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1 **Decrease in alarm call response among tufted capuchin monkeys in**  
2 **competitive feeding contexts: possible evidence for counterdeception**

3

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12

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15

16

17 **Abstract**

18 Animal signals function to elicit behaviors in receivers that ultimately benefit the signaler, while  
19 receivers should respond in a way that maximizes their own fitness. However, the best response  
20 may be difficult for receivers to determine when unreliable signaling is common. “Deceptive”  
21 alarm calling is common among tufted capuchin monkeys (*Cebus apella nigrinus*) in competitive  
22 feeding contexts, and responding to these calls is costly. Receivers should thus vary their  
23 responses based on whether a call is likely to be reliable. If capuchins are indeed able to assess  
24 reliability, I predicted that receivers will be less likely to respond to alarms that are given during  
25 competitive feeding contexts than in noncompetitive contexts, and, within feeding contexts, that  
26 individuals inside or adjacent to a food patch will be less likely to respond to alarms than those  
27 further from the resource. I tested these predictions in a group of wild capuchins by observing  
28 the reactions of focal animals to alarm calls in both noncompetitive contexts and experimental  
29 feeding contexts. Antipredator escape reactions, but not vigilance reactions, occurred  
30 significantly less often in competitive feeding contexts than in noncompetitive contexts and  
31 individuals adjacent to food patches were more likely to respond to alarm calls than were those  
32 inside or further from food patches. Although not all predictions were fully supported, the  
33 findings demonstrate that receivers vary their behavior in a way that minimizes the costs  
34 associated with “deceptive” alarms, but further research is needed to determine whether or not  
35 this can be attributed to counterdeception.

36

37 **Key words: communication; deception; skeptical responding; antipredator behaviors; New**

38 **World primates**

39

40 **Introduction**

41 Signaling systems are argued to often present a conflict between signal senders and receivers.  
42 Senders aim to benefit by influencing the behavior of receivers and receivers attempt to respond  
43 to signals in such a way that they benefit themselves (Krebs and Dawkins 1984; Rendall *et al.*  
44 2009). In order for a given signal to successfully influence receiver behavior to the benefit of the  
45 signaler, the reliability of the signal must surpass some certain threshold because habitually  
46 unreliable signals are likely to be ignored by receivers (Wiley 1994; Zahavi and Zahavi 1997). In  
47 cases in which reliability surpasses that threshold but is still variable, there should be selection  
48 for receivers to accurately assess reliability and be more likely to ignore those signals which are  
49 less likely to be reliable (Hauser 1996). Indeed, several studies have shown that receivers more  
50 often fail to respond to signals produced by individuals (or classes of individuals) that are less  
51 likely to be reliable (Cheney and Seyfarth 1988; Gouzoules *et al.* 1996; Ramakrishnan and Coss  
52 2000; Hanson and Coss 2001; Hare and Atkins 2001; but see Blumstein and Daniel 2004).

53         Recent work has shown that among tufted capuchin monkeys (*Cebus apella nigrinus*),  
54 signalers likely benefit both by alerting conspecifics to the presence of a predator through the  
55 production of terrestrial predator-associated calls (“hiccups”; see Methods) (Wheeler 2008), and  
56 by producing these same calls in the absence of predators but when the group is feeding on high-  
57 value resources (Wheeler 2009a). These latter calls are functionally deceptive because they often  
58 elicit antipredator escape reactions in neighboring individuals, thereby allowing the caller to gain  
59 access to the contested resource (Wheeler 2009a). Further, these false alarms are given by  
60 individuals who are the least likely to win contests over resources (i.e., subordinate individuals;  
61 see Janson 1985), most often when those individuals are in a spatial position in which they could

62 potentially take advantage of any conspecific reactions (i.e., immediately adjacent to a food  
63 patch occupied by others).

