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

3

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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 nigrinus*) 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.

47 **Introduction**

48

49 Many gregarious birds and mammals produce alarm calls upon encountering a predator. Such
50 calls typically function to alert conspecifics to the presence of danger and/or communicate to the
51 predator that it has been detected (Caro 2005). While some species have a generalized alarm call
52 system, producing similar calls in different threatening situations, other species demonstrate
53 “situationally variable” alarm calls (reviewed in Fichtel & Kappeler 2002; Caro 2005). In the
54 latter case, individuals may produce acoustically distinct call types, vary the number of calls
55 given, and/or vary the intensity of calls based on the context in which they are produced
56 (Blumstein 1999a). Such situationally variable calls can potentially evoke reactions in call
57 receivers that are appropriate for the context in which they were given (e.g., Seyfarth et al. 1980;
58 Blumstein 1999b). Among those species that produce situationally variable alarm calls, two
59 distinct types of call systems have been identified: those that vary based on the degree of urgency
60 posed by the threat (e.g., high versus low) and those that vary based on threat type (e.g.,
61 carnivore versus raptor; termed “functionally referential”: Macedonia & Evans 1993), although
62 systems that combine both simultaneously are possible (Marler et al. 1992; Manser 2001).

63 Urgency-based alarm call systems are exemplified by yellow-bellied marmots (*Marmota*
64 *flaviventris*), which vary their alarm calling based on a combination of the distance from the
65 caller to the predator and the type of predator encountered, but not based on predator type alone
66 (Blumstein & Armitage 1997). Such risk is also reflected in call perception; high-risk alarms
67 evoke high arousal responses (e.g., flee to burrow) in marmots more often than low-risk alarms,
68 although the different calls do not evoke distinct types of reactions (Blumstein & Armitage 1997;
69 see also Leavesley & Magrath 2005). While urgency-based alarm call systems have long been

70 recognized in the sciurid rodents (reviewed in Blumstein 2007), such alarm call systems have
71 more recently been reported in birds (e.g., Baker & Becker 2002; Leavesley & Magrath 2005;
72 Templeton et al. 2005), carnivores (Manser 2001; Furrer & Manser 2009), and some primates
73 (bonnet macaques: *Macaca radiata*; Coss et al. 2007). In addition, Fichtel & Kappeler (2002)
74 argued that the terrestrial predator-associated alarm calls of redfronted lemurs (*Eulemur fulvus*)
75 and Verreaux's sifakas (*Propithecus verreauxi*) may reflect the caller's perceived threat-urgency
76 because these calls were also given in non-predatory contexts characterized by high arousal.

77 Functionally referential alarm calls, in contrast to urgency-based calls, show both *context*
78 *specificity* of call production and *stimulus independence* (or *perception specificity*) in call
79 response (Marler et al. 1992; Macedonia & Evans 1993). Context specificity of production is
80 demonstrated if only a narrow range of stimuli elicit the calls; this range can be as specific as a
81 single species (e.g., leopard) or as general as group of species with common characteristics (e.g.,
82 any terrestrial predator; Blumstein 1999a). Stimulus independence of call reaction is shown if the
83 call alone elicits an appropriate reaction (i.e., even if supposed referent is absent)

84 The two criteria of functionally referential signals are illustrated by the now classic
85 studies of vervet monkeys (*Chlorocebus aethiops*) which indicated that not only do raptors,
86 carnivores, and constricting snakes each elicit an acoustically distinct call type (Struhsaker
87 1967), but also that playbacks of each call type alone are sufficient to evoke predator-specific
88 responses in receivers of the call (Seyfarth et al. 1980). While referential alarm calls are more
89 common in primates than other taxa (reviewed in Fichtel & Kappeler 2002; Caro 2005), there is
90 support for such alarm call systems in both suricates (*Suricata suricatta*), which simultaneously
91 vary aspects of the calls with risk-urgency (Manser 2001; Manser et al. 2001), and several avian
92 taxa (e.g., Seddon et al. 2002; Gill & Sealy 2004). Among primates, alarm calls that show both

93 context and perception specificity have been documented only in lemurs (e.g., Macedonia &
94 Evans 1993; Fichtel & Kappeler 2002) and Old World monkeys (e.g., Cheney & Seyfarth 1990;
95 Zuberbühler 2000), but not New World monkeys or apes.

96 Several additional studies of alarm calls in primates and rodents have tested only one of
97 the two criteria of functionally referential calling (see Blumstein 2007). Among primates, both
98 white-faced capuchins (*Cebus capucinus*) and white-handed gibbons (*Hylobates lar*) show some
99 degree of context specificity in alarm call production (Digweed et al. 2005; Fichtel et al. 2005;
100 Clarke et al. 2006; see also Crockford & Boesch 2003; Notman & Rendall 2005), but the
101 evidence of stimulus independent responses in these cases is limited because playback
102 experiments were not conducted. In another study of New World primates, alarm call playbacks
103 conducted with two sympatric species of tamarins indicated that *Saguinus mystax* responded to
104 each of the two call types commonly elicited by aerial and terrestrial stimuli respectively with
105 predator-specific reactions, while only aerial predator alarm calls elicited such responses in *S.*
106 *fuscicollis* (Kirchhof & Hammerschmidt 2006). However, data regarding the context of
107 production of the alarm calls were not given for either of these tamarin species and it is thus
108 unclear if their calls are indeed predator-specific. Examination of both call production and
109 perception is important because situational variation in call production does not necessarily lead
110 to distinct responses in call receivers (Blumstein 1995) and predator specific responses to alarms
111 can be elicited by calls that are not specific to predator encounters (e.g., Fichtel & Kappeler
112 2002).

