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1 Decrease in alarm call response among tufted capuchin monkeys in

2 competitive feeding contexts: possible evidence for counterdeception

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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 nigritus*) 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.

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

38 **World primates**

39

Introduction

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

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

Methods

Study site and subjects

I conducted the study from May, 2005 to December, 2006 in Iguazú National Park, northeastern

Argentina (25º40'S, 54 º 30'W). The site sits at the southwestern edge of the South American

Atlantic Forest and is characterized by humid, semi-deciduous, subtropical forest. A more

detailed description of the study site can be found in Di Bitetti *et al*. (2000).

Tufted capuchin monkeys are medium-sized (~3 kg), arboreal primates that are primarily

frugivorous but who spend a large proportion of their active time searching for dispersed insect

prey (Fragaszy et al. 2004). All data from the current study are based on a single group, the

Macuco Group, which ranged in size from 23 to 28 individuals during the study period. This

group has been under almost continuous observation since 1991 and is well habituated to both

human observers and the experimental conditions utilized in this study (see Janson 1996, 2007a).

All individuals were readily recognizable based on facial characteristics and fur patterns.

Tufted capuchins in Iguazú face threats from hawk-eagles (*Spizaetus* spp.), carnivores

(including tayras: *Eira barbara*; ocelots: *Leopardus pardalis*; pumas: *Puma concolor*; and

jaguars: *Panthera onca*), and vipers (*Crotalus durissus*, *Bothrops* spp.). In response to these

threats, the monkeys regularly produce one or more of three discrete alarm call types: "barks" are

given in response to aerial threats, while "hiccups" and/or "peeps" are given in response to

carnivores and snakes (Wheeler in press). The alarm hiccup is not specific to predator

encounters; the call is also frequently given in other contexts in which the caller would

likely benefit by eliciting antipredator reactions in receivers (Wheeler in press). However,

callers tend to produce two or more intense hiccups in quick succession in high-risk

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 <u>Observational and experimental protocols</u>

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 to 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   <u>Statistical methods</u>

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, χ^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   χ^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 that 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

References

Blumstein, D. T., & Daniel, J. C. (2004). Yellow-bellied marmots discriminate between the
     alarm calls of individuals and are more responsive to calls from juveniles. *Animal
     Behaviour*, *68*, 1257-1265.

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

Cheney, D., & Seyfarth, R. (1988). Assessment of meaning and the detection of unreliable
     signals by vervet monkeys. *Animal Behaviour*, *36*, 477-486.

Di Bitetti, M. S. (2001). Food Associated Calls in the Tufted Capuchin Monkey (*Cebus apella*).
     Ph.D. dissertation, State University of New York, Stony Brook, NY.

337   Di Bitetti, M. S., Vidal, E. M. L., Baldovino, M. C., & Benesovsky, V. (2000). Sleeping site

338   preference in tufted capuchin monkeys (*Cebus apella nigritus*). *American Journal of*

339   *Primatology*, *50*, 257-274.

340   Fischer, J. (1998). Barbary macaques categorize shrill barks into two call types. *Animal*

341   *Behaviour*, *55*, 799-807.

342   Fischer, J., & Hammerschmidt, K. (2001). Functional referents and acoustic similarity revisited:

343   the case of Barbary macaque alarm calls. *Animal Cognition*, *4*, 29-35.

344   Fragaszy DM, Visalberghi E, Fedigan LM. (2004). *The Complete Capuchin: The Biology of the*

345   *Genus* Cebus. Cambridge: Cambridge University Press.

346   Gouzoules, H., & Gouzoules, S. (2002). Primate communication: by nature honest, or by

347   experience wise? *International Journal of Primatology*, *23*, 821-848.

348   Gouzoules, H., Gouzoules, S., & Miller, K. (1996). Skeptical responding in rhesus monkeys

349   (*Macaca mulatta*). *International Journal of Primatology*, *17*, 549-568.

350   Hanson, M., & Coss, R. (2001). Age differences in the response of California ground squirrels

351   (*Spermophilus beecheyi*) to conspecific alarm calls. *Ethology*, *107*, 259-275.

352   Hare, J. F., & Atkins, B. A. (2001). The squirrel that cried wolf: reliability detection by juvenile

353   Richardson's ground squirrels (*Spermophilus richardsonii*). *Behavioral Ecology and*

354   *Sociobiology*, *51*, 108-112.

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

356   Janson, C.H. (1985). Aggressive competition and individual food consumption in wild brown

357   capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology, 18,* 125-138.

358   Janson, C. H. (1996). Toward an experimental socioecology of primates. In M. A. Norconk, A.

359   L. Rosenberger & P. A. Garber (Eds.), *Adaptive Radiations of Neotropical Primates*. (pp.

360 309-325). New York: Plenum Press.

361 Janson, C. H. (2007a). Experimental evidence for route integration and strategic planning in wild

362 capuchin monkeys. *Animal Cognition*, *10*, 341-356.

363 Janson, C. H. (2007b). Predator detection and the evolution of primate sociality: insights from

364 experiments on a rain forest primate. *American Journal of Physical Anthropology*, *S44*,

365 136.