64         When deceptive signaling is common, there should be selection for individuals to  
65 anticipate such behaviors and employ counterstrategies to reduce the likelihood of being  
66 deceived (see Krebs and Dawkins 1984). Behaviors that are not necessarily deceptive themselves  
67 but which function to reduce the success of another's attempted deception have been termed  
68 "counterdeceptive", although evidence that primates employ such behaviors is largely anecdotal  
69 (Byrne and Whiten 1990; but see Gouzoules *et al.* 1996). In the case of tufted capuchin alarm  
70 calls, antipredator reactions are beneficial for receivers when the calls reliably indicate the  
71 presence of a predator but are costly when the calls are "deceptive". The ability to determine  
72 when such behaviors should be employed upon hearing an alarm call should therefore be  
73 favored. Since the potential for individuals to benefit by providing unreliable predator-associated  
74 signals is high in competitive feeding situations but relatively low in noncompetitive contexts,  
75 one would expect calls produced in the former context to be ignored more often than those  
76 produced in the latter context. Further, within the feeding contexts, individuals within or adjacent  
77 to food patches should be more likely to ignore alarm calls than those further from the food  
78 because antipredator reactions would be more costly for the former than the latter in terms of lost  
79 access to resources. Here I test these predictions by comparing the responses (or lack thereof) of  
80 tufted capuchins to terrestrial predator-associated alarm calls produced in an experimental  
81 feeding context with such responses in natural, noncompetitive situations. Support for this  
82 prediction would provide initial (but not necessarily conclusive) evidence that capuchins employ  
83 counterdeception to reduce the costs associated with deceptive alarm calls.

84

## 85 **Methods**

### 86 Study site and subjects

87 I conducted the study from May, 2005 to December, 2006 in Iguazú National Park, northeastern  
88 Argentina (25°40'S, 54 ° 30'W). The site sits at the southwestern edge of the South American  
89 Atlantic Forest and is characterized by humid, semi-deciduous, subtropical forest. A more  
90 detailed description of the study site can be found in Di Bitetti *et al.* (2000).

91 Tufted capuchin monkeys are medium-sized (~3 kg), arboreal primates that are primarily  
92 frugivorous but who spend a large proportion of their active time searching for dispersed insect  
93 prey (Fragaszy et al. 2004). All data from the current study are based on a single group, the  
94 Macuco Group, which ranged in size from 23 to 28 individuals during the study period. This  
95 group has been under almost continuous observation since 1991 and is well habituated to both  
96 human observers and the experimental conditions utilized in this study (see Janson 1996, 2007a).  
97 All individuals were readily recognizable based on facial characteristics and fur patterns.

98 Tufted capuchins in Iguazú face threats from hawk-eagles (*Spizaetus* spp.), carnivores  
99 (including tayras: *Eira barbara*; ocelots: *Leopardus pardalis*; pumas: *Puma concolor*; and  
100 jaguars: *Panthera onca*), and vipers (*Crotalus durissus*, *Bothrops* spp.). In response to these  
101 threats, the monkeys regularly produce one or more of three discrete alarm call types: “barks” are  
102 given in response to aerial threats, while “hiccups” and/or “peeps” are given in response to  
103 carnivores and snakes (Wheeler in press). The alarm hiccup is not specific to predator  
104 encounters; the call is also frequently given in other contexts in which the caller would  
105 likely benefit by eliciting antipredator reactions in receivers (Wheeler in press). However,  
106 callers tend to produce two or more intense hiccups in quick succession in high-risk  
107 situations such as encounters with felids, and playbacks of such call bouts (hereafter ‘high-

108 urgency hiccups') regularly elicit reactions in listeners that would allow them to escape  
109 from or locate a terrestrial predator (Wheeler in press). In contrast, hiccups given in  
110 nonpredatory contexts tend to consist of only a single, low intensity call (Wheeler in press), and  
111 such call bouts rarely elicit vigilance (but never escape) reactions in natural contexts (Wheeler,  
112 *unpub. data*); I thus did not consider hiccup bouts consisting of only a single call (in either  
113 experimental or natural contexts) for the current analysis. I also did not examine responses to  
114 barks or peeps because there is no evidence that these call types are produced in nonpredatory  
115 contexts (Wheeler in press).

#### 116 Observational and experimental protocols

117 I collected data on responses to bouts of high-urgency hiccups on all adult and juvenile  
118 individuals over one year of age using a continuous focal sampling protocol (Martin and Bateson  
119 2007) in natural and experimental feeding contexts. Juveniles were included in the analysis  
120 because previous work has shown that reactions of individuals in this age class do not differ from  
121 those of adults (Wheeler 2009b). In both contexts, I examined responses only for those bouts in  
122 which: 1) two or more hiccups were given in quick succession (i.e., high-urgency bouts) and 2)  
123 there was no identified eliciting stimulus. The second condition reduces the possibility that focal  
124 animals' reactions (or lack thereof) were a response to this stimulus rather than to the alarm call.  
125 Eliciting stimuli potentially included any real threat (such as a felid) or any other stimulus which  
126 could reasonably be misconstrued by the monkeys to be a real threat (such as a medium to large-  
127 sized mammal moving through the understory or the observer stepping on and cracking a small  
128 branch). In addition, because aggressive interactions frequently elicit bouts of hiccups (Di Bitetti  
129 2001; Wheeler 2009a), I did not include responses to hiccups that were produced following an  
130 aggressive interaction (normally assessed through the production of additional vocalizations

131 associated with aggressive interactions; see Di Bitetti 2001) in the analysis. Bouts in which there  
132 was no identifiable eliciting stimulus are hereafter referred to as “spontaneous” hiccups.