113 This study experimentally tests whether variation in alarm call production and response
114 in a New World primate, the tufted capuchin monkey (*Cebus apella nigrurus*), indicates an
115 urgency-based and/or a functionally referential alarm call system in a species in which food-

116 associated call have been shown to be functionally referential (Di Bitetti 2003). To address
117 questions regarding alarm call production, the study subjects were observed in experimental
118 contexts in which they detected models of raptors, felids, and snakes at varying distances to
119 determine the call types and rates of calling elicited by these three stimulus types at difference
120 levels of risk-urgency. These experiments were complemented with observations in natural
121 contexts to determine if the call types produced in the experimental contexts are produced in any
122 additional contexts. To test whether responses to the calls are stimulus independent, playbacks of
123 the call types elicited by the predator models were conducted.

124

125 **Methods**

126

127 Study Site and Subjects

128 Data were collected from July - September 2004 and May 2005 - December 2006 in Iguazú
129 National Park, Argentina (25°40'S, 54°30'W; see Di Bitetti et al. 2000 for a detailed description
130 of the study site). Initial predator model experiments were conducted during the first period
131 while all experimental protocols and natural observations were implemented during the second
132 study period. Tufted capuchins are medium-sized (~ 3 kg), diurnal, and omnivorous primates that
133 typically live in groups of 7-30 individuals characterized by female philopatry and male dispersal
134 (Di Bitetti 2001). The population is highly arboreal with individuals spending the majority of
135 time at 3 to 10 m above the ground and less than 3% of daytime activity occurring terrestrially
136 (Wheeler unpublished data). Data were collected on three fully habituated multimale-
137 multifemale groups (“Macuco”: 23-28 individuals; “Gundolf”: 15 individuals; “Guenon”: 9
138 individuals). All individuals were easily recognizable based on physical characteristics and were

139 of known age and sex. While all protocols were conducted with all three study groups, most
140 experiments and observations were conducted with the Macuco group because this group
141 allowed for a greater number of individuals to be sampled.

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

148 Tufted capuchins produce at least three acoustically distinct call types in response to
149 predators and snakes (Fig. 1), each of which is easily distinguishable by ear in humans. Two of
150 these, the “bark” (Fig. 1a) and the “hiccup” (Fig. 1b), were described by Di Bitetti (2001) and
151 labeled the “aerial predator alarm call” (APAC) and the “ground predator alarm call” (GPAC)
152 respectively. *Ad libitum* observations by Di Bitetti (2001) indicated that APACs were elicited
153 exclusively by flying stimuli while GPACs were elicited by terrestrial stimuli including felids
154 and, possibly, venomous snakes as well as in response to conspecific aggression (Di Bitetti
155 2001). Di Bitetti (2001) also noted the use of “hiku” calls, which were not acoustically
156 distinguishable from GPACs, by animals foraging in suspensory positions. Because of the lack
157 of acoustic variation between the GPAC and the hiku, they are here considered a single call type
158 (i.e., the hiccup). In addition to these two alarm call types identified by Di Bitetti (2001), a third
159 call type, the “peep” (Fig. 1c), was identified during the course of the current study. While this
160 call sounds and appears (spectrographically) to be similar to the species’ contact note (CN; Fig.
161 1d), it is differentiated from the CN by the rapid repetition of calls over a period of a few seconds

162 to several minutes (as opposed to a single CN given on average every 20 s per individual; Di
163 Bitetti 2001). None of the three alarm call types were age or sex specific, being produced by all
164 age-sex classes with the exception of very young infants (Di Bitetti 2001, pers. obs.). Peeps and
165 hiccups were often given together as a single call series in response to potentially threatening
166 stimuli. For these reasons, a call was considered a peep rather than a contact note if an individual
167 produced four or more notes in a two second period, or if the call was given between two hiccups
168 separated by less than five seconds. Although no quantitative data are available on call
169 amplitude, both the bark and hiccup appear to vary considerably in call intensity, while peeps are
170 always relatively low-intensity calls.

171

172 Call production

173 To determine if alarm call production by tufted capuchins varies situationally, indicating either
174 an urgency-based or a functionally referential call system, the types of calls and the rates in
175 which they were given were noted during experimental predator encounters. During experiments,
176 study subjects were presented with models of perched or flying hawk eagles, ocelots, vipers, or
177 non-threatening snakes (see Fig. 1 in Wheeler 2008). During most experiments, audio recordings
178 were made and analyzed to determine the number of calls of each type that were given following
179 the detection (described in further detail below).

180 Models were placed 50-150 m in front of the group in the direction of movement.

181 Perched raptor models were hung from tree branches by a rope thrown over the branch (normally
182 at a height of 10 to 12 m, but on a few occasions lower if canopy height was especially low).

183 Experiments with flying eagle models were conducted at sites prepared beforehand; the model
184 glided down a fishing line tied between two tree trunks from a height of 10-15 m down to 1.5 m

185 as the group approached the site, but before any individuals detected the model. Ocelot models
186 were placed on the ground or in trees at a height of up to 5m while snake models were always
187 placed on the ground or fallen tree trunks. The placement of the models in terms of the
188 surrounding vegetation was varied in order to ensure that the distance in which they were
189 detected was varied. To avoid habituation, a particular model type (e.g., raptor, felid, snake) was
190 not used for one week following a detection, while a specific model was not used more than once
191 in any 15 day period. In total, 50 experiments were conducted with the ocelot models, 30 with
192 perched raptor models, 8 with flying raptor models, 47 with venomous snake models, and 28
193 with non-venomous snake models. Of these, 97 were conducted with the Macuco Group, 30 with
194 the Gundolf Group, and 36 with the Guenon Group

