

Kent Academic Repository

Full text document (pdf)

Citation for published version

Wheeler, Brandon C. (2009) Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. *Proceedings of the Royal Society B: Biological Sciences*, 276 (1669). pp. 3013-3018. ISSN 0962-8452.

DOI

<https://doi.org/10.1098/rspb.2009.0544>

Link to record in KAR

<http://kar.kent.ac.uk/54730/>

Document Version

Author's Accepted Manuscript

Copyright & reuse

Content in the Kent Academic Repository is made available for research purposes. Unless otherwise stated all content is protected by copyright and in the absence of an open licence (eg Creative Commons), permissions for further reuse of content should be sought from the publisher, author or other copyright holder.

Versions of research

The version in the Kent Academic Repository may differ from the final published version.

Users are advised to check <http://kar.kent.ac.uk> for the status of the paper. **Users should always cite the published version of record.**

Enquiries

For any further enquiries regarding the licence status of this document, please contact:

researchsupport@kent.ac.uk

If you believe this document infringes copyright then please contact the KAR admin team with the take-down information provided at <http://kar.kent.ac.uk/contact.html>

1 **Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to**
2 **usurp resources from conspecifics**

3
4 Published in *Proceedings of the Royal Society Series B* 276: 3013-3018.

5 <http://rspb.royalsocietypublishing.org/content/276/1669/3013>

6
7 Brandon C. Wheeler

8 Interdepartmental Doctoral Program in Anthropological Sciences

9 Stony Brook University

10 Stony Brook, NY 11794-4364 USA

11 E-mail: bcwheeler43@gmail.com

12

13 **SUMMARY**

14 The use of “tactical deception” is argued to have been important in the cognitive evolution of
15 the Order Primates, but systematic studies of active deception in wild nonhuman primates are
16 scant. This study tests whether wild tufted capuchin monkeys (*Cebus apella nigrinus*) use alarm
17 calls in a functionally deceptive manner to usurp food resources. If capuchins use alarm calls
18 “deceptively”, it was predicted that false alarms should be: 1) given by subordinates more than
19 by dominants, 2) more frequent when food is most contestable, 3) more frequent when less food
20 is available, and 4) given when the caller is in a spatial position in which it could increase its
21 feeding success if conspecifics react to the call. These predictions were tested by observing
22 subjects in experimental contexts in which the amount and distribution of a high value resource

23 (banana pieces) were manipulated using wooden platforms suspended from tree branches. While
24 false alarms were non-significantly more common when more food was available, the three
25 remaining predictions were supported. These results generally support the hypothesis that alarm
26 calls are used by capuchins to reduce the effects of feeding competition. Whether this is
27 intentional on the part of the caller requires further investigation.

28 **KEYWORDS:** alarm calls, feeding competition, deception, communication, primates, *Cebus*
29 *apella nigrinus*

30

31 **1. INTRODUCTION**

32 Animal signals are argued to function to manipulate the behaviour of signal receivers in a way
33 that preferentially benefits the signaller (Dawkins & Krebs 1978; Krebs & Dawkins 1984). Anti-
34 predator signals have long been challenging to explain because of the danger that the signaller
35 imparts on itself in an apparent attempt to warn others of impending danger. While numerous
36 hypotheses potentially explain how an individual who has detected a predator can benefit
37 directly or indirectly by eliciting anti-predator behaviour in conspecifics (reviewed in Hauser
38 1996; Wheeler 2008), individuals could also use alarm calls in the absence of a predator to
39 distract signal receivers and take advantage of the momentary diversion of attention. Cases such
40 as this wherein individuals produce a signal outside its “normal” context in order to distract
41 listeners is a form of what has been termed tactical or functional deception (Whiten & Byrne
42 1988; Hauser 1996, 1997).

43 Functionally deceptive behaviours are expected to be uncommon, especially in social
44 animals where the need to cooperate with group members is common and the potential for
45 targets to habituate to such behaviours is high (Cheney & Seyfarth 1990). This prediction has
46 been largely supported by the fact that observation of behaviours that can be interpreted as
47 functionally deceptive are rare and largely anecdotal (Byrne & Whiten 1990). However,
48 functionally deceptive behaviours can in theory be relatively common if the cost of not
49 responding with an “appropriate” reaction is high (Mitchell 1988) or if targets are largely unable
50 to determine whether or not the agent’s behaviour was indeed deceptive or honest (Whiten &
51 Byrne 1988). Both of these criteria may apply to alarm calls, as the cost of not responding with
52 an anti-predatory behaviour is potentially death, and because false alarms due to

53 misclassification of innocuous stimuli may be common (e.g. Haftorn 2000), especially in
54 environments with poor visibility (see Evans 1997).

