Kent Academic Repository

Full text document (pdf)

Citation for published version

Wheeler, Brandon C (2010) Decrease in alarm call response among tufted capuchins in competitive feeding contexts: possible evidence for counterdeception. International Journal of Primatology, 31 (4). pp. 665-675. ISSN 0164-0291.

DOI

http://doi.org/10.1007/s10764-010-9419-1

Link to record in KAR

http://kar.kent.ac.uk/54728/

Document Version

Author's Accepted Manuscript

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

The final publication is available at Springer via http://dx.doi.org/10.1007/s10764-010-9419-1

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

Short title: Possible counterdeception in capuchins
Word count: 5,206

Abstract

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

Key words: communication; deception; skeptical responding; antipredator behaviors; New World primates

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

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

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

Observational and experimental protocols

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

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

To record data on alarm call response during competitive feeding situations, I conducted experiments in which the group was provided with bananas cut into 2.5 cm pieces and placed in wooden platforms suspended from tree branches at a height of 3 to 10 m above the ground (additional details of the feeding experiments can be found in Janson 1996, 2007a; Wheeler 2009a). Each experimental site consisted of one to six individual platforms that were placed with at least 15 m separating each platform from all others. At least two sites were set up within the study group's home range each month, and I provided bananas at each site for at least 13 consecutive days each month. During most months, up to two experiments were conducted per day (one at each site); during the austral winter (June-August), eight sites were set up within the group's homerange simultaneously, resulting in as many as eight experiments per day for the current analysis. Banana pieces were placed in the platforms as the group approached the site but before the first individuals arrived. I chose a focal animal opportunistically as the group arrived at the site and followed that individual until all banana pieces had been eaten (usually within 10 minutes of arriving at the site) or the individual was lost. I noted the occurrence of all high-urgency alarm hiccups produced by group members other than the focal individual as well as the focal individual's reaction (or lack thereof) using the same methods and definitions described above for spontaneous high-urgency alarm hiccups produced in natural contexts. In addition, the focal animal's spatial position relative to the feeding platforms was also noted; I scored spatial position as on a feeding platform with food, adjacent to (within 2 m of) a platform with food, or more than 2 m from a platform with food. Because alarm calling was relatively common during the feeding experiments, with multiple alarm calls bouts often being produced during a single experiment, only the first bout of hiccups given during a particular experiment was considered; this reduces the likelihood that focal animals ignored a particular alarm call simply because it was immediately preceded by a similar acoustic stimulus (Zuberbühler *et al*. 1999).

Statistical methods

I tested the effect of context (i.e., natural or experimental) on alarm call response using a within subject logistic regression with the software Stata 10.0. Context was entered as the independent variable, antipredator response (yes or no) as the dependent variable, and individual identity as a fixed-effect. This method was chosen because it takes into account the fact individuals contribute more than one data point and allows for unbalanced data sets (van de Pol and Wright 2009). I ran two separate regressions, one with escape reaction (yes or no) as the dependent variable, and the second with vigilance reaction (yes or no) as the dependent variable. Stata automatically dropped those individuals from the analysis that were not focal animals when alarm calls were given in both of the two contexts or if the individual always employed the same response regardless of the context in which the call was given.

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

Results

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

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

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

Discussion

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

Although the observed differences between contexts support the counterdeception hypothesis, the responses within the competitive feeding contexts did not vary as I predicted in terms of the spatial position of the signal receiver. Specifically, there was little difference between individuals on platforms and those further than 2 m from a platform in the likelihood of a response, while those adjacent to the platforms were the most likely to respond (reacting even more frequently than did individuals in natural contexts). Still, while the observed trend seems to somewhat weaken support for the idea that the capuchins employ counterdeception, it is possible that the methods employed in this study did not take into account a parameter that is likely quite important for receivers in determining how to respond to an alarm call: the distance from the caller to the receiver. Because capuchins in Iguazú tend to detect terrestrial predators from extremely short distances (Janson 2007b), individuals in proximity to the alarm caller are also likely close to the predator (if one is actually present), while individuals at a greater distance from the caller are unlikely to be in immediate proximity to the predator and can therefore afford to ignore alarm calls without putting themselves in immediate danger. Thus which type of response (escape, vigilance, or ignore) is, on average, most beneficial should vary based on the distance to the caller. Because deceptive alarm calls tend to be given by individuals adjacent to the feeding platforms (Wheeler 2009a), individuals on or near the platforms would be more likely than those further from the platforms to be near the caller; this may explain why those adjacent to platforms reacted more often than did those more than 2 m from the platforms. While those individuals on the platforms were probably as likely to be near the caller as those adjacent to the platforms (and thus as likely to be at high risk), the costs of responding to false alarms are higher for those on the platforms since an escape reaction is more likely to result in the loss of resources for individuals within a food patch than for those adjacent to a food patch. The idea that distance to the caller is important is supported by the fact that, from the caller's perspective, 40.0% of deceptive alarm calls caused an escape reaction in at least one neighboring conspecific (Wheeler 2009a), much higher than the 7.6% of focal animals who responded to spontaneous alarm calls in the current study.