133 In natural contexts, focal samples were two minutes in length and were conducted from  
134 6:00 to 19:30, but I eliminated data collected in the two hours following encounters with actual  
135 or decoy predators (see Wheeler 2008, in press) as well as data collected while the group was  
136 feeding on high quality, contestable resources (i.e., foods occurring in discrete patches smaller  
137 than group spread; see Koenig and Borries 2006). I chose focal animals opportunistically,  
138 although an effort was made to choose individuals who were undersampled. No individual was  
139 sampled more than once in a one hour period, and usually not more than once in a day (mean  
140 number of samples per individual per day: 0.6; range: 0-4). If a bout of spontaneous high-  
141 urgency alarm call “hiccups” was produced at any point during the focal sample by any group  
142 member other than the focal animal, I noted whether or not the focal animal reacted with an  
143 antipredator behavior appropriate for a terrestrial predator at any point from the initiation of the  
144 call bout to two seconds after the bout ended. Behaviors considered included both escape (run at  
145 least 1 meter either up or horizontally) and vigilance (look to the caller, look toward the ground,  
146 and/or scan surroundings) responses. It should be noted that escape responses were always  
147 accompanied by vigilance responses, and so reactions scored as “vigilance” imply that this was  
148 the only reaction (i.e., there was no escape response).

149 To record data on alarm call response during competitive feeding situations, I conducted  
150 experiments in which the group was provided with bananas cut into 2.5 cm pieces and placed in  
151 wooden platforms suspended from tree branches at a height of 3 to 10 m above the ground  
152 (additional details of the feeding experiments can be found in Janson 1996, 2007a; Wheeler  
153 2009a). Each experimental site consisted of one to six individual platforms that were placed with



154 at least 15 m separating each platform from all others. At least two sites were set up within the  
155 study group's home range each month, and I provided bananas at each site for at least 13  
156 consecutive days each month. During most months, up to two experiments were conducted per  
157 day (one at each site); during the austral winter (June-August), eight sites were set up within the  
158 group's homerange simultaneously, resulting in as many as eight experiments per day for the  
159 current analysis. Banana pieces were placed in the platforms as the group approached the site but  
160 before the first individuals arrived. I chose a focal animal opportunistically as the group arrived  
161 at the site and followed that individual until all banana pieces had been eaten (usually within 10  
162 minutes of arriving at the site) or the individual was lost. I noted the occurrence of all high-  
163 urgency alarm hiccups produced by group members other than the focal individual as well as the  
164 focal individual's reaction (or lack thereof) using the same methods and definitions described  
165 above for spontaneous high-urgency alarm hiccups produced in natural contexts. In addition, the  
166 focal animal's spatial position relative to the feeding platforms was also noted; I scored spatial  
167 position as on a feeding platform with food, adjacent to (within 2 m of) a platform with food, or  
168 more than 2 m from a platform with food. Because alarm calling was relatively common during  
169 the feeding experiments, with multiple alarm calls bouts often being produced during a single  
170 experiment, only the first bout of hiccups given during a particular experiment was considered;  
171 this reduces the likelihood that focal animals ignored a particular alarm call simply because it  
172 was immediately preceded by a similar acoustic stimulus (Zuberbühler *et al.* 1999).

### 173 Statistical methods

174 I tested the effect of context (i.e., natural or experimental) on alarm call response using a within  
175 subject logistic regression with the software Stata 10.0. Context was entered as the independent  
176 variable, antipredator response (yes or no) as the dependent variable, and individual identity as a

177 fixed-effect. This method was chosen because it takes into account the fact individuals contribute  
178 more than one data point and allows for unbalanced data sets (van de Pol and Wright 2009). I ran  
179 two separate regressions, one with escape reaction (yes or no) as the dependent variable, and the  
180 second with vigilance reaction (yes or no) as the dependent variable. Stata automatically dropped  
181 those individuals from the analysis that were not focal animals when alarm calls were given in  
182 both of the two contexts or if the individual always employed the same response regardless of the  
183 context in which the call was given.