195 Data on vocal behavior during the experiments was collected using an all-occurrence
196 sampling method (Martin & Bateson 2007). Three observers (the author and two assistants)
197 standing within a 15 m radius of the model noted the identity of the first individual to vocalize
198 upon detecting a model, the type(s) of call given, as well as the caller's height and distance to the
199 model at the moment the vocalizations commenced. All age and sex classes were observed to
200 react vocally to all model types and, with the exception of infants, were included in the analyses.
201 A call was considered to be in response to the model if the caller was looking directly towards
202 the model or simultaneously employing an appropriate escape reaction. Only the first caller from
203 each experiment was included in the analysis, as subsequent detectors' perceived risk could be
204 affected by the behavior of previous detectors. The first caller's risk-urgency was classified as
205 high, medium, or low depending on the type of predator encountered and the distance to the
206 model. Predators which could likely successfully attack the caller from their current position
207 (i.e., low probability of escape for the caller) were considered a high urgency threat; these

208 included stationary predators at a distance of less than 5 m and flying stimuli at a distance of less
209 than 25 m. Encounters at greater distances were considered medium (stationary predators at 5 to
210 25 m; flying raptors at 25 to 100 m) or low urgency threats (stationary predators at more than 25
211 m; flying raptors at more than 100 m). Venomous snakes were always considered a low urgency
212 threat because these species seem to be extremely unlikely prey on capuchins (see above) and in
213 no case did a capuchin detect a venomous snake within a likely striking distance (i.e., less than 1
214 m). Vocalizations given during the predator model experiments were recorded onto a Sony MZ-
215 NH 900 Hi-MD MiniDisc recorder, or a Marantz PMD-660 digital audio recorder using either a
216 Sennheiser ME-67/K6 or MKH-60 directional microphone. In nearly all cases, vocalizing
217 animals were within 10 m of the microphone. Calls were recorded at a sampling rate of 44.1 kHz
218 with a 16 bit resolution and saved in an uncompressed digital format. Recordings were examined
219 to determine the number of each alarm type that was given in the 10 second period beginning
220 with the initiation of the first call. A 10 second period was chosen for two reasons. First, the
221 initial calls given should be the most likely to reflect the caller's perceived risk (see Blumstein &
222 Armitage 1997). Second, because alarm calling among tufted capuchins tends to attract
223 conspecific mobbers (Wheeler 2008) who often begin to call once they have detected the
224 predator model, calls given after this initial period could not always be easily assigned to a
225 particular individual. Only those call bouts that did not overlap with calls from other group
226 members and which were of sufficiently high quality (e.g., with low background noise) were
227 used to determine how many calls were given over the first 10 seconds. This, together with
228 equipment failure on seven occasions, led to a larger number of experimental observations of call
229 types given (N=82) than observations of call rate (N=58).

230 To determine if the call types produced in response to the predator models were given in
231 any additional (i.e., non-predatory) situations, two-minute continuous focal samples were
232 conducted in natural contexts. Focal samples were conducted on all adults and juveniles over two
233 years of age throughout the day, but no such data were collected in the two hours following
234 predator model or playback experiments. Focal animals were chosen opportunistically, although
235 an effort was made to choose individuals who were undersampled, and no individual was
236 sampled more than once in a one hour period. If a focal animal gave an alarm call, the number of
237 calls given and the eliciting stimulus were noted. Eliciting stimuli were divided into four main
238 categories: 1) actual/potential aerial threats, 2) actual/potential terrestrial threats, 3) any other
239 stimuli, and 4) unknown. Actual threats included predators and vipers. Potential threats included
240 alarm calls of conspecifics or heterospecific animals as well as stimuli which could be
241 reasonably misclassified as a predator or viper. Stimuli included in the latter category included
242 large, non-predatory birds in flight (including vultures and toucans), medium-sized to large
243 animals in the understory (including rodents and ungulates), and non-venomous snakes.
244 Misclassification of non-predators as potential threats is expected in a dense forest where callers
245 may not be able to see a stimulus well enough to correctly identify it (Evans 1997). Such stimuli
246 were classified as “other” (not potential predators) in cases where the focal animal had an
247 unobstructed view of the stimulus and the individual could reasonably be assumed to have
248 recognized it as a non-threatening stimulus. Non-predatory stressors, including conspecific
249 aggression, attacks by stinging insects, and “precarious positional behaviors”, were also assigned
250 to the “other” category. Precarious positional behaviors were those in which the individual could
251 reasonably be assumed to be at a relatively high risk of falling and included suspensory positions

252 and the use of unstable substrates (dead vegetation or highly flexible substrates less than 1 cm in
253 diameter).

254

255 Call response

256 To determine if alarm calls elicit predator-specific responses in call receivers, observations of
257 focal animals following the playback of conspecific alarm calls were made. Only alarm calls
258 produced in response to a known threat (i.e., the predator models or potential predators
259 encountered in natural contexts) were used as playbacks. Recordings of actual call sequences
260 given in response to threatening stimuli were used for playbacks. Because bouts of barks
261 normally included only a few calls (often only a single call) while hiccups were given repeatedly,
262 playbacks of these call types reflected this. Due to a lack of a sufficient number of high quality
263 recordings of sequences of peeps, I was unable to conduct enough playback experiments to test
264 for responses to this call type. In addition to playbacks of alarm calls, playbacks of 1) non-alarm
265 vocalizations of sympatric avian and mammalian taxa (to determine the effect of playing back
266 other familiar sounds through speakers) and 2) capuchin alarm calls played in reverse (since
267 these were acoustically similar to alarm calls) were conducted as control experiments. Playbacks
268 were conducted with a compact-disc player or an Apple iPod connected to a RadioShack (#277-
269 1008) or Saul Mineroff Electronics (SME-AFS) amplified speaker hidden in vegetation at a
270 height of 2 ± 0.5 m. Call intensity was adjusted to mimic that observed during the predator
271 model experiments (75-85 dB as measured by a RadioShack 33-2055 digital sound level meter
272 placed 1 meter from the speaker). Only a single playback was conducted per day and
273 experiments were conducted only in cases when no alarm calls had been heard for at least 15
274 minutes and when no stimuli which could be mistaken for predators were present (e.g., terrestrial

275 mammals or low-flying vultures). Each individual was tested only once for a given stimulus type
276 (bark, hiccup, and control). While not all individuals were tested for all three stimulus types,
277 each age-sex class was tested multiple times for each stimulus. While I initially intended to use a
278 unique call sequence for each playback, this was not possible due to a lack of recordings of
279 sufficiently high quality. Thus some call series were used for more than one playback experiment
280 (but not more than twice with a particular group), although these were spaced out by more than a
281 month in order to ensure that individuals did not habituate to a particular call. A total of eight
282 distinct bouts of barks, nine distinct bouts of hiccups, and ten different control recordings were
283 used in the playbacks.

