observations of call rate (N=58).

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 in the latter category included large, non-predatory birds in flight (including vultures and toucans), medium-sized to large animals in the understory (including rodents and ungulates), and non-venomous snakes. Misclassification of non-predators as potential threats is expected in a dense forest where callers may not be able to see a stimulus well enough to correctly identify it (Evans 1997). Such stimuli were classified as “other” (not potential predators) in cases where the focal animal had an unobstructed view of the stimulus and the individual could reasonably be assumed to have recognized it as a non-threatening stimulus. Non-predatory stressors, including conspecific aggression, attacks by stinging insects, and “precarious positional behaviors”, were also assigned to the “other” category. Precarious positional behaviors were those in which the individual could reasonably be assumed to be at a relatively high risk of falling and included suspensory positions and the use of unstable substrates (dead vegetation or highly flexible substrates less than 1 cm in diameter).

Call response

To determine if alarm calls elicit predator-specific responses 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. Because bouts of barks normally included only a few calls (often only a single call) while hiccups were given repeatedly, playbacks of these call types reflected this. Due to a lack of a sufficient number of high quality recordings of sequences of peeps, I was unable to conduct enough playback experiments to test for responses to this call type. In addition to playbacks of alarm calls, playbacks of 1) non-alarm vocalizations of sympatric avian and mammalian taxa (to determine the effect of playing back other familiar sounds through speakers) and 2) capuchin alarm calls played in reverse (since these were acoustically similar to alarm calls) 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 ± 0.5 m. 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., terrestrial mammals or low-flying vultures). Each individual was tested only once for a given stimulus type (bark, hiccup, and control). While not all individuals were tested for all three stimulus types, each age-sex class was tested multiple times for each stimulus. While I initially intended to use a unique call sequence for each playback, this was not possible due to a lack of recordings of sufficiently high quality. Thus some call series were used for more than one playback experiment (but not more than twice with a particular group), 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 eight distinct bouts of barks, nine distinct bouts of hiccups, and ten different control recordings were used in the playbacks.

For each playback experiment, a single adult or juvenile animal resting, grooming, or foraging (with little or no directional movement) approximately 15 m from the playback speaker was chosen as a focal animal; because focal animals often changed positions before the playback started, its distance to the speaker varied at the moment of playback but in nearly all cases (39 of 44 playbacks) the focal was 10 to 20 m from the speaker. All age-sex classes received all playback treatments and no one class was overrepresented in the dataset. Juveniles were considered appropriate focal animals because their reactions did not differ from those of adults (Wheeler 2009a). 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 s 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 anti-aerial predator, anti-terrestrial predator, or generalized anti-predator behaviors (see Table 1 for definitions). Generalized anti-predator behaviors were those which would be appropriate responses to both terrestrial and aerial predators and therefore cannot be considered to be "predator specific".

Statistical analyses and data selection

To test the factors that affect call production in experimental contexts, a multinomial logistic regression was used with call type of the first individual to call in an experiment as the dependent variable and stimulus category (raptor, felid, or snake) and risk-urgency (high, medium, or low) as the predictor variables. Although some individuals were observed to give the first bout of calls in response to a model on more than one occasion, each individual was included in the logistic regression only once in order to avoid pseudoreplication. In most cases (27 of 32 individuals), the first observation of a particular individual was the one chosen to include in the analysis. However, because choosing the first observation for all individuals led to a relatively small sample size for detections of raptors and detections in high-urgency situations, calling bouts in these two contexts were chosen over an individual's first observed calling bout. 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. General linear mixed models (GLMM) with stimulus type or risk-urgency as the independent variable, call rate over the first 10 s as the independent variable, and caller identity as a random factor were used test if call rate varies based on the context in which the calls are produced. Fisher's exact tests were used to examine differences in the occurrence of anti-predator responses across the playback types. The logistic regression and binomial tests were conducted with SPSS 15.0. Fisher's exact tests were calculated using the VassarStats web utility (http://faculty.vassar.edu/lowry/VassarStats.html). GLMMs were conducted with STATA 10.0.