366 Koenig, A., & Borries, C. (2006). The predictive power of socioecological models: a

367 reconsideration of resource characteristics, agonism, and dominance hierarchies. In G.

368 Hohmann, M. M. Robbins & C. Boesch (Eds.), *Feeding Ecology in Apes and Other*

369 *Primates: Ecological, Physical and Behavioral Aspects*. (pp. 263-284). New York:

370 Cambridge University Press.

371 Krebs, J., & Dawkins, R. (1984). Animal signals: mind-reading and manipulation. In J. Krebs &

372 N. Davies (Eds.), *Behavioural Ecology: An Evolutionary Approach*. (pp. 380-402).

373 Sunderland, MA: Sinauer.

374 Martin, P., & Bateson, P. (2007). *Measuring Behaviour: An Introductory Guide*. New York:

375 Cambridge University Press

376 Ramakrishnan, U., & Coss, R. (2000). Age differences in the responses to adult and juvenile

377 alarm calls by bonnet macaques (*Macaca radiata)*. *Ethology*, *106*, 131-144.

378 Randler, C. (2005). Coots *Fulica atra* reduce their vigilance under increased competition.

379 *Behavioural Processes, 68*, 173-178.

380 Rendall, D., Owren, M. J., & Ryan, M. J. (2009). What do animal signals mean? *Animal*

381 *Behaviour, 78,* 233-240.

382 Rendall, D., Seyfarth, R. M., Cheney, D. L., & Owren, M. J. (1999). The meaning and function

of grunt variants in baboons. *Animal Behaviour*, *57*, 583–592.

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

Tibbetts, E. A. (2008). Resource value and the context dependence of receiver behaviour. *Proceedings of the Royal Society of London Series B*, *275*, 2201-2206.

van de Pol, M., & Wright, J. (2009). A simple method for distinguishing within-versus between-subject effects using mixed models. *Animal Behaviour, 77*, 753-758.

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

Wheeler, B. C. (2009a). Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. *Proceedings of the Royal Society of London Series B*, *276*, 3013-3018.

Wheeler, B. C. (2009b). *An Experimental Analysis of Alarm Calling Behavior in Wild Tufted Capuchin Monkeys* (Cebus apella nigritus). Ph.D. dissertation, State University of New York, Stony Brook, NY.

Wheeler, B. C. (in press). Production and perception of situationally variable alarm calls in wild tufted capuchin monkeys (*Cebus apella nigritus*). *Behavioral Ecology and Sociobiology*.

Wiley, R. H. (1994). Errors, exaggeration, and deception in animal communication. In L. A. Real (Ed.), *Behavioral Mechanisms in Evolutionary Ecology*. (pp. 157–189). Chicago: University of Chicago Press.

Zahavi, A., & Zahavi, A. (1997). *The handicap principle: A missing piece of Darwin's puzzle*. Oxford: Oxford University Press.

406   Zuberbühler, K., Cheney, D.L., & Seyfarth, R.M. (1999). Conceptual semantics in a nonhuman

407   primate. *Journal of Comparative Psychology*, *113*, 33-42.
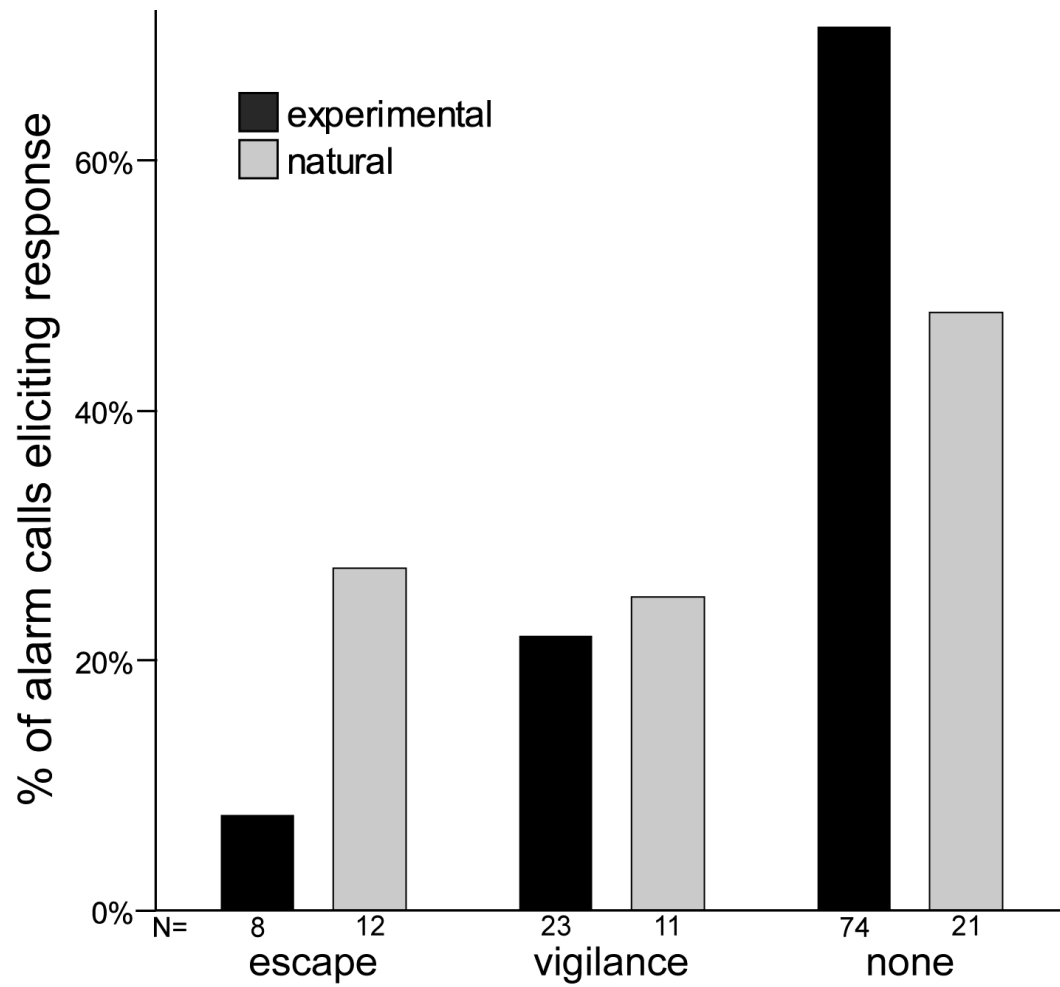
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Figure caption