284 For each playback experiment, a single adult or juvenile animal resting, grooming, or
285 foraging (with little or no directional movement) approximately 15 m from the playback speaker
286 was chosen as a focal animal; because focal animals often changed positions before the playback
287 started, its distance to the speaker varied at the moment of playback but in nearly all cases (39 of
288 44 playbacks) the focal was 10 to 20 m from the speaker. All age-sex classes received all
289 playback treatments and no one class was overrepresented in the dataset. Juveniles were
290 considered appropriate focal animals because their reactions did not differ from those of adults
291 (Wheeler 2009a). Focal individuals were videotaped with a Canon Elura 80 MiniDV camcorder
292 for at least 20 seconds prior to the initiation of the playback and for up to one minute following
293 the playback. However, because of the density of the forest and the fact that the playbacks often
294 elicited movement in the focal animals causing them to move out of view, only the first 10 s
295 following the initiation of the playback were analyzed; increasing the amount of time analyzed
296 following the playback greatly decreased the number of analyzable experiments. Following the
297 playback, notes were taken on the focal animal's height and distance to the speaker at the

298 initiation of the playback and its qualitative reaction to the playback. In addition, a map was
299 drawn indicating the position of the focal animal, the video camera, and the playback speaker.
300 Videos were analyzed to determine if focal animals performed any anti-aerial predator, anti-
301 terrestrial predator, or generalized anti-predator behaviors (see Table 1 for definitions).
302 Generalized anti-predator behaviors were those which would be appropriate responses to both
303 terrestrial and aerial predators and therefore cannot be considered to be “predator specific”.

304

305 Statistical analyses and data selection

306 To test the factors that affect call production in experimental contexts, a multinomial logistic
307 regression was used with call type of the first individual to call in an experiment as the
308 dependent variable and stimulus category (raptor, felid, or snake) and risk-urgency (high,
309 medium, or low) as the predictor variables. Although some individuals were observed to give the
310 first bout of calls in response to a model on more than one occasion, each individual was
311 included in the logistic regression only once in order to avoid pseudoreplication. In most cases
312 (27 of 32 individuals), the first observation of a particular individual was the one chosen to
313 include in the analysis. However, because choosing the first observation for all individuals led to
314 a relatively small sample size for detections of raptors and detections in high-urgency situations,
315 calling bouts in these two contexts were chosen over an individual’s first observed calling bout.
316 Context specificity of call production was determined by categorizing all alarm calls given by
317 focal animals in both natural contexts and during the predator model experiments and assigning
318 them to one of three contexts: actual/potential aerial threat, actual/potential terrestrial threat, or
319 other (defined above). To be conservative, calls produced in unknown contexts were classified as
320 “other”. Production of a call type was considered to be specific for a particular threat category if

321 a binomial test indicated that the number of calls given in that context did not differ significantly
322 from an expected value of 95%; this value was chosen because it requires that call production
323 approaches total specificity, but allows for some observer error in context classification. General
324 linear mixed models (GLMM) with stimulus type or risk-urgency as the independent variable,
325 call rate over the first 10 s as the independent variable, and caller identity as a random factor
326 were used test if call rate varies based on the context in which the calls are produced. Fisher's
327 exact tests were used to examine differences in the occurrence of anti-predator responses across
328 the playback types. The logistic regression and binomial tests were conducted with SPSS 15.0.
329 Fisher's exact tests were calculated using the VassarStats web utility ([http://faculty.vassar.edu/](http://faculty.vassar.edu/lowry/VassarStats.html)
330 [lowry/VassarStats.html](http://faculty.vassar.edu/lowry/VassarStats.html)). GLMMs were conducted with STATA 10.0.

331

332 **Results**

333

334 Call production

335 *Call types given in experimental contexts*

336 The types of calls given to raptor models were recorded on 13 occasions, to ocelot models on 35
337 occasions, and to snake models on 34 occasions (see Wheeler 2008 for discussion of detections
338 which did not result in a vocal response). When considering only one reaction per individual, the
339 call type or series produced in response to a model was better explained by stimulus category
340 (i.e., raptor, felid, or snake; multinomial logistic regression: $N=32$, $\chi^2=35.51$, $df=6$, $p<0.0001$)
341 than by risk-urgency (same logistic regression: $\chi^2=2.54$, $df=6$, $p=0.863$; Fig. 2). Focal animals
342 produced only barks, and never hiccups or peeps, in response to models of flying and perched
343 raptors (Fig. 2a). In contrast, focal animals produced hiccups, peeps, or a combination of the two

344 call types in response to both felid and snake models, but barks were never given in this context
345 (Fig. 2a). The urgency of the threat presented by the predator or snake model was less tightly
346 associated with the vocal responses; barks were given at all levels of risk (but only once in a low-
347 risk context), as were both hiccups and peeps, although peeps given in high risk situations were
348 always accompanied by hiccups (Fig. 2b).

349

350 *Context specificity of barks, hiccups, and peeps*

351 In addition to the alarms given in the experimental contexts, another 142 alarm calls were given
352 by focal animals in natural contexts. When these data are factored in, clear differences between
353 the three alarm calls types emerge in the degree to which production of the calls is context
354 specific. Seven barks were given by focal animals in natural contexts. Six of these were in
355 response to flying stimuli, only one of which was a small raptor that may have posed a threat to
356 infants (but not to the adult male who called), while the others fell into the category of potential
357 aerial threats (i.e., innocuous flying stimuli). The eliciting stimulus could not be determined in
358 the seventh case. When these calls are considered together with the calls given in the
359 experimental contexts, 19 of 20 observed barks (95%) were associated with an actual or potential
360 aerial threat, not significantly difference from the value expected for a context specific call
361 (binomial test: $p=0.736$).