Results

Call production

Call types given in experimental contexts

The types of calls given to raptor models were recorded on 13 occasions, to ocelot models on 35 occasions, and to snake models on 34 occasions (see Wheeler 2008 for discussion of detections which did not result in a vocal response). When considering only one reaction per individual, the call type or series produced in response to a model was better explained by stimulus category (i.e., raptor, felid, or snake; multinomial logistic regression: $N=32$, $\chi^2=35.51$, $df=6$, $p<0.0001$) than by risk-urgency (same logistic regression: $\chi^2=2.54$, $df=6$, $p=0.863$; Fig. 2). Focal animals produced only barks, and never hiccups or peeps, in response to models of flying and perched raptors (Fig. 2a). 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 (Fig. 2a). The urgency of the threat presented by the predator or snake model was less tightly associated with the vocal responses; barks were given at all levels of risk (but only once in a low-risk context), as were both hiccups and peeps, although peeps given in high risk situations were always accompanied by hiccups (Fig. 2b).

Context specificity of barks, hiccups, and peeps

In addition to the alarms given in the experimental contexts, another 142 alarm calls were given by focal animals in natural contexts. When these data are factored in, clear differences between the three alarm calls types emerge in the degree to which production of the calls is context specific. Seven barks were given by focal animals in natural contexts. Six of these were in response to flying stimuli, only one of which 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 (i.e., innocuous flying stimuli). 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 barks (95%) were associated with an actual or potential aerial threat, not significantly difference from the value expected for a context specific call (binomial test: p=0.736).

Focal animals were observed to produce hiccups in natural contexts on 135 occasions. Only seven of these (5.2%) were in response to potential threats: one in response to a medium-sized terrestrial rodent (agouti: *Dasyprocta azarae*) moving quickly through the understory, three following hiccups given by other capuchins, and one following agouti grunt vocalizations (apparently the species' alarm call). Of the remaining calls, the vast majority (N=96; 71.1%)

were given in situations in which the caller was employing a precarious positional behavior and could reasonably be assumed to be at risk of falling. A single bout (0.7%) was given by an individual while receiving aggression from another groupmate. No eliciting stimulus could be identified in the 31 cases (23.0%), but these were most often given when the group was foraging close to the ground in dense bamboo forest where visibility was greatly limited. When the contexts in which these calls were given are combined with those given during the predator model experiments, only 58 of 193 hiccups (30.1%) were in response to actual or potential terrestrial threats, significantly less than expected for a context specific call type (binomial test; $p<0.0001$).

Focal animals were never observed in natural contexts to produce a long call series resembling the peeps that were given in response to the ocelot and snake models. However, given the ubiquity of the acoustically similar contact call, the low intensity of the call, and the inconspicuous behavior that normally accompanies the production of contact calls, it is possible that short bouts were produced at a rate similar to that observed during short bouts of peeps, but that this went unnoticed by the observer. If the lack of observations of calls similar to peeps indeed reflects a lack of production of such call series (or if further analysis indicates that the calls are acoustically distinct from contact calls), then it appears that peeps are indeed context specific, with all 37 observed bouts occurring in the context of a terrestrial threat (Table 2): 16 bouts were given in response to felid models, while 15 were given to venomous snake models and 6 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 s) were observed on 18 occasions (Table 2), five times in response to felid models, 10 to venomous snake models, and three to non-venomous snakes. However, in nearly all of these cases (except four involving non-venomous snakes and one with a viper) at least one hiccup was given within the first 30 s of the calling bout (but not within the first 10 s 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 s of a calling bout varied from 1 to 9. Fewer barks were on average given in high-urgency situations (mean ± SE: 3.67 ± 1.3 calls; N=3) than to medium or low-urgency aerial predators (5.17 ± 1.4 calls, N=6), but statistical analyses were not performed due to the small sample size available. The number of hiccups an individual gave in the first 10 s of a calling bout varied from 1 to 11. Significantly more hiccups were given in response to felids (5.77 ± 0.8 calls; N=22) than to snakes (1.73 ± 0.2 calls; N=15) (GLMM: $F_{1,15}$=6.1, *P*=0.024). Likewise, more hiccups were given in response to higher risk relative to lower risk threats (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) (GLMM: $F_{1,15}$=9.18, *P*=0.008). This trend is even more pronounced when one considers that precarious positional behaviors (a non-urgent situation) almost always elicit only a single hiccup (Fig. 3). The number of peeps an individual gave during the first 10 s of a calling bout varied from one to 23, but did not vary significantly across the situations examined. The number of peeps given in response to felids (6.80 ± 1.6 calls; N=15) did not differ from that given to snakes (7.33 ± 1.6 calls; N=15) (GLMM: $F_{1,11}$=0.08, *P*=0.786), and there was no variation in the number of peeps based on the caller's risk-urgency (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) (GLMM: $F_{1,11}$=0.14, *P*=0.714). Finally, when considering an entire call series consisting of both hiccups and peeps, felids elicited significantly more calls in the first 10 s (8.8 ± 0.9 calls; N=26) than did snakes (5.9 ± 1.2 calls, N=23) (GLMM: $F_{1,22}$=4.69, *P*=0.042) and there was a tendency for more calls to be given in higher risk than lower risk situations (high risk: 10.40 ± 1.2 calls, N=5; medium risk: 8.75 ± 1.0 calls, N=20; low risk: 5.75 ± 1.1 calls, N=24) (GLMM: $F_{1,22}$=3.33, *P*=0.082).

