Kent Academic Repository

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.**

Downloaded from

https://kar.kent.ac.uk/54730/ The University of Kent's Academic Repository KAR

The version of record is available from

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

This document version

Author's Accepted Manuscript

DOI for this version

Licence for this version

UNSPECIFIED

Additional information

Versions of research works

Versions of Record

If this version is the version of record, it is the same as the published version available on the publisher's web site. Cite as the published version.

Author Accepted Manuscripts

If this document is identified as the Author Accepted Manuscript it is the version after peer review but before type setting, copy editing or publisher branding. Cite as Surname, Initial. (Year) 'Title of article'. To be published in *Title of Journal* , Volume and issue numbers [peer-reviewed accepted version]. Available at: DOI or URL (Accessed: date).

Enquiries

If you have questions about this document contact ResearchSupport@kent.ac.uk. Please include the URL of the record in KAR. If you believe that your, or a third party's rights have been compromised through this document please see our Take Down policy (available from https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies).

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

Published in *Proceedings of the Royal Society Series B* 276: 3013-3018.
http://rspb.royalsocietypublishing.org/content/276/1669/3013

Brandon C. Wheeler
Interdepartmental Doctoral Program in Anthropological Sciences
Stony Brook University
Stony Brook, NY 11794-4364 USA
E-mail: bcwheeler43@gmail.com

SUMMARY

The use of "tactical deception" is argued to have been important in the cognitive evolution of the Order Primates, but systematic studies of active deception in wild nonhuman primates are scant. This study tests whether wild tufted capuchin monkeys (*Cebus apella nigritus*) use alarm calls in a functionally deceptive manner to usurp food resources. If capuchins use alarm calls "deceptively", it was predicted that false alarms should be: 1) given by subordinates more than by dominants, 2) more frequent when food is most contestable, 3) more frequent when less food is available, and 4) given when the caller is in a spatial position in which it could increase its feeding success if conspecifics react to the call. These predictions were tested by observing subjects in experimental contexts in which the amount and distribution of a high value resource (banana pieces) were manipulated using wooden platforms suspended from tree branches. While false alarms were non-significantly more common when more food was available, the three remaining predictions were supported. These results generally support the hypothesis that alarm calls are used by capuchins to reduce the effects of feeding competition. Whether this is intentional on the part of the caller requires further investigation.

KEYWORDS: alarm calls, feeding competition, deception, communication, primates, *Cebus apella nigritus*

1. INTRODUCTION

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

Functionally deceptive behaviours are expected to be uncommon, especially in social animals where the need to cooperate with group members is common and the potential for targets to habituate to such behaviours is high (Cheney & Seyfarth 1990). This prediction has been largely supported by the fact that observation of behaviours that can be interpreted as functionally deceptive are rare and largely anecdotal (Byrne & Whiten 1990). However, functionally deceptive behaviours can in theory be relatively common if the cost of not responding with an "appropriate" reaction is high (Mitchell 1988) or if targets are largely unable to determine whether or not the agent's behaviour was indeed deceptive or honest (Whiten & Byrne 1988). Both of these criteria may apply to alarm calls, as the cost of not responding with an anti-predatory behaviour is potentially death, and because false alarms due to misclassification of innocuous stimuli may be common (e.g. Haftorn 2000), especially in environments with poor visibility (see Evans 1997).

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

An additional study conducted under experimental conditions similarly showed that great tits (*Parus major*) successfully used false alarms to distract competitors during feeding (Møller 1988). Here it was found that individuals did not give false alarms if they were only in the presence of individuals whom they could easily displace with threat displays (i.e. subordinate individuals), but did when in the presence of those that could not be easily displaced (i.e. individuals of similar or higher rank). In addition, false alarms were more common when the food was more clumped, and therefore more easily monopolized by dominants, than when it was more dispersed. Similar uses of false alarms in feeding contexts have been observed anecdotally in a number of taxa including nuthatches (Tramer 1994), foxes (Rüppell 1986), and primates (Byrne & Whiten 1990; Gouzoules et al. 1996).

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

This study examines the use of terrestrial predator-associated calls by tufted capuchin monkeys (*Cebus apella nigritus*) in experimental feeding contexts when no predators or other potentially threatening stimuli are present. This study was undertaken after initial *ad libitum* observations indicated that these calls were given far more often in these experimental contexts than in natural contexts, although it was not clear if this increased production of alarm calls reflected a strategy for usurping resources, as has been shown in the avian taxa discussed above. If anti-predator calls are indeed used during feeding to usurp resources from conspecifics, several testable predictions can be made. First, because dominants can easily usurp resources from subordinates through displacements (although the reverse is not true), false alarms should be given more often by subordinates than by dominants (see Møller, 1988). Second, false alarms should be more common when food is more clumped, and therefore more contestable, than when more dispersed. Third, false alarms are expected to be more common when less food is available. Fourth, false alarms should be given when the caller is close enough to the contested resource to take advantage of any conspecific reactions. Finally, the false alarms should elicit anti-predator reactions, just as alarm calls given in response to real threats do (Wheeler in preparation).