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

367 were given in situations in which the caller was employing a precarious positional behavior and
368 could reasonably be assumed to be at risk of falling. A single bout (0.7%) was given by an
369 individual while receiving aggression from another groupmate. No eliciting stimulus could be
370 identified in the 31 cases (23.0%), but these were most often given when the group was foraging
371 close to the ground in dense bamboo forest where visibility was greatly limited. When the
372 contexts in which these calls were given are combined with those given during the predator
373 model experiments, only 58 of 193 hiccups (30.1%) were in response to actual or potential
374 terrestrial threats, significantly less than expected for a context specific call type (binomial test;
375 $p < 0.0001$).

376 Focal animals were never observed in natural contexts to produce a long call series
377 resembling the peeps that were given in response to the ocelot and snake models. However,
378 given the ubiquity of the acoustically similar contact call, the low intensity of the call, and the
379 inconspicuous behavior that normally accompanies the production of contact calls, it is possible
380 that short bouts were produced at a rate similar to that observed during short bouts of peeps, but
381 that this went unnoticed by the observer. If the lack of observations of calls similar to peeps
382 indeed reflects a lack of production of such call series (or if further analysis indicates that the
383 calls are acoustically distinct from contact calls), then it appears that peeps are indeed context
384 specific, with all 37 observed bouts occurring in the context of a terrestrial threat (Table 2): 16
385 bouts were given in response to felid models, while 15 were given to venomous snake models
386 and 6 to non-venomous snake models. These calls were most often given together with hiccups;
387 bouts of peeps alone (i.e., without hiccups in the first 10 s) were observed on 18 occasions (Table
388 2), five times in response to felid models, 10 to venomous snake models, and three to non-
389 venomous snakes. However, in nearly all of these cases (except four involving non-venomous

390 snakes and one with a viper) at least one hiccup was given within the first 30 s of the calling bout
391 (but not within the first 10 s as considered here).

392

393 *Call rate*

394 In addition to variation in the types of calls that were produced, there was also considerable
395 situational variation in the number of alarm calls produced by a caller in a single calling bout.
396 The number of barks produced by an individual in the first 10 s of a calling bout varied from 1 to
397 9. Fewer barks were on average given in high-urgency situations (mean \pm SE: 3.67 ± 1.3 calls;
398 $N=3$) than to medium or low-urgency aerial predators (5.17 ± 1.4 calls, $N=6$), but statistical
399 analyses were not performed due to the small sample size available. The number of hiccups an
400 individual gave in the first 10 s of a calling bout varied from 1 to 11. Significantly more hiccups
401 were given in response to felids (5.77 ± 0.8 calls; $N=22$) than to snakes (1.73 ± 0.2 calls; $N=15$)
402 (GLMM: $F_{1,15}=6.1$, $P=0.024$). Likewise, more hiccups were given in response to higher risk
403 relative to lower risk threats (high risk: 7.40 ± 1.7 calls, $N=5$; medium risk: 5.50 ± 0.9 calls,
404 $N=16$; low risk: 1.75 ± 0.2 calls, $N=16$) (GLMM: $F_{1,15}=9.18$, $P=0.008$). This trend is even more
405 pronounced when one considers that precarious positional behaviors (a non-urgent situation)
406 almost always elicit only a single hiccup (Fig. 3). The number of peeps an individual gave during
407 the first 10 s of a calling bout varied from one to 23, but did not vary significantly across the
408 situations examined. The number of peeps given in response to felids (6.80 ± 1.6 calls; $N=15$)
409 did not differ from that given to snakes (7.33 ± 1.6 calls; $N=15$) (GLMM: $F_{1,11}=0.08$, $P=0.786$),
410 and there was no variation in the number of peeps based on the caller's risk-urgency (high risk:
411 5.00 ± 3.5 calls, $N=3$; medium risk: 7.25 ± 1.8 calls, $N=12$; low risk: 7.33 ± 1.6 calls, $N=15$)
412 (GLMM: $F_{1,11}=0.14$, $P=0.714$). Finally, when considering an entire call series consisting of both

413 hiccups and peeps, felids elicited significantly more calls in the first 10 s (8.8 ± 0.9 calls; $N=26$)
414 than did snakes (5.9 ± 1.2 calls, $N=23$) (GLMM: $F_{1,22}=4.69$, $P=0.042$) and there was a tendency
415 for more calls to be given in higher risk than lower risk situations (high risk: 10.40 ± 1.2 calls,
416 $N=5$; medium risk: 8.75 ± 1.0 calls, $N=20$; low risk: 5.75 ± 1.1 calls, $N=24$) (GLMM: $F_{1,22}=3.33$,
417 $P=0.082$).

418

419 Call response

420 A total of 44 playbacks experiments were conducted including 15 controls, 14 barks, and 15
421 hiccups; reactions to these are summarized in Table 3. Anti-predator reactions were employed by
422 focal animals more often following playbacks of alarm calls (i.e., barks and hiccups; 26 of 29
423 experiments) than following control playbacks (7 of 15 experiments) (Fisher's exact test,
424 $p=0.003$), but there was no difference in this regard between the two alarm call types (barks: 13
425 of 14 playbacks; hiccups: 13 of 15 playbacks) (Fisher's exact test; $p=1.0$). Generalized anti-
426 predator reactions were the most common reaction to both alarm call types (barks: 11 of 14
427 playbacks; hiccups: 12 of 15 playbacks), and such reactions occurred significantly more often
428 following the alarms than the controls (6 of 15 playbacks) (2 x 3 Fisher's exact test: $p=0.04$).