Call response

A total of 44 playbacks experiments were conducted including 15 controls, 14 barks, and 15 hiccups; reactions to these are summarized in Table 3. Anti-predator reactions were employed by focal animals more often following playbacks of alarm calls (i.e., barks and hiccups; 26 of 29 experiments) than following control playbacks (7 of 15 experiments) (Fisher's exact test, p=0.003), but there was no difference in this regard between the two alarm call types (barks: 13 of 14 playbacks; hiccups: 13 of 15 playbacks) (Fisher's exact test; p=1.0). Generalized anti-predator reactions were the most common reaction to both alarm call types (barks: 11 of 14 playbacks; hiccups: 12 of 15 playbacks), and such reactions occurred significantly more often following the alarms than the controls (6 of 15 playbacks) (2 x 3 Fisher's exact test: p=0.04). There were differences between the alarm call types in the occurrence of predator-specific reactions. Anti-aerial predator behaviors occurred more often following playbacks of barks (8 of 14 playbacks) than following playbacks of hiccups (3 of 15 playbacks) or controls (2 of 15 playbacks) (2 x 3 Fisher's exact test: p=0.03), while anti-terrestrial predator behaviors occurred more often following playbacks of hiccups (5 of 15 playbacks) than following playbacks of barks (0 of 15 playbacks) or controls (1 of 15 playbacks) (2 x 3 Fisher's exact test: p=0.04).

Discussion

The three alarm call types produced by tufted capuchins showed varying degrees of production specificity: production of the bark was highly specific, being elicited almost exclusively by aerial threats, while the hiccup was given both in response to terrestrial (but never aerial) threats and in non-predatory contexts in which the caller was likely experiencing some degree of stress. Peeps seem to be elicited only by terrestrial threats, but additional research is needed to confirm that similar call bouts are not also given in the absence of felids and snakes. All three alarm call types were observed at least once in each of high, medium, and low-urgency situations, thus indicating that call types do not vary uniquely with threat urgency. However, the number of hiccups given during the first 10 s 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 and hiccups elicited anti-predator reactions at a similar rate and, although generalized anti-predator reactions were the most common response to both alarm call types, barks more often elicited anti-aerial predator behaviors while only hiccups elicited anti-terrestrial predator behaviors. 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, but initial observations indicate that the calls draw the attention of listeners towards the caller. The observed trends of alarm call production and response were similar across groups. These results suggest that situational variation in the types of alarm calls produced by tufted capuchins reflects the type of threat encountered rather than the risk-urgency presented by that threat, but that in at least some cases the rate of calling is affected by the caller's perceived risk. Likewise, responses to calls are strongly linked to the types of threats that elicit the calls, but additional research is needed to determine if variation within call types affects call the receiver's perception of risk-urgency.