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

70 An additional study conducted under experimental conditions similarly showed that great
71 tits (*Parus major*) successfully used false alarms to distract competitors during feeding (Møller
72 1988). Here it was found that individuals did not give false alarms if they were only in the
73 presence of individuals whom they could easily displace with threat displays (i.e. subordinate
74 individuals), but did when in the presence of those that could not be easily displaced (i.e.
75 individuals of similar or higher rank). In addition, false alarms were more common when the

76 food was more clumped, and therefore more easily monopolized by dominants, than when it was
77 more dispersed. Similar uses of false alarms in feeding contexts have been observed anecdotally
78 in a number of taxa including nuthatches (Tramer 1994), foxes (Rüppell 1986), and primates
79 (Byrne & Whiten 1990; Gouzoules et al. 1996).

80 To date, only a pair of studies have examined passive deception (i.e. the withholding of
81 information) in free ranging primates by showing that some species selectively withhold food
82 calls on some occasions (Hauser 1992; Di Bitetti 2005). Passive deception is likely more
83 common among animals than active deception (i.e. providing false information, such as
84 producing food calls in the absence of food) due the difficulty in detecting the behaviour
85 (Cheney & Seyfarth 1990). However, the classification of instances in which individuals do not
86 provide information to others as deceptive has been criticized on the basis that the withholding of
87 an altruistic act is not necessarily “cheating” (see Owings & Morton 1998). In contrast, actively
88 providing false information is more widely accepted as a functionally deceptive behaviour (see
89 Searcy & Nowicki 2005). There is not yet systematic evidence that any primates actively use
90 signals outside their “appropriate” context (but see Slocombe & Zuberbühler 2007 for evidence
91 of functionally deceptive exaggeration of signals in chimpanzees, *Pan troglodytes*). Systematic
92 studies of such behaviour with wild primates are important given that the ability to use tactical
93 deception is argued to have been an important factor in the cognitive evolution of primates
94 (Whiten & Byrne, 1988).

95 This study examines the use of terrestrial predator-associated calls by tufted capuchin
96 monkeys (*Cebus apella nigrinus*) in experimental feeding contexts when no predators or other
97 potentially threatening stimuli are present. This study was undertaken after initial *ad libitum*
98 observations indicated that these calls were given far more often in these experimental contexts

99 than in natural contexts, although it was not clear if this increased production of alarm calls
100 reflected a strategy for usurping resources, as has been shown in the avian taxa discussed above.
101 If anti-predator calls are indeed used during feeding to usurp resources from conspecifics, several
102 testable predictions can be made. First, because dominants can easily usurp resources from
103 subordinates through displacements (although the reverse is not true), false alarms should be
104 given more often by subordinates than by dominants (see Møller, 1988). Second, false alarms
105 should be more common when food is more clumped, and therefore more contestable, than when
106 more dispersed. Third, false alarms are expected to be more common when less food is available.
107 Fourth, false alarms should be given when the caller is close enough to the contested resource to
108 take advantage of any conspecific reactions. Finally, the false alarms should elicit anti-predator
109 reactions, just as alarm calls given in response to real threats do (Wheeler in preparation).

110

111 **2. METHODS**

112 (a) *Study site and subjects*

113 Data were collected between May 2005 and December 2006 in Iguazú National Park,
114 Argentina (25°40'S, 54°30'W), a semi-deciduous and sub-tropical forest (see Di Bitetti et al.
115 2006 for additional details regarding the study site). Tufted capuchins are largely frugivorous
116 primates, although a considerable portion of their diet consists of insect prey (Brown & Zunino
117 1990). In Iguazú, capuchin groups typically range in size from 7-30 individuals (Di Bitetti 2001),
118 although groups of up to 45 individuals have been observed (C. Janson unpublished data).
119 Dominance hierarchies are linear with dominant individuals winning contests over food and
120 spatial position (Janson 1985, 1990; Di Bitetti & Janson 2001). The species is mostly arboreal,
121 primarily inhabiting the mid to lower canopy (Fleagle & Mittermeier 1980). All data for this

122 study came from a single study group, the Macuco Group, which ranged in size from 23-28
123 individuals during the study period. All study subjects were readily recognizable based on facial
124 characteristics.