429 There were differences between the alarm call types in the occurrence of predator-specific
430 reactions. Anti-aerial predator behaviors occurred more often following playbacks of barks (8 of
431 14 playbacks) than following playbacks of hiccups (3 of 15 playbacks) or controls (2 of 15
432 playbacks) (2 x 3 Fisher's exact test: $p=0.03$), while anti-terrestrial predator behaviors occurred
433 more often following playbacks of hiccups (5 of 15 playbacks) than following playbacks of barks
434 (0 of 15 playbacks) or controls (1 of 15 playbacks) (2 x 3 Fisher's exact test: $p=0.04$).

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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

459 research is needed to determine if variation within call types affects call the receiver's perception
460 of risk-urgency.

461 These findings match well with most previous studies of primates that indicate that
462 terrestrial and aerial predators respectively elicit distinct alarm call types (e.g., Seyfarth et al.
463 1980; Macedonia & Evans 1993; Zuberbühler 2000 2001; Fichtel & Kappeler 2002; Range &
464 Fischer 2004; Digweed et al. 2005; Ouattara et al. 2009a; Schel et al. 2009), in contrast to many
465 sciurid rodent and avian taxa (reviewed in Fichtel & Kappeler 2002; Caro 2005). Likewise, the
466 regular production of terrestrial predator-associated calls in the absence of predators appears to
467 be common, especially among non-catarrhine primates (Fichtel & Kappeler 2002; Digweed et al.
468 2005; Fichtel et al. 2005; Kirchhof & Hammerschmidt 2006; see also Ouattara et al. 2009a for
469 similar trends in a catarrhine primate). Finally, an increase in call rate with an increase in risk
470 facing the caller is consistent with several studies of avian and rodent taxa (Blumstein &
471 Armitage 1997; Blumstein 1999b; Warkentin et al. 2001; Baker & Becker 2002; Leavesley &
472 Magrath 2005) and a recent study of Old World monkeys (Ouattara et al. 2009b; see also Schel
473 et al. 2009).

474 The use of the same call for carnivores and snakes among arboreal (e.g., Fichtel &
475 Kappeler 2002; Digweed et al. 2005; Ouattara et al. 2009a; this study) but not terrestrial
476 (Seyfarth et al. 1980; Range & Fischer 2004) primates fits well with the prediction that the need
477 for distinct escape reactions for different threat types are the main driving force behind the
478 evolution of functionally referential alarm calls (Macedonia & Evans 1993). However, in the
479 current study apparent attempts to locate the predator were a far more common response to
480 playbacks than were escape reactions, indicating that the ability to quickly locate a predator may
481 also be important (Kirchhof & Hammerschmidt 2006; see also Ouattara et al. 2009c for

482 additional evidence that different predator types favor distinct non-escape reactions in forest
483 primates). The low rate of escape reactions in the current study may be explained by the
484 extremely short distances in which raptors, felids, and snakes are detected in the study population
485 (Janson 2007). When predators rely on ambush, average detection distances may be extremely
486 short, in which case the detector would likely be in far more danger than are other group
487 members. If this is the case, then an escape response by call receivers may not be the most
488 beneficial reaction, particularly if the caller is not in the receiver's immediate vicinity. In
489 addition, given that a large proportion of the alarms given in natural contexts were to innocuous
490 stimuli, call receivers may lower the costs associated with responding to such false alarms by
491 relying on additional cues before employing a time and energy consuming escape response (see
492 Beauchamp & Ruxton 2007).

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

504 Functional deception may also play a role in other primate taxa reported to use predator-
505 associated calls in the absence of predators (precarious positional behaviors: Ouattara et al.
506 2009a; conspecific aggression: Cheney & Seyfarth 1990; Fichtel & Kappeler 2002; Fichtel et al.
507 2005; Kirchhof & Hammerschmidt 2006; see also Digweed & Rendall 2009 for similar trends in
508 a sciurid rodent). Additional research should be conducted to determine if these calls are
509 functionally deceptive by examining if they cause anti-predator reactions that would be
510 beneficial to the caller (e.g., elicitation of vigilance in neighbors or distraction of conspecific
511 competitors). Potentially “deceptive” uses of calls should be explicitly considered when
512 examining context specificity of production, as a low degree of context specificity may be
513 favored when callers benefit by influencing receiver behavior in a similar way across a range of
514 contexts (see Rendall et al. 2009). Indeed, several studies have shown that predator-associated
515 calls that are also given in non-predatory contexts still regularly elicit predator-specific reactions
516 despite their low levels of context specificity (e.g., Fichtel & Kappeler 2002; Kirchhof &
517 Hammerschmidt 2006; current study). This should occur when such responses are on average
518 beneficial for recipients (see Wiley 1994). It is interesting that, among non-catarrhine primates, it
519 is consistently the terrestrial predator-associated call that shows a low degree of context
520 specificity, while primate aerial predator alarm calls tend to be highly specific in this regard.
521 Such trends may be related to a lack of ability to use aerial predator alarms “deceptively” (e.g., if
522 a greater ability to locate flying stimuli reduces reactions to false alarms) or to higher risk of
523 predation by aerial relative to terrestrial predators. The latter factor could favor a high degree of
524 context specificity if a decrease in call reliability reduces the benefits callers receive by giving
525 “honest” alarms (see Wheeler 2008). At this point, though, the benefit of evolving a functionally
526 referential call for aerial but not terrestrial predators is unclear, as are the selective pressures

527 which would favor the apparently higher degree of context specificity in the terrestrial predator-
528 associated calls of Old World monkeys relative to Neotropical and Malagasy primates.