These findings match well with most previous studies of primates that indicate that terrestrial and aerial predators respectively elicit distinct alarm call types (e.g., Seyfarth et al. 1980; Macedonia & Evans 1993; Zuberbühler 2000 2001; Fichtel & Kappeler 2002; Range & Fischer 2004; Digweed et al. 2005; Ouattara et al. 2009a; Schel et al. 2009), in contrast to many sciurid rodent and avian taxa (reviewed in Fichtel & Kappeler 2002; Caro 2005). Likewise, the regular production of terrestrial predator-associated calls in the absence of predators appears to be common, especially among non-catarrhine primates (Fichtel & Kappeler 2002; Digweed et al. 2005; Fichtel et al. 2005; Kirchhof & Hammerschmidt 2006; see also Ouattara et al. 2009a for similar trends in a catarrhine primate). Finally, an increase in call rate with an increase in risk facing the caller is consistent with several studies of avian and rodent taxa (Blumstein & Armitage 1997; Blumstein 1999b; Warkentin et al. 2001; Baker & Becker 2002; Leavesley & Magrath 2005) and a recent study of Old World monkeys (Ouattara et al. 2009b; see also Schel et al. 2009).

The use of the same call for carnivores and snakes among arboreal (e.g., Fichtel & Kappeler 2002; Digweed et al. 2005; Ouattara et al. 2009a; this study) but not terrestrial (Seyfarth et al. 1980; Range & Fischer 2004) primates fits well with the prediction that the need for distinct escape reactions for different threat types are the main driving force behind the evolution of functionally referential alarm calls (Macedonia & Evans 1993). However, in the current study apparent attempts to locate the predator were a far more common response to playbacks than were escape reactions, indicating that the ability to quickly locate a predator may also be important (Kirchhof & Hammerschmidt 2006; see also Ouattara et al. 2009c for additional evidence that different predator types favor distinct non-escape reactions in forest primates). The low rate of escape reactions in the current study may be explained by the extremely short distances in which raptors, felids, and snakes are detected in the study population (Janson 2007). When predators rely on ambush, average detection distances may be extremely short, in which case the detector would likely be in far more danger than are other group members. If this is the case, then an escape response by call receivers may not be the most beneficial reaction, particularly if the caller is not in the receiver's immediate vicinity. 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 (see Beauchamp & Ruxton 2007).

The data presented here indicate that although the hiccup is not specific to encounters with felids and snakes, bouts that consist of two or more hiccups may be. However, while not apparent in the results of the current study, such bouts are often produced in response to moderately intense to intense conspecific aggression (Di Bitetti 2001; Wheeler 2009b) and during feeding experiments in which within group contest competition for food is intense (Wheeler 2009b). In both cases, the calls are likely functionally deceptive because the anti-predator reactions of call receivers would benefit the caller despite the absence of any terrestrial threats. The single hiccups produced while engaged in precarious positional behaviors may also be functionally deceptive; the calls sometimes, albeit rarely, elicit sudden vigilance in immediate neighbors, a behavior which would be seemingly be beneficial for an individual at risk of falling to the ground.

Functional deception may also play a role in other primate taxa reported to use predator-associated calls in the absence of predators (precarious positional behaviors: Ouattara et al. 2009a; conspecific aggression: Cheney & Seyfarth 1990; Fichtel & Kappeler 2002; Fichtel et al. 2005; Kirchhof & Hammerschmidt 2006; see also Digweed & Rendall 2009 for similar trends in a sciurid rodent). Additional research should be conducted to determine if these calls are functionally deceptive by examining if they cause anti-predator reactions that would be beneficial to the caller (e.g., elicitation of vigilance in neighbors or distraction of conspecific competitors). Potentially "deceptive" uses of calls should be explicitly considered when examining context specificity of production, as a low degree of context specificity may be favored when callers benefit by influencing receiver behavior in a similar way across a range of contexts (see Rendall et al. 2009). Indeed, several studies have shown that predator-associated calls that are also given in non-predatory contexts still regularly elicit predator-specific reactions despite their low levels of context specificity (e.g., Fichtel & Kappeler 2002; Kirchhof & Hammerschmidt 2006; current study). This should occur when such responses are on average beneficial for recipients (see Wiley 1994). It is interesting that, among non-catarrhine primates, it is consistently the terrestrial predator-associated call that shows a low degree of context specificity, while primate aerial predator alarm calls tend to be highly specific in this regard. Such trends may be related to a lack of ability to use aerial predator alarms "deceptively" (e.g., if a greater ability to locate flying stimuli reduces reactions to false alarms) or to higher risk of predation by aerial relative to terrestrial predators. The latter factor could favor a high degree of context specificity if a decrease in call reliability reduces the benefits callers receive by giving "honest" alarms (see Wheeler 2008). At this point, though, the benefit of evolving a functionally referential call for aerial but not terrestrial predators is unclear, as are the selective pressures which would favor the apparently higher degree of context specificity in the terrestrial predator-associated calls of Old World monkeys relative to Neotropical and Malagasy primates.