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

138

139 (b) *Experimental protocol*

140 Data on false alarm call production during feeding were collected in experimental
141 contexts wherein the quantity and distribution of a high quality resource (banana pieces
142 measuring approximately 2.5 cm) were manipulated using 1m x 1m platforms suspended from
143 tree branches by a system of ropes and pulleys at 3 to 10m above the ground (see also Janson
144 1996; Di Bitetti & Janson 2001 for additional descriptions of feeding platform experiments).

145 Within a given experimental site, the fruit pieces were distributed across one to six platforms in
146 order to vary the degree of monopolizability of the resource. The quantity of food available was
147 manipulated by varying the number of bananas provided from two to 30. Within a site,
148 individual platforms were spaced at least 15 m apart, but the site was spread over no more than
149 40 m. Different experimental sites were separated by at least 250 m and were placed at least 150
150 m from naturally occurring fruit patches. The spatial distribution of the platforms within and
151 between sites, relative to group spread, allowed each site to mimic a single food patch, while
152 different sites mimicked distinct patches. During most months, two experimental sites were used
153 simultaneously; the sites were set up on the final day of the month and were provisioned once a
154 day for thirteen consecutive days following their discovery by the study group. During the three
155 months of the Argentine winter there were 8 sites used simultaneously and bananas were
156 provided at each site everyday that the study group visited for the entire three month period.

157 The banana pieces were placed in the platforms as the group approached the experimental
158 site, but before arriving. When the group arrived, one or two observers each chose a focal
159 individual over six months in age (when they begin to spend most of their time away from their
160 mothers), following it until all banana pieces had been eaten, and collected data on its behaviour
161 using both instantaneous and continuous sampling methods (Martin & Bateson 2007). All data
162 were spoken into an audio recorder. Every thirty seconds, observers noted the focal animal's
163 location (within 2 m of a platform with food or greater than 2 m from a platform with food). All
164 hiccups given by the focal animal were noted continuously, and the animal's location at the
165 moment the call was given was recorded. All occurrences of anti-predator escape reactions
166 employed by other group members within a 10 m radius of the focal animal following an alarm
167 call by the focal were noted.

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

187

188 (c) *Data analysis*

189 For each individual focal follow (of which there were one or two per individual
190 experiment), it was noted simply whether or not the focal animal gave an RRDA at any point

191 during the experiment. Unless otherwise stated, the tests described below are based on whether
192 or not RRDA's were produced during an observation period, not the number of RRDA's given. A
193 Fisher's exact test was used to test whether or not subordinate individuals were more likely to
194 produce RRDA's than dominants. The six highest ranking individuals (as determined through
195 analysis of dyadic agonistic interactions; see Wheeler 2008 for additional details), including the
196 group's four adult males and the two highest ranking adult females, were placed in the
197 "dominant" category as these are the only individuals who were able to effectively exclude more
198 subordinate individuals (18 of which were sampled) from accessing the platforms (pers. obs.).
199 For this test, each individual was scored based on whether or not it was observed to give an
200 RRDA at least once during any of the first 20 experiments in which it was a focal animal. Many
201 animals were sampled more than 20 times, but additional experiments were not included in this
202 analysis in order to avoid oversampling certain individuals. A few individuals from the study
203 group were sampled less than 20 times (e.g. due to death or dispersal). Although some of these
204 individuals were observed to produce RRDA's, all undersampled individuals were excluded from
205 this analysis in order to prevent a bias towards calling. Wilcoxon signed ranks tests for small
206 sample sizes (Siegel & Castellan 1988) were used to test whether or not individuals produced
207 RRDA's more often when food was more monopolizable (i.e. distributed across 1 to 3 platforms)
208 than when less contestable (4 to 6 platforms). To be included in this analysis, each individual had
209 to be sampled at least 5 times in each of the two conditions. Because most individuals were not
210 sampled an equal number of time in both conditions, additional experiments of the oversampled
211 condition were not included in the analysis. For example, if an individual was sampled 10 times
212 with 1 to 3 platforms and 15 times with 4 to 6 platforms, then only the first 10 experiments with
213 4 to 6 platforms were included in the analysis; alarm calls given in any subsequent experiments