184         To test for differences in alarm call response within the feeding contexts based on the  
185 focal animal's spatial position relative to the feeding platforms, I conducted Fisher's exact tests  
186 based on 2 x 3 tables using the VassarStats web utility  
187 (<http://faculty.vassar.edu/lowry/VassarStats.html>). Two separate tests were run; the first tested  
188 for differences in the likelihood of escape reactions between the three spatial categories while the  
189 second tested for differences in the likelihood of vigilance reactions between these categories.  
190 While I initially intended to analyze these data based on how each individual responds in each of  
191 the spatial contexts (i.e., using the same type of regression analysis as described above), very  
192 few individuals (N=6) were observed in each of the spatial categories when an alarm call was  
193 given. The use of the Fisher's exact test allows all observations to be included in the analysis but  
194 introduces some pseudoreplication (with individuals contributing more than one data point) and  
195 the results should therefore be interpreted with some caution.

196

## 197 **Results**

198 I conducted over 134 hours of focal sampling in natural contexts, during which individuals other  
199 than the focal animal initiated a total of 44 bouts of spontaneous high-urgency hiccups. Of these

200 44 call bouts, 12 (27.3%) elicited escape reactions, 11 (25.0%) elicited vigilance reactions, and  
201 21 (47.7%) elicited no antipredator reaction in the focal animal (Fig. 1). I also conducted 321  
202 individual feeding platform experiments resulting in 31 hours of data on focal individuals.  
203 During these experiments, 105 bouts of alarm calls met the criteria to be included in the present  
204 analysis. Of these, 8 (7.6%) elicited escape reactions, 23 (21.9%) elicited vigilance reactions, and  
205 74 (70.5%) elicited no antipredator reaction in the focal animal (Fig. 1). The context in which the  
206 alarm call was given significantly predicted whether or not focal animals employed an escape  
207 response (within subject logistic regression: N=14 individuals,  $\chi^2=10.13$ , df=1, p=0.002) but did  
208 not significantly predict if a vigilance-only response followed the call (N=19 individuals,  
209  $\chi^2=0.02$ , df=1, p=0.887).

210         When considering only those calls given in the experimental feeding context, the  
211 responses of focal animals varied significantly based on their spatial position relative to the food.  
212 Focal animals responded with escape reactions significantly more often when they were adjacent  
213 to a platform (4 of 17 observations; 23.5%) than when on a platform (2 of 30 observations;  
214 6.7%) or more than 2 m from a platform (2 of 54 observations; 3.7%) (2 x 3 Fisher's exact test:  
215 N=101 calls; p=0.041; Fig. 2). However, the propensity to employ a vigilance-only reaction did  
216 not vary with location (2 x 3 Fisher's exact test: N=101 calls; p=0.360); individuals on platforms  
217 employed such reactions during 5 of 30 observations (16.7%), individuals adjacent to platforms  
218 did so during 6 of 17 observations (35.3%), and individuals more than 2 m from a platform did  
219 so during 12 of 54 observations (22.2 %) (Fig. 2).

220

221 **Discussion**

222 Tufted capuchin monkeys in this study responded significantly less often to conspecific  
223 terrestrial predator alarm calls with antipredator escape reactions in experimental feeding  
224 contexts than in natural contexts, but the rate in which vigilance reactions were employed  
225 differed little between the two contexts. Given that functionally deceptive alarm calls are  
226 frequently produced during these competitive feeding contexts (Wheeler 2009a), such a decrease  
227 in the rate of escape reactions may be due to the frequent production of unreliable (“deceptive”)  
228 alarm calls in competitive feeding contexts (Wheeler 2009a). Escape reactions in response to  
229 deceptive alarm calls can be costly because, in addition to the expenditure of time and energy  
230 associated with the response, they potentially result in decreased food consumption. In contrast,  
231 vigilance reactions are less costly since they are not as energetically costly and do not leave the  
232 food patch unoccupied. By varying their rate of escape responses to alarm calls, tufted capuchins  
233 are able to alleviate some of the costs associated with deceptive alarm calling. While these  
234 findings support the hypothesis that capuchins employ counterdeception (sensu Byrne and  
235 Whiten 1990) in response to frequent use of functionally deceptive alarm calls, further research  
236 is needed to determine if this is indeed the best interpretation of the observed trends.