Despite the observed differences in production specificity, both barks and hiccups elicited predator-specific reactions, although both calls most often elicited generalized anti-predator reactions. The single most common response to both alarm call types was to simply look towards the speaker, and playbacks frequently resulted in individuals approaching the speaker (although often after the initial 10 s of the playback analyzed here). 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; see also Partan & Marler 1999). Second, given the short detection distances in which predators and snakes are typically detected (Janson 2007), 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.

While this study examined only situational variation in the production of different call types and rates of calling, acoustic variation within call types may also be associated with the context of production (e.g., Manser 2001; Range & Fischer 2004) and receivers may be able to cue in on these differences (e.g., Fischer 1998; 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 2001) as seen in Fig. 1. Variation in syllable number may be associated with particular threat types or the caller's risk-urgency (e.g., Templeton et al. 2005). Likewise, although quantitative data on call intensity is not available from this study, there was clearly variation in this regard for both hiccups and barks, and variation appeared to be related to risk-urgency (see also Marler et al. 1992; Seyfarth & Cheney 2003): I perceived barks given to flying raptors as generally higher amplitude than those given to perched raptors, and hiccups given to felids as generally higher amplitude than those given to snakes or in non-urgent contexts. Finally, different combinations of calls may be given in response to different types of threats (e.g., Arnold & Zuberbühler 2006; Schel et al. 2009; Ouattara et al. 2009b). While there was no obvious variation in the combination of, for example, hiccups and peeps to differentiate between detections of felids and snakes, further investigation may be warranted to determine if this is indeed possible.

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Table 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 horiz.	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. Vocal responses during experimental exposure to models of raptors, felids, and snakes at different levels of risk-urgency*

	perched raptors			flying raptors			felids			vipers		other snakes		total
call type	h	m	l	h	m	l	h	m	l	h	l	h	l	
barks only	▨	7	1	5						▨		▨		13
hiccups only	▨						3	15	1	▨	7	▨	6	32
peeps only	▨							5		▨	10	▨	3	18
hiccups plus peeps	▨						3	8		▨	5	▨	3	19

Shaded cells indicate that no detections of a particular threat type at that level of risk-urgency; blank cells indicate a zero value. h = high risk-urgency, m = medium risk-urgency, l = low risk-urgency. *Note that these values include multiple observations of some individuals.

Table 3. Anti-predator behaviors elicited by the alarm call playbacks*

					anti-aerial predator	generalized anti-predator					anti-terrestrial predator		
	# of PBs	no rxn	look up	run to cover	**≥1 AAP**	run horiz	appr spkr	scan	look spkr	**≥1 GAP**	run up	look down	**≥1 ATP**
Control	15	9	2	0	**2**	0	1	1	5	**6**	0	1	**1**
Bark	14	3	6	2	**8**	1	0	4	7	**11**	0	0	**0**
Hiccup	15	4	2	1	**3**	0	5	0	12	**12**	2	4	**5**

PBs = playbacks; no rxn = no reaction; AAP = anti-aerial predator specific behavior; appr spkr = approach playback speaker; look speaker = look towards playback speaker; GAP = general anti-predator behavior; ATP = anti-terrestrial predator specific behavior. * Note that the rows do not sum to 100% because some playbacks elicited more than one anti-predator behavior.

Figure 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 a different adult female while foraging. Additional descriptions and spectrograms of calls a, b, & d are provided in Di Bitetti (2001).

Figure 2. Call types given to: a) different threat types, and b) different levels of risk-urgency. Black bars = barks only, dark grey bars = hiccups only, light grey bars = both hiccups and peeps, white bars = peeps only.