214 were not counted. The percent of experiments which elicited RRDA's was then calculated for
215 each individual in each of the two experimental conditions. This same methodology was used to
216 test if false alarms were more common when less food was available (i.e. when 10 bananas or
217 less were presented) than when more than food was available (more than 10 bananas). A
218 binomial test was used to determine if RRDA's were given more often than expected when an
219 individual was within 2 m of a platform with food, as callers could easily take advantage of any
220 escape reactions the calls elicited from this short distance. The expected values for this test were
221 calculated as the mean of the percent time (based on the instantaneous focal samples) the callers
222 spent within 2 m of a platform during each experiment in which an RRDA was produced.
223 Although some individuals were observed to produce RRDA's during more than one experiment,
224 only the first such observation by each individual was included in this analysis in order to avoid
225 pseudoreplication. Fisher's exact tests were conducted using SPSS 15.0. Wilcoxon signed ranks
226 tests for small sample sizes were calculated following Siegel and Castellan (1988).

227 **3. RESULTS**

228 A total of 321 individual feeding platform experiments were successfully conducted
229 during the study period. This resulted in a total of 499 focal follows and a total of 45 hours of
230 focal animal observation. The total number of focal follows conducted with a given number of
231 platforms and food quantity are provided in table 1. Focal animals did not produce high-urgency
232 hiccups in the vast majority of experiments; such bouts were observed during 60 focal follows,
233 while bouts that met the criteria to be considered a resource-related deceptive alarm were given
234 by 13 different animals during 25 individual experiments (5% of all focal follows; see table 2).

235 Production of RRDA's was non-random in terms of which individuals called and in what
236 contexts they did so. Twenty four of the 25 RRDA's were given by subordinate individuals.

237 When considering only those individuals sampled at least 20 times, none of the four dominant
238 individuals was observed to produce an RRDA during the first 20 experiments in which they
239 were sampled, while 7 of 8 subordinate individuals did so, a significant difference (Fisher's exact
240 test: $N=12$, $p=0.010$). The remaining subordinate individual produced an RRDA on one
241 occasion, but not until the 22nd experiment in which it was the focal. Among those individuals
242 who were observed to give one or more RRDA, 8 gave the calls more when the banana pieces
243 were distributed across 1 to 3 platforms, 2 did so more often when 4 to 6 platforms were used,
244 and one individual showed no difference between the two treatments (two-tailed Wilcoxon
245 signed ranks test: $T^- = 6$; $N=10$; $p=0.027$). Indeed, closer examination shows that the calls were
246 most common when food was distributed across 1 or 2 platforms than across 3 or more platforms
247 (figure 1). However, the frequency of RRDA did not vary based on food quantity. While 8
248 individuals called more when more than 10 bananas were presented and only 3 called more when
249 10 or fewer bananas were given, the difference was not significant (two-tailed Wilcoxon signed
250 ranks test: $T^+ = 18.5$; $N=11$, $p=0.206$).

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

260 The false alarm calls elicited anti-predator escape reactions in one or more neighboring
261 conspecifics in 10 of 25 cases (40%). In seven of these 10 cases, the caller likely increased its
262 feeding success as a result of the conspecific reactions. On four occasions, the caller entered a
263 feeding platform and obtained banana pieces immediately after others jumped out in response to
264 the false alarm. On three occasions, the caller was already in a platform, but the false alarm
265 caused others also in the platform to jump out, while the caller stayed and continued feeding. In
266 the three remaining cases, the caller was unable to enter the platform because, although at least
267 one neighboring individual reacted, one or more individuals did not and remained on the feeding
268 platform.

269

270 **4. DISCUSSION**

271 The resource usurpation hypothesis for false alarm call production was broadly
272 supported, with four of the five predictions finding support in this study: subordinate individuals
273 produced the calls far more often than dominants, the calls were given more often when the
274 contested resources could most easily be monopolized by dominants, callers tended to be well
275 positioned spatially to take advantage of any potential anti-predator reactions the calls elicited,
276 and the RRDA's distracted conspecifics by eliciting anti-predator escape reactions (doing so
277 nearly twice as often as did playbacks of "honest" alarm calls; Wheeler in preparation), with
278 callers most often taking advantage of these reactions. The only prediction not supported was
279 that RRDA's would be more common when less food was available. In fact, RRDA's were
280 slightly, but non-significantly, more common when more food was available. Even without
281 support for the latter prediction, it seems that capuchin monkeys, like some avian and rodent taxa

282 (e.g. Munn 1986; Tamura 1995), use alarm calls to distract others during competitive situations,
283 alleviating some of the costs associated with contest competition for food.