2. METHODS

(a) *Study site and subjects*

Data were collected between May 2005 and December 2006 in Iguazú National Park, Argentina (25°40'S, 54°30'W), a semi-deciduous and sub-tropical forest (see Di Bitetti et al. 2006 for additional details regarding the study site). Tufted capuchins are largely frugivorous primates, although a considerable portion of their diet consists of insect prey (Brown & Zunino 1990). In Iguazú, capuchin groups typically range in size from 7-30 individuals (Di Bitetti 2001), although groups of up to 45 individuals have been observed (C. Janson unpublished data). Dominance hierarchies are linear with dominant individuals winning contests over food and spatial position (Janson 1985, 1990; Di Bitetti & Janson 2001). The species is mostly arboreal, primarily inhabiting the mid to lower canopy (Fleagle & Mittermeier 1980). All data for this study came from a single study group, the Macuco Group, which ranged in size from 23-28 individuals during the study period. All study subjects were readily recognizable based on facial characteristics.

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

(b) *Experimental protocol*

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

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

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

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

(c) *Data analysis*

For each individual focal follow (of which there were one or two per individual experiment), it was noted simply whether or not the focal animal gave an RRDA at any point during the experiment. Unless otherwise stated, the tests described below are based on whether or not RRDAs were produced during an observation period, not the number of RRDAs given. A Fisher's exact test was used to test whether or not subordinate individuals were more likely to produce RRDAs than dominants. The six highest ranking individuals (as determined through analysis of dyadic agonistic interactions; see Wheeler 2008 for additional details), including the group's four adult males and the two highest ranking adult females, were placed in the "dominant" category as these are the only individuals who were able to effectively exclude more subordinate individuals (18 of which were sampled) from accessing the platforms (pers. obs.). For this test, each individual was scored based on whether or not it was observed to give an RRDA at least once during any of the first 20 experiments in which it was a focal animal. Many animals were sampled more than 20 times, but additional experiments were not included in this analysis in order to avoid oversampling certain individuals. A few individuals from the study group were sampled less than 20 times (e.g. due to death or dispersal). Although some of these individuals were observed to produce RRDAs, all undersampled individuals were excluded from this analysis in order to prevent a bias towards calling. Wilcoxon signed ranks tests for small sample sizes (Siegel & Castellan 1988) were used to test whether or not individuals produced RRDAs more often when food was more monopolizable (i.e. distributed across 1 to 3 platforms) than when less contestable (4 to 6 platforms). To be included in this analysis, each individual had to be sampled at least 5 times in each of the two conditions. Because most individuals were not sampled an equal number of time in both conditions, additional experiments of the oversampled condition were not included in the analysis. For example, if an individual was sampled 10 times with 1 to 3 platforms and 15 times with 4 to 6 platforms, then only the first 10 experiments with 4 to 6 platforms were included in the analysis; alarm calls given in any subsequent experiments were not counted. The percent of experiments which elicited RRDAs was then calculated for each individual in each of the two experimental conditions. This same methodology was used to test if false alarms were more common when less food was available (i.e. when 10 bananas or less were presented) than when more than food was available (more than 10 bananas). A binomial test was used to determine if RRDAs were given more often than expected when an individual was within 2 m of a platform with food, as callers could easily take advantage of any escape reactions the calls elicited from this short distance. The expected values for this test were calculated as the mean of the percent time (based on the instantaneous focal samples) the callers spent within 2 m of a platform during each experiment in which an RRDA was produced. Although some individuals were observed to produce RRDAs during more than one experiment, only the first such observation by each individual was included in this analysis in order to avoid pseudoreplication. Fisher's exact tests were conducted using SPSS 15.0. Wilcoxon signed ranks tests for small sample sizes were calculated following Siegel and Castellan (1988).