Figure 3. The number of hiccups in the first 10 s of calling bouts given in response to stimuli representing the three levels of risk-urgency and in non-urgent contexts. Box plots show median (dark line), first and third quartiles (box), range (whiskers), extreme values (open circles), and outliers (asterisks). Note that calls given in non-urgent contexts were not included in the GLMM analysis.

Figure 1

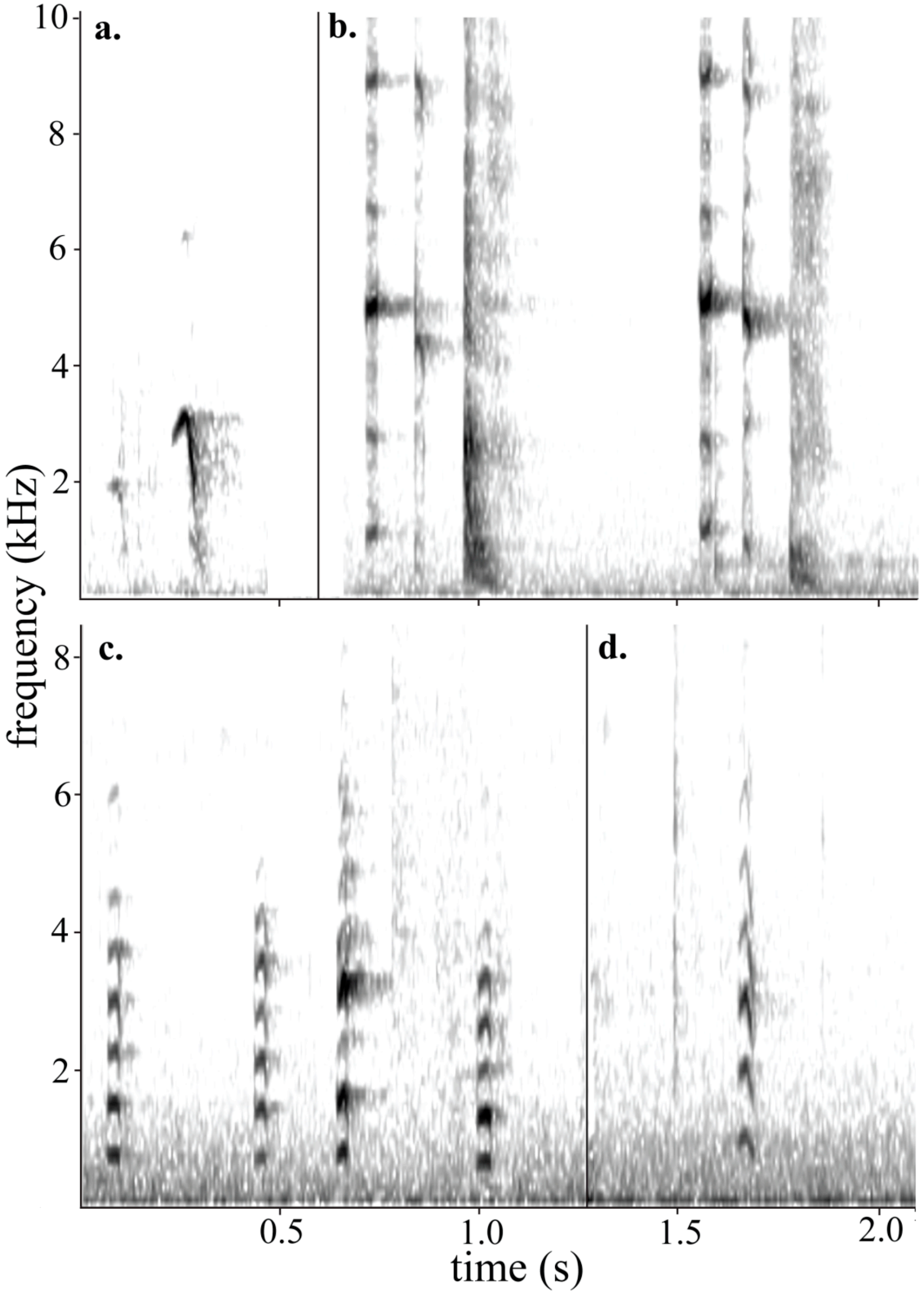


Figure 2

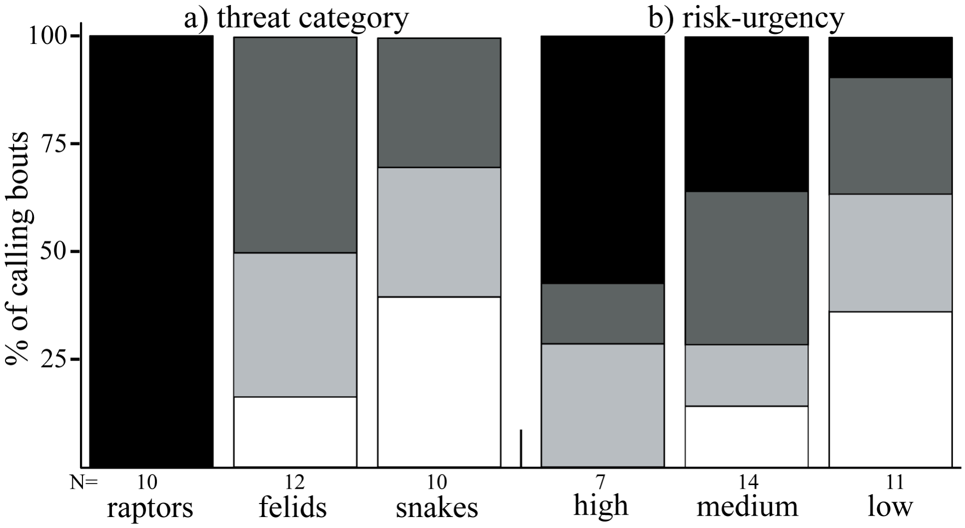
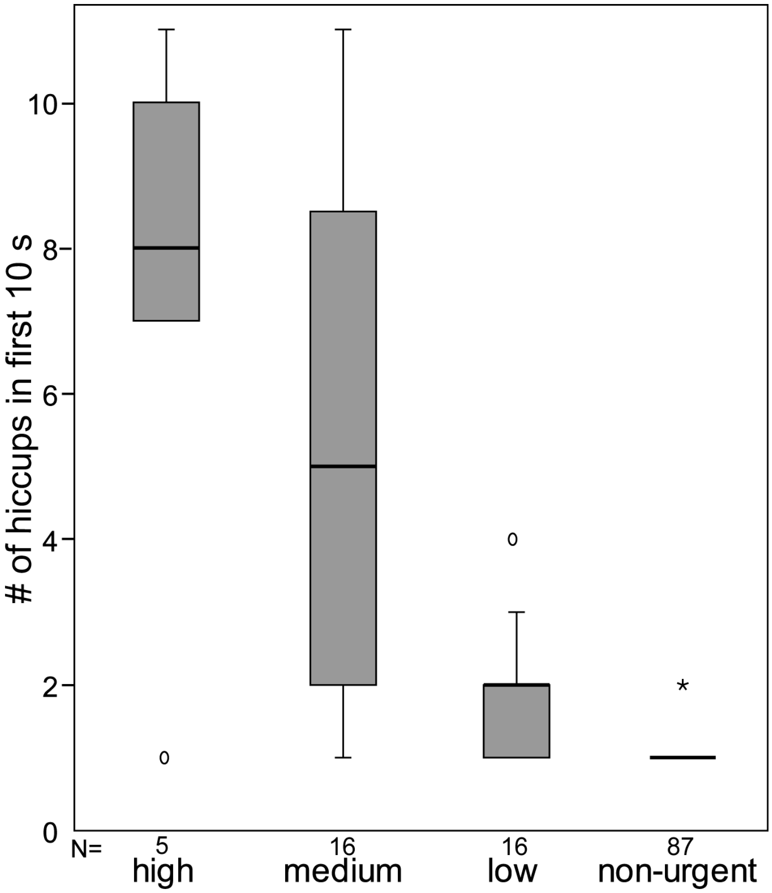

a) threat category
b) risk-urgency
% of calling bouts
100
75
50
25
N=
10
12
10
7
14
11
raptors
felids
snakes
high
medium
low

Figure 3


10
8
6
4
2
0
# of hiccups in first 10 s
N=
5
16
16
87
high
medium
low
non-urgent