237 Although the observed differences between contexts support the counterdeception  
238 hypothesis, the responses within the competitive feeding contexts did not vary as I predicted in  
239 terms of the spatial position of the signal receiver. Specifically, there was little difference  
240 between individuals on platforms and those further than 2 m from a platform in the likelihood of  
241 a response, while those adjacent to the platforms were the most likely to respond (reacting even  
242 more frequently than did individuals in natural contexts). Still, while the observed trend seems to  
243 somewhat weaken support for the idea that the capuchins employ counterdeception, it is possible  
244 that the methods employed in this study did not take into account a parameter that is likely quite

245 important for receivers in determining how to respond to an alarm call: the distance from the  
246 caller to the receiver. Because capuchins in Iguazú tend to detect terrestrial predators from  
247 extremely short distances (Janson 2007b), individuals in proximity to the alarm caller are also  
248 likely close to the predator (if one is actually present), while individuals at a greater distance  
249 from the caller are unlikely to be in immediate proximity to the predator and can therefore afford  
250 to ignore alarm calls without putting themselves in immediate danger. Thus which type of  
251 response (escape, vigilance, or ignore) is, on average, most beneficial should vary based on the  
252 distance to the caller. Because deceptive alarm calls tend to be given by individuals adjacent to  
253 the feeding platforms (Wheeler 2009a), individuals on or near the platforms would be more  
254 likely than those further from the platforms to be near the caller; this may explain why those  
255 adjacent to platforms reacted more often than did those more than 2 m from the platforms. While  
256 those individuals on the platforms were probably as likely to be near the caller as those adjacent  
257 to the platforms (and thus as likely to be at high risk), the costs of responding to false alarms are  
258 higher for those on the platforms since an escape reaction is more likely to result in the loss of  
259 resources for individuals within a food patch than for those adjacent to a food patch. The idea  
260 that distance to the caller is important is supported by the fact that, from the caller's perspective,  
261 40.0% of deceptive alarm calls caused an escape reaction in at least one neighboring conspecific  
262 (Wheeler 2009a), much higher than the 7.6% of focal animals who responded to spontaneous  
263 alarm calls in the current study.

264         The proximate mechanisms underlying the decreased response rate of terrestrial predator-  
265 associated alarm calls in the experimental feeding contexts remain unclear and may be explained  
266 by at least one of several factors, not all of which fully support the hypothesis that the observed  
267 trends are due to counterdeception. First, the calls given in the experimental feeding contexts,

268 despite an overall acoustic similarity, may differ slightly in acoustic structure from the calls  
269 given in response to actual predatory threats. The capuchins may be able to (sometimes) cue in  
270 on these differences and respond appropriately (Fischer 1998). Acoustic analysis of “honest” and  
271 “deceptive” alarms and playbacks of “deceptive” alarms in non-competitive contexts are needed  
272 to determine if this is the case. Second, whether or not acoustic variation exists, calls given in the  
273 experimental feeding contexts may be less likely to elicit reactions than those given in nonfeeding  
274 contexts because receivers are more “skeptical” of the former (Smith 1986; Gouzoules and  
275 Gouzoules 2002). Such skepticism could be due to the perceived unreliability of the calling  
276 individual (Cheney and Seyfarth 1988; Hare and Atkins 2001), but because the identity of callers  
277 was unknown in most cases, this cannot yet be tested. However, because subordinate individuals  
278 are far more likely to produce false alarm calls during these experiments than are dominants  
279 (Wheeler 2009a), and greater skepticism of alarm calls given by subordinate individuals relative  
280 to dominants has been previously demonstrated in captive rhesus macaques (*Macaca mulatta*)  
281 (Gouzoules *et al.* 1996), it is possible that the observed trends in the current study are due to  
282 skepticism of antipredator signals given by subordinates. A second possible factor which could  
283 drive skeptical responding is the behavioral context in which the call is produced. Several studies  
284 have demonstrated that the context in which a particular signal is produced can affect receiver  
285 responses (Rendall *et al.* 1999; Fischer and Hammerschmidt 2001; Tibbetts 2008). In the current  
286 case, receivers may be skeptical of alarm calls produced during competitive feeding situations,  
287 with or without taking caller identity or acoustic characteristics of the call into account, since  
288 false alarms are more likely to be given in this context than in noncompetitive situations. Finally,  
289 receivers may be less likely to respond to signals in general, not just terrestrial predator-  
290 associated alarm calls specifically, in competitive contexts due to greater attention being given to