3. RESULTS

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

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

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

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

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

4. DISCUSSION

The resource usurpation hypothesis for false alarm call production was broadly supported, with four of the five predictions finding support in this study: subordinate individuals produced the calls far more often than dominants, the calls were given more often when the contested resources could most easily be monopolized by dominants, callers tended to be well positioned spatially to take advantage of any potential anti-predator reactions the calls elicited, and the RRDAs distracted conspecifics by eliciting anti-predator escape reactions (doing so nearly twice as often as did playbacks of "honest" alarm calls; Wheeler in preparation), with callers most often taking advantage of these reactions. The only prediction not supported was that RRDAs would be more common when less food was available. In fact, RRDAs were slightly, but non-significantly, more common when more food was available. Even without support for the latter prediction, it seems that capuchin monkeys, like some avian and rodent taxa (e.g. Munn 1986; Tamura 1995), use alarm calls to distract others during competitive situations, alleviating some of the costs associated with contest competition for food.

Functionally deceptive signaling is thought to have to be rare and/or have a low cost for the “deceived”, otherwise the signal will simply be ignored and become ineffective (Fitch & Hauser 2002; Searcy & Nowicki 2005). In the current study, RRDAs were quite common, being given at a rate of 0.56 deceptive calls/individual/hr in the experimental feeding contexts. Previous studies have shown that false alarm call rates can exceed the rates in which alarm calls are given in response to real threats and still regularly elicit anti-predator reactions (Munn 1986; Møller 1988). It seems likely that in these cases the cost of being deceived is indeed relatively low (loss of a small amount of food) compared to the cost to not responding to a real threat (potentially death). Call receivers may therefore employ a “better safe than sorry” approach in response to alarm calls (Haftorn 2000) as the cost of being deceived, even on a regular basis, may be less costly than ignoring all calls given in competitive situations.

While these results support a *functionally* deceptive interpretation for the production of false alarms during feeding, it is difficult to prove that this behaviour is *intentionally* deceptive (see Hauser, 1997). A study of the proximate causes of call production would be needed to provide more insight in this regard (Fitch & Hauser 2002). Intentionally deceptive calls would be driven proximately by the cognitive ability to understand the “beliefs” of others (Hauser, 1997). Alternatively, false alarms may be common during feeding because, after having once produced an alarm call in this context, observed the reaction of neighboring conspecifics, and acquired food as a result, individuals associate call production with access to food. While such an explanation requires that individuals learn to associate false alarm production with a food reward, it does not require special cognitive abilities. It is also plausible that call production is driven proximately by physiological mechanisms. Previous work has shown that captive tufted capuchin monkeys who experience high cortisol levels due to chronic stress produce these calls more often than those under less stress (Boinski et al. 1999; see also Bercovitch et al. 1995; Blumstein et al. 2006). Subordinates may experience elevated stress (and increased cortisol levels) when the group is feeding on high quality food resources that are highly clumped in their distribution because dominant individuals can easily exclude subordinates from feeding (e.g. Janson 1985, Koenig et al. 1998). Additional research is needed to confirm if stress is indeed a possible proximate explanation for call production.

ACKNOWLEDGMENTS

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

REFERENCES

Bercovitch, F. B., Hauser, M. D. & Jones, J. H. 1995 The endocrine stress response and alarm vocalizations in Rhesus macaques. *Animal Behaviour* **49**, 1703-1706.

Blumstein, D. T., Patton, M. L. & Saltzman, W. 2006 Faecal glucocorticoid metabolites and alarm calling in free-living yellow-bellied marmots. *Biology Letters* **2**, 29-32.

Boinski, S., Gross, T. S. & Davis, J. K. 1999 Terrestrial predator alarm vocalizations are a valid monitor of stress in captive brown capuchins (*Cebus apella*). *Zoo Biology* **18**, 295-312.

Brown, A. & Zunino, G. 1990 Dietary variability in *Cebus apella* in extreme habitats: evidence for adaptability. *Folia Primatologica* **54**, 187-195.

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

Cheney, D. & Seyfarth, R. 1990 *How Monkeys See the World: Inside the Mind of Another Species*. Chicago: University of Chicago Press.

Dawkins, R. & Krebs, J. 1978 Animal signals: information or manipulation. In *Behavioural Ecology: An Evolutionary Approach* (ed. J. Krebs & N. Davies), pp. 282-309. Oxford: Blackwell Scientific Publications.

Di Bitetti, M.S. 2001 Food associated calls in the tufted capuchin monkey (*Cebus apella*). Ph.D. Dissertation: SUNY Stony Brook.

Di Bitetti, M.S. 2005 Food-associated calls and audience effects in tufted capuchin monkeys, *Cebus apella nigritus*. *Animal Behaviour* **69**, 911-919.

Di Bitetti, M. S. & Janson, C. H. 2001 Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. *Animal Behaviour* **62**, 47-56.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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.

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

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

# of platforms	# of bananas 2-4.9	5-9.9	10-19.9	20-30	total
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

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

Figure legends

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

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

Short title for page headings:

Deceptive alarm calling in capuchins