284 Functionally deceptive signaling is thought to have to be rare and/or have a low cost for
285 the “deceived”, otherwise the signal will simply be ignored and become ineffective (Fitch &
286 Hauser 2002; Searcy & Nowicki 2005). In the current study, RRDAAs were quite common, being
287 given at a rate of 0.56 deceptive calls/individual/hr in the experimental feeding contexts.

288 Previous studies have shown that false alarm call rates can exceed the rates in which alarm calls
289 are given in response to real threats and still regularly elicit anti-predator reactions (Munn 1986;
290 Møller 1988). It seems likely that in these cases the cost of being deceived is indeed relatively
291 low (loss of a small amount of food) compared to the cost to not responding to a real threat
292 (potentially death). Call receivers may therefore employ a “better safe than sorry” approach in
293 response to alarm calls (Haftorn 2000) as the cost of being deceived, even on a regular basis,
294 may be less costly than ignoring all calls given in competitive situations.

295 While these results support a *functionally* deceptive interpretation for the production of
296 false alarms during feeding, it is difficult to prove that this behaviour is *intentionally* deceptive
297 (see Hauser, 1997). A study of the proximate causes of call production would be needed to
298 provide more insight in this regard (Fitch & Hauser 2002). Intentionally deceptive calls would be
299 driven proximately by the cognitive ability to understand the “beliefs” of others (Hauser, 1997).
300 Alternatively, false alarms may be common during feeding because, after having once produced
301 an alarm call in this context, observed the reaction of neighboring conspecifics, and acquired
302 food as a result, individuals associate call production with access to food. While such an
303 explanation requires that individuals learn to associate false alarm production with a food
304 reward, it does not require special cognitive abilities. It is also plausible that call production is

305 driven proximately by physiological mechanisms. Previous work has shown that captive tufted
306 capuchin monkeys who experience high cortisol levels due to chronic stress produce these calls
307 more often than those under less stress (Boinski et al. 1999; see also Bercovitch et al. 1995;
308 Blumstein et al. 2006). Subordinates may experience elevated stress (and increased cortisol
309 levels) when the group is feeding on high quality food resources that are highly clumped in their
310 distribution because dominant individuals can easily exclude subordinates from feeding (e.g.
311 Janson 1985, Koenig et al. 1998). Additional research is needed to confirm if stress is indeed a
312 possible proximate explanation for call production.

313

314 **ACKNOWLEDGMENTS**

315 This study would not have been possible without the years of work Charles Janson put in
316 to developing platform experiments with the Macuco group. Andreas Koenig and Charles Janson
317 provided indispensable advice during all phases of this project. Helpful advice was also provided
318 by Sue Boinski, Mario Di Bitetti, John Fleagle, and Barbara Tiddi. Comments by Julia Fischer,
319 Kate Lessells, Robert Seyfarth, and an anonymous reviewer greatly improved this manuscript. I
320 thank the Centro de Investigaciones Ecológicas Subtropicales (CIES) and the Delegación
321 Técnica of the Argentine Administration of National Parks for permission to live and work in the
322 park. I owe a debt of gratitude to many for assistance in the field, especially Fermino Silva.
323 Funding was provided by the American Society of Primatologists, the Wenner-Gren Foundation
324 (Grant #7244), the National Science Foundation (DDIG # 0550971 and BCS-0515007 to C.
325 Janson), and the National Geographic Society Committee on Research and Exploration (grant to
326 C. Janson). The study received IACUC approval from Stony Brook University (ID numbers
327 2005-1448 and 2006-1448).