291 competitive task (see also Randler 2005). If this does indeed explain the observed trends, then  
292 the decrease in alarm call response would arguably not be counterdeceptive, but perhaps part of a  
293 broader adaptive strategy to reduce the likelihood of being distracted (even by reliable signals)  
294 while engaged in a competitive situation. The fact that individuals on platforms reacted less often  
295 to alarm calls than did those immediately outside the platforms lends some support to this idea,  
296 but it is less supported by the fact that even those individuals not in the immediate vicinity of a  
297 platform rarely responded to alarm calls given during the feeding experiments. Playback  
298 experiments of alarm barks, which more reliably indicate the presence of an aerial predator than  
299 hiccups do a terrestrial predator (Wheeler in press), during the feeding experiments may give an  
300 indication of whether or not even typically reliable signals are also more likely to be ignored in  
301 this context. Whatever proximate mechanism underlies the observed trend, a decreased response  
302 rate to alarm signals in competitive contexts seems likely to ultimately function to reduce the  
303 costs of being distracted in competitive contexts, but determining whether or not the behavior is  
304 truly counterdeceptive (i.e., a direct result of the “deceptive” uses of the hiccups) requires  
305 additional research.

306

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325

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411 **Figure caption**

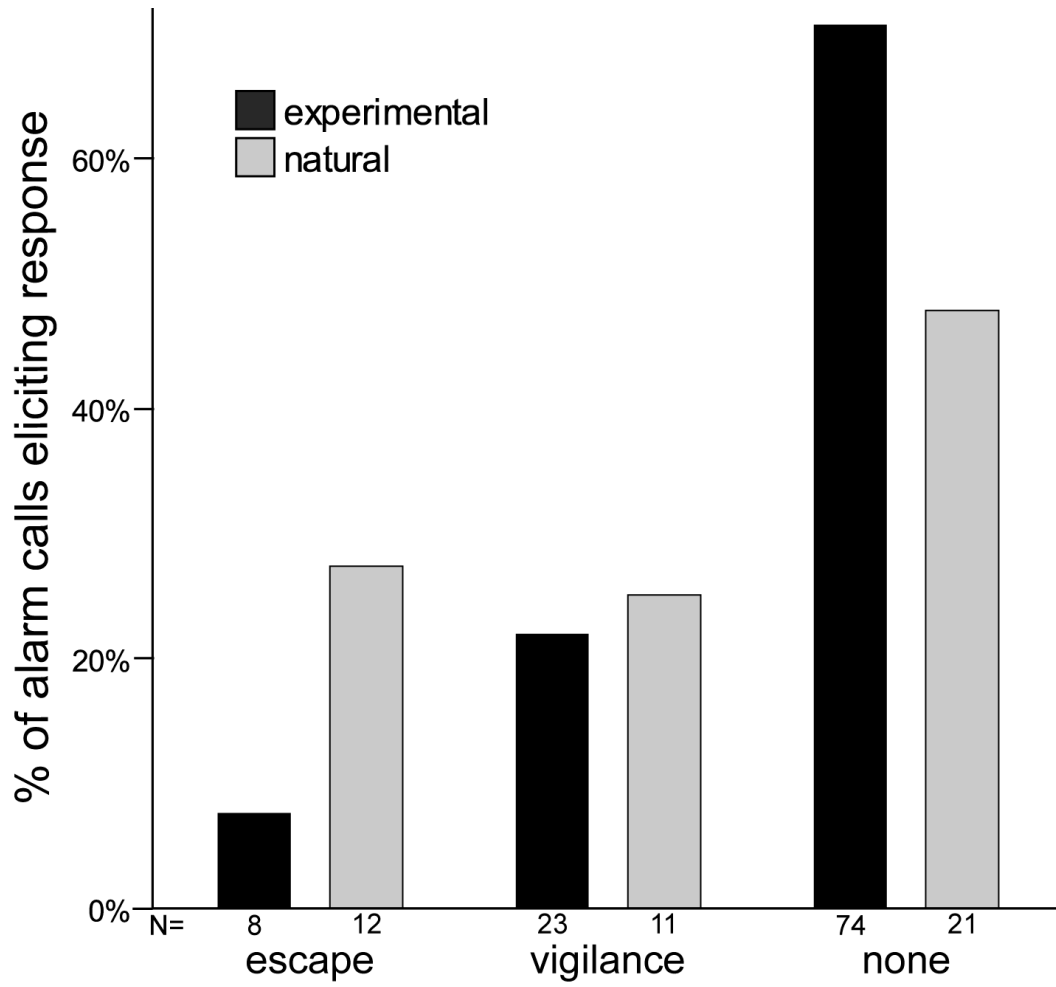
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413 **Fig. 1.** The percent of alarm calls that elicited terrestrial predator-associated escape reactions,  
414 vigilance reactions, or no reaction in focal animals in each of experimental feeding contexts and  
415 natural contexts.