529 Despite the observed differences in production specificity, both barks and hiccups elicited
530 predator-specific reactions, although both calls most often elicited generalized anti-predator
531 reactions. The single most common response to both alarm call types was to simply look towards
532 the speaker, and playbacks frequently resulted in individuals approaching the speaker (although
533 often after the initial 10 s of the playback analyzed here). Such reactions may be adaptive for two
534 distinct reasons. First, examining the behavior of the caller may provide the receiver with
535 additional clues as to what elicited the call (Fischer & Hammerschmidt 2001; see also Partan &
536 Marler 1999). Second, given the short detection distances in which predators and snakes are
537 typically detected (Janson 2007), a likely place to locate the threat will most often be near the
538 caller. Since a clear view of the caller would in most cases be impeded because of the typical
539 distance that separated the playback speaker from the focal animal, approaching the speaker may
540 often be necessary to either locate the predator or to obtain additional cues based on the caller's
541 behavior.

542 While this study examined only situational variation in the production of different call
543 types and rates of calling, acoustic variation within call types may also be associated with the
544 context of production (e.g., Manser 2001; Range & Fischer 2004) and receivers may be able to
545 cue in on these differences (e.g., Fischer 1998; Manser et al. 2001). For example, while hiccups
546 are most often a two-syllable call (*hic-cup*), they sometimes contain three syllables (*hic-hic-up*;
547 Di Bitetti 2001) as seen in Fig. 1. Variation in syllable number may be associated with particular
548 threat types or the caller's risk-urgency (e.g., Templeton et al. 2005). Likewise, although
549 quantitative data on call intensity is not available from this study, there was clearly variation in

550 this regard for both hiccups and barks, and variation appeared to be related to risk-urgency (see
551 also Marler et al. 1992; Seyfarth & Cheney 2003): I perceived barks given to flying raptors as
552 generally higher amplitude than those given to perched raptors, and hiccups given to felids as
553 generally higher amplitude than those given to snakes or in non-urgent contexts. Finally,
554 different combinations of calls may be given in response to different types of threats (e.g.,
555 Arnold & Zuberbühler 2006; Schel et al. 2009; Ouattara et al. 2009b). While there was no
556 obvious variation in the combination of, for example, hiccups and peeps to differentiate between
557 detections of felids and snakes, further investigation may be warranted to determine if this is
558 indeed possible.

559

560

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561

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695

696 **Table 1.** List of behaviors falling into the different anti-predator behavioral categories and their
 697 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
anti- terrestrial predator	look to speaker	looking beyond immediate substrate, and within 45° of a straight line between the focal animal and the speaker
	look down	looking beyond immediate substrate, with head at least 45° below the horizontal
	run up	quick vertical movement of at least two meters

698

699

700 **Table 2.** Vocal responses during experimental exposure to models of raptors, felids, and snakes
 701 at different levels of risk-urgency*

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

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

705

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

707

	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

708 PBs = playbacks; no rxn = no reaction; AAP = anti-aerial predator specific behavior; appr spkr =

709 approach playback speaker; look speaker = look towards playback speaker; GAP = general anti-

710 predator behavior; ATP = anti-terrestrial predator specific behavior. * Note that the rows do not

711 sum to 100% because some playbacks elicited more than one anti-predator behavior.

712

713 **Figure 1.** Spectrograms of characteristic alarm calls: a) one bark given by an adult male in
714 response to a flying eagle model, b) two hiccups given by a juvenile female in response to an
715 ocelot model, and c) four peeps given by an adult female in response to a venomous snake
716 model; d) a single contact note given by a different adult female while foraging. Additional
717 descriptions and spectrograms of calls a, b, & d are provided in Di Bitetti (2001).

718

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

722

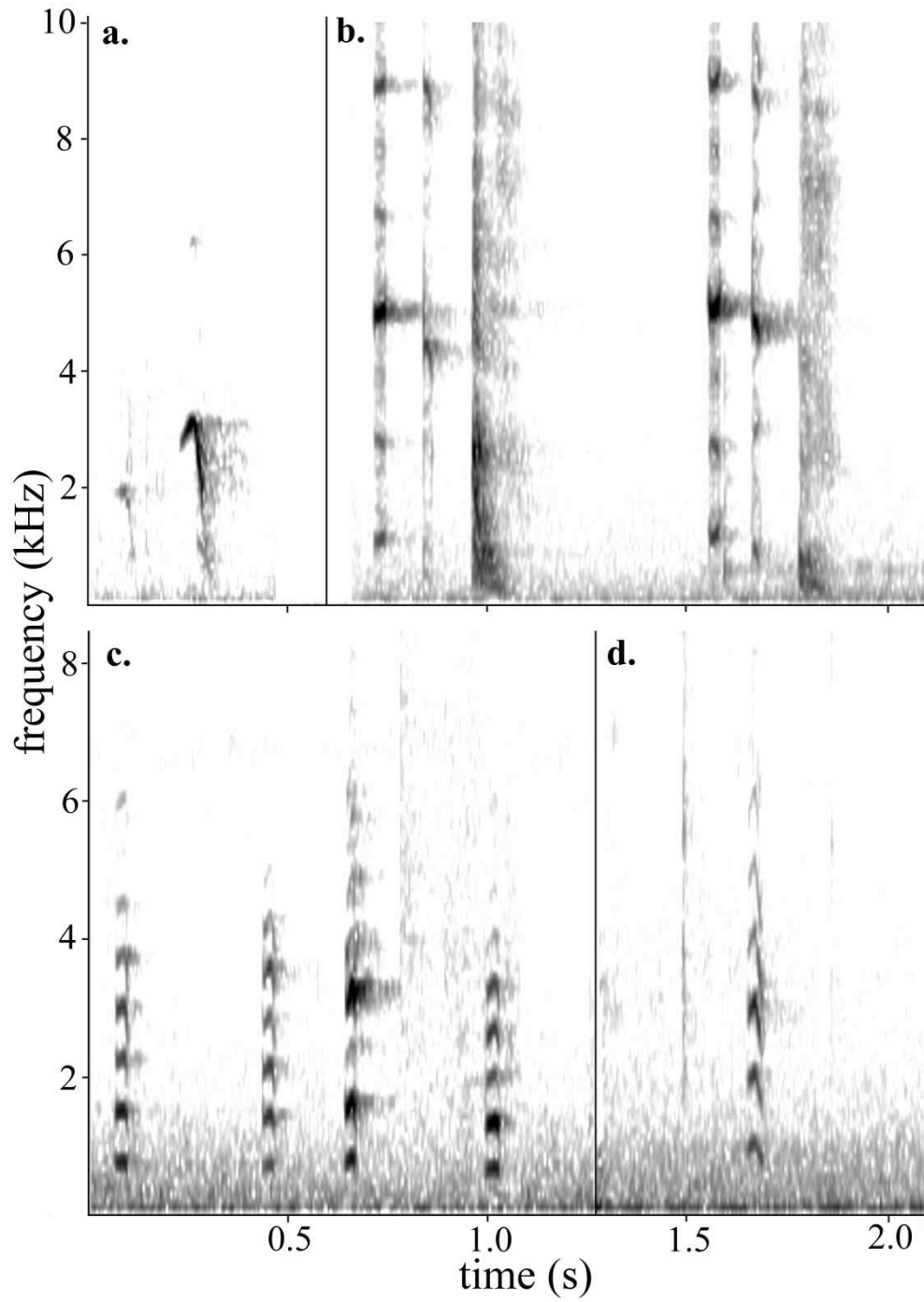
723 **Figure 3.** The number of hiccups in the first 10 s of calling bouts given in response to stimuli
724 representing the three levels of risk-urgency and in non-urgent contexts. Box plots show median
725 (dark line), first and third quartiles (box), range (whiskers), extreme values (open circles),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