328

329 **REFERENCES**

- 330 Bercovitch, F. B., Hauser, M. D. & Jones, J. H. 1995 The endocrine stress response and alarm
331 vocalizations in Rhesus macaques. *Animal Behaviour* **49**, 1703-1706.
- 332 Blumstein, D. T., Patton, M. L. & Saltzman, W. 2006 Faecal glucocorticoid metabolites and
333 alarm calling in free-living yellow-bellied marmots. *Biology Letters* **2**, 29-32.
- 334 Boinski, S., Gross, T. S. & Davis, J. K. 1999 Terrestrial predator alarm vocalizations are a valid
335 monitor of stress in captive brown capuchins (*Cebus apella*). *Zoo Biology* **18**, 295-312.
- 336 Brown, A. & Zunino, G. 1990 Dietary variability in *Cebus apella* in extreme habitats: evidence
337 for adaptability. *Folia Primatologica* **54**, 187-195.
- 338 Byrne, R. & Whiten, A. 1990 Tactical deception in primates: the 1990 database. *Primate Report*
339 **27**, 1-101.
- 340 Cheney, D. & Seyfarth, R. 1990 *How Monkeys See the World: Inside the Mind of Another*
341 *Species*. Chicago: University of Chicago Press.
- 342 Dawkins, R. & Krebs, J. 1978 Animal signals: information or manipulation. In *Behavioural*
343 *Ecology: An Evolutionary Approach* (ed. J. Krebs & N. Davies), pp. 282-309. Oxford:
344 Blackwell Scientific Publications.
- 345 Di Bitetti, M.S. 2001 Food associated calls in the tufted capuchin monkey (*Cebus apella*). Ph.D.
346 Dissertation: SUNY Stony Brook.
- 347 Di Bitetti, M.S. 2005 Food-associated calls and audience effects in tufted capuchin monkeys,
348 *Cebus apella nigritus*. *Animal Behaviour* **69**, 911-919.
- 349 Di Bitetti, M. S. & Janson, C. H. 2001 Social foraging and the finder's share in capuchin
350 monkeys, *Cebus apella*. *Animal Behaviour* **62**, 47-56.

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

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

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

359 Fleagle, J. G. & Mittermeier, R. A. 1980 Locomotor behavior, body size, and comparative
360 ecology of seven Surinam monkeys. *American Journal of Physical Anthropology* **52**,
361 301-314.

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

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

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

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

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

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

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

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

379 Koenig, A., Beise, J., Chalise, M. K. & Ganzhorn, J. U. 1998 When females should contest for
380 food - testing hypotheses about resource density, distribution, size, and quality with
381 Hanuman langurs (*Presbytis entellus*). *Behavioral Ecology and Sociobiology* **42**, 225-
382 237.

383 Krebs, J. & Dawkins, R. 1984 Animal signals: mind-reading and manipulation. In *Behavioural*
384 *Ecology: An Evolutionary Approach* (ed. J. Krebs & N. Davies), pp. 380-402: Sinaver
385 Associates.

386 Martin, P. & Bateson, P. 2007 *Measuring Behaviour: An Introductory Guide*. New York:
387 Cambridge University Press

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

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

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

394 Munn, C. 1986 Birds that 'cry wolf'. *Nature* **319**, 143-145.

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

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

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

402 Siegel, S. & Castellan, N. J. 1988. *Nonparametric statistics for the behavioral sciences*. New
403 York: McGraw-Hill.

404 Slocombe, K. E. & Zuberbühler, K. 2007 Chimpanzees modify recruitment screams as a function
405 of audience composition. *Proceedings of the National Academy of Sciences* **104**, 17228-
406 17233.

407 Tamura, N. 1995 Postcopulatory mate guarding by vocalization in the Formosan squirrel.
408 *Behavioral Ecology and Sociobiology* **36**, 377-386.

409 Tramer, E. J. 1994 Feeder Access: Deceptive Use of Alarm Calls by a White-Breasted Nuthatch.
410 *Wilson Bulletin* **106**, 573.

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

413 Whiten, A. & Byrne, R. 1988 Tactical deception in primates. *Behavioral and Brain Sciences* **11**,
414 233-273.

415

416 Table 1. The total number of focal follows conducted with a given number of bananas distributed
417 across a given number of platforms.

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

418

419

420 Table 2. The number of high-urgency hiccups produced by focal animals attributed to each
421 eliciting stimulus.

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

422

423 **Figure legends**

424 **Figure 1** The number of experiments with a given number of platforms in which a focal animal
425 did and did not produce resource-related deceptive alarm calls. Deceptive alarm calls were given
426 more often than expected when food was distributed across fewer platforms.

427

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

434

- 435 Short title for page headings:
- 436 Deceptive alarm calling in capuchins
- 437