416

417 **Fig. 2.** The percent of alarm calls that elicited terrestrial predator-associated escape reactions,  
418 vigilance reactions, or no reaction in focal animals for each of the three spatial positions  
419 considered during the experimental feeding contexts.

420 **Figure 1**

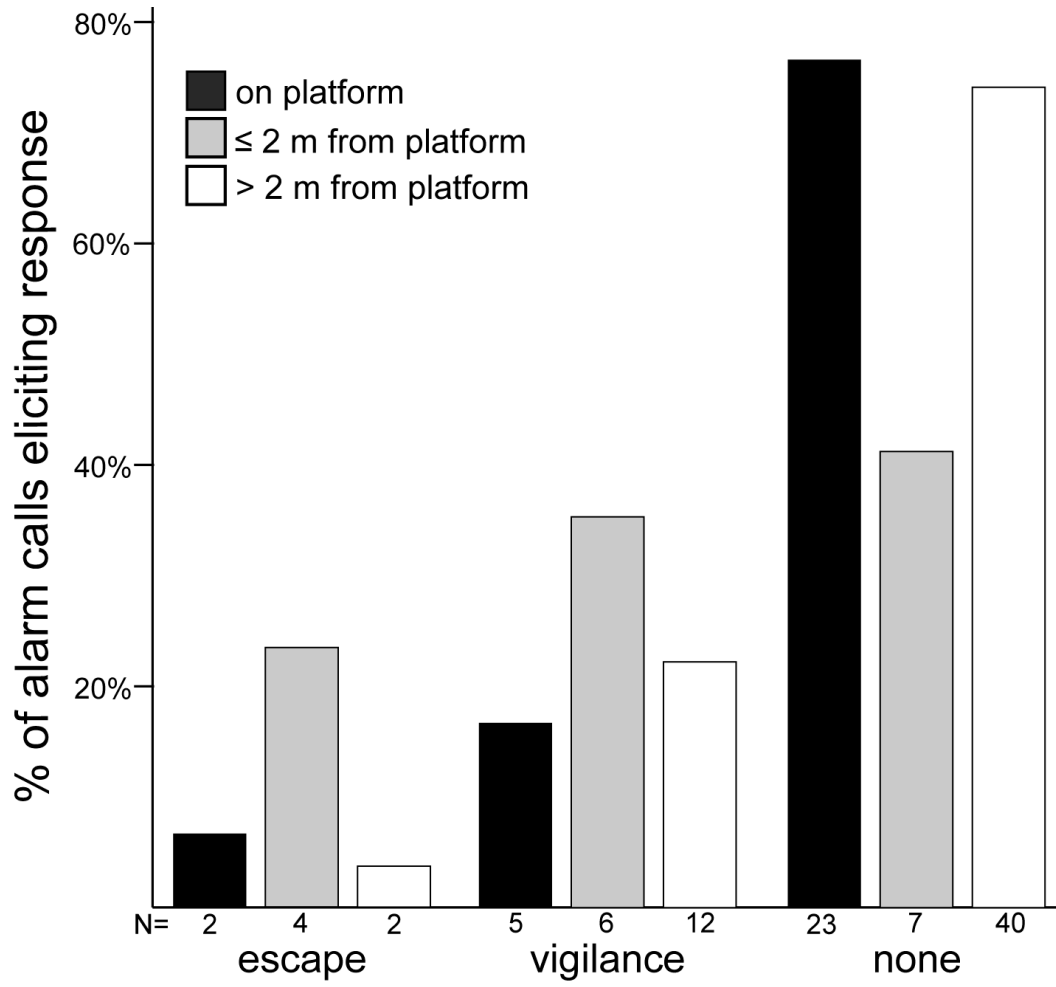


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424 **Figure 2**



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