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731 **Figure 1**

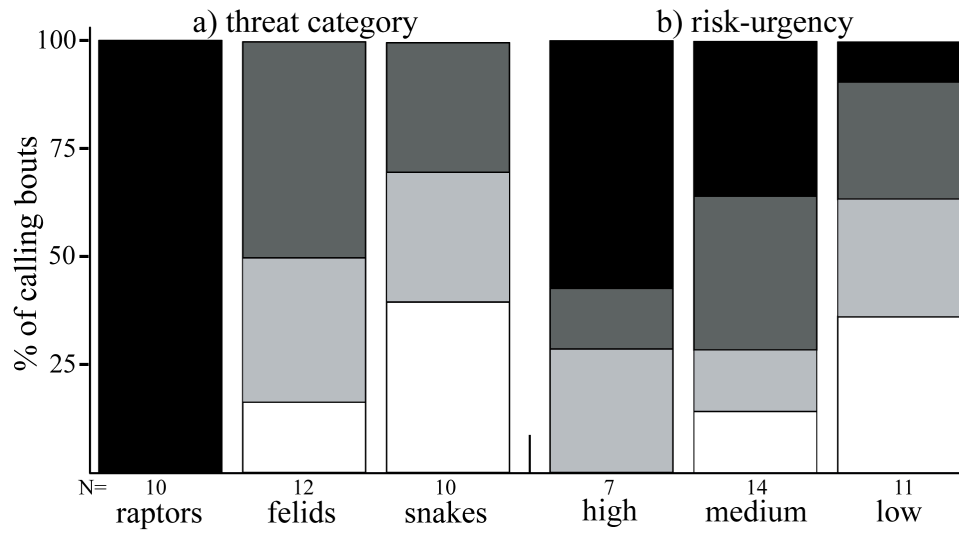


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735 **Figure 2**



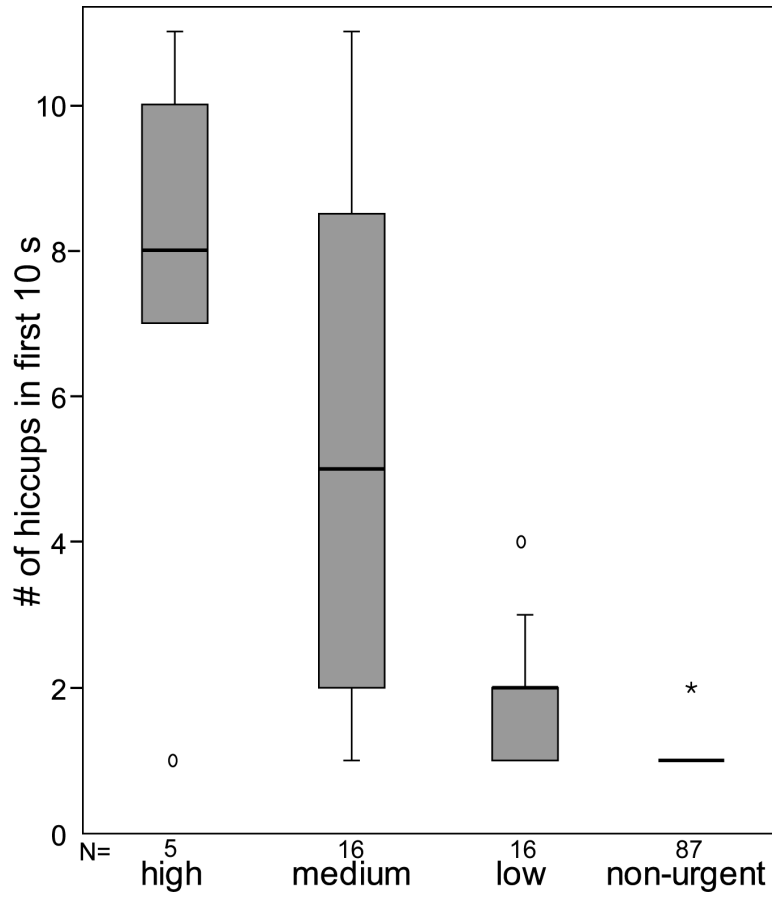
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740 **Figure 3**



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