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

Fig. 2. The percent of alarm calls that elicited terrestrial predator-associated escape reactions, vigilance reactions, or no reaction in focal animals for each of the three spatial positions considered during the experimental feeding contexts.
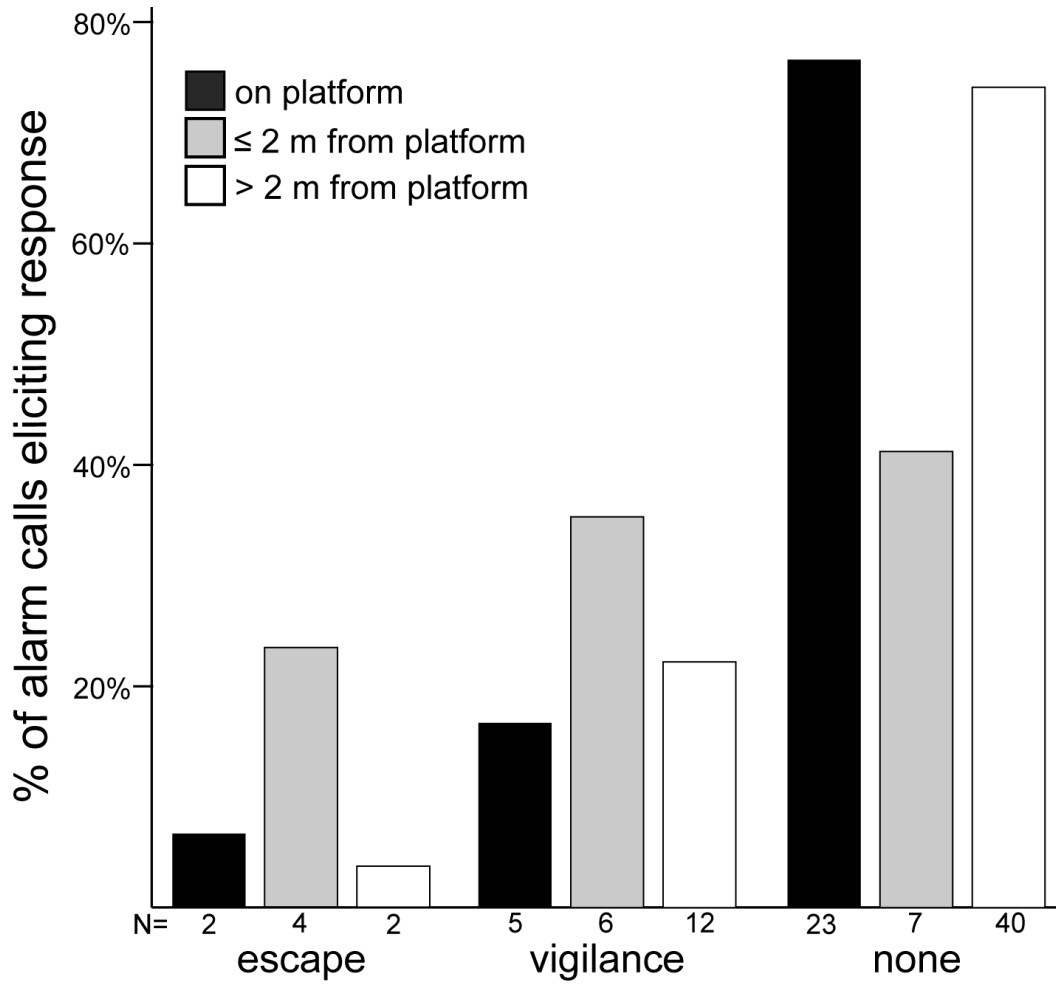
420   **Figure 1**

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424 **Figure 2**