The proximate mechanisms underlying the decreased response rate of terrestrial predator-associated alarm calls in the experimental feeding contexts remain unclear and may be explained by at least one of several factors, not all of which fully support the hypothesis that the observed trends are due to counterdeception. First, the calls given in the experimental feeding contexts, despite an overall acoustic similarity, may differ slightly in acoustic structure from the calls given in response to actual predatory threats. The capuchins may be able to (sometimes) cue in on these differences and respond appropriately (Fischer 1998). Acoustic analysis of “honest” and “deceptive” alarms and playbacks of “deceptive” alarms in non-competitive contexts are needed to determine if this is the case. Second, whether or not acoustic variation exists, calls given in the experimental feeding contexts may be less likely to elicit reactions that those given in nonfeeding contexts because receivers are more “skeptical” of the former (Smith 1986; Gouzoules and Gouzoules 2002). Such skepticism could be due to the perceived unreliability of the calling individual (Cheney and Seyfarth 1988; Hare and Atkins 2001), but because the identity of callers was unknown in most cases, this cannot yet be tested. However, because subordinate individuals are far more likely to produce false alarm calls during these experiments than are dominants (Wheeler 2009a), and greater skepticism of alarm calls given by subordinate individuals relative to dominants has been previously demonstrated in captive rhesus macaques (*Macaca mulatta*) (Gouzoules *et al*. 1996), it is possible that the observed trends in the current study are due to skepticism of antipredator signals given by subordinates. A second possible factor which could drive skeptical responding is the behavioral context in which the call is produced. Several studies have demonstrated that the context in which a particular signal is produced can affect receiver responses (Rendall *et al*. 1999; Fischer and Hammerschmidt 2001; Tibbetts 2008). In the current case, receivers may be skeptical of alarm calls produced during competitive feeding situations, with or without taking caller identity or acoustic characteristics of the call into account, since false alarms are more likely to be given in this context than in noncompetitive situations. Finally, receivers may be less likely to respond to signals in general, not just terrestrial predator-associated alarm calls specifically, in competitive contexts due to greater attention being given to competitive task (see also Randler 2005). If this does indeed explain the observed trends, then the decrease in alarm call response would arguably not be counterdeceptive, but perhaps part of a broader adaptive strategy to reduce the likelihood of being distracted (even by reliable signals) while engaged in a competitive situation. The fact that individuals on platforms reacted less often to alarm calls than did those immediately outside the platforms lends some support to this idea, but it is less supported by the fact that even those individuals not in the immediate vicinity of a platform rarely responded to alarm calls given during the feeding experiments. Playback experiments of alarm barks, which more reliably indicate the presence of an aerial predator than hiccups do a terrestrial predator (Wheeler in press), during the feeding experiments may give an indication of whether or not even typically reliable signals are also more likely to be ignored in this context. Whatever proximate mechanism underlies the observed trend, a decreased response rate to alarm signals in competitive contexts seems likely to ultimately function to reduce the costs of being distracted in competitive contexts, but determining whether or not the behavior is truly counterdeceptive (i.e., a direct result of the "deceptive" uses of the hiccups) requires additional research.

Acknowledgements

I owe a large debt of gratitude to Charles Janson, whose work developing platform experiments with the study group made this project possible. Andreas Koenig and Charles Janson provided much helpful advice and support during all phases of this project. Fruitful discussion was also provided by Sue Boinski, Mario Di Bitetti, Julia Fischer, John Fleagle, and Barbara Tiddi. Barbara Tiddi and Gabriele Schino also provided helpful statistical advice. Several anonymous reviewers provided helpful comments on a previous draft of this manuscript. I am extremely grateful to the Delegación Tecnica of the Argentine Administration of National Parks for permission to conduct research in the park, and to the Centro Investigaciones Ecológicas Subtropicales for support and permission to live in the park. Thanks are due to many for assistance in the field, especially Eugenia Acevedo, Mariana Bischoff, Peter Cooper, Eugenia di Sorrentino, Rocio Prieto Gaona, Fermino Silva, Barbara Tiddi, and Eugenia Vidal. Financial support was provided by the American Society of Primatologists, the Wenner-Gren Foundation (grant no. 7244), and the National Science Foundation (DDIG # 0550971). Pilot work was supported by grants to Charles Janson (NSF BCS-0515007 and a grant from the National Geographic Society Committee on Research and Exploration). The protocols used in this study received IACUC approval from Stony Brook University (ID numbers 2005-1448 and 2006-1448) and complied with all applicable laws of the United States and Argentina.

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.

Di Bitetti, M. S., Vidal, E. M. L., Baldovino, M. C., & Benesovsky, V. (2000). Sleeping site preference in tufted capuchin monkeys (*Cebus apella nigritus*). *American Journal of Primatology*, *50*, 257-274.

Fischer, J. (1998). Barbary macaques categorize shrill barks into two call types. *Animal Behaviour*, *55*, 799-807.

Fischer, J., & Hammerschmidt, K. (2001). Functional referents and acoustic similarity revisited: the case of Barbary macaque alarm calls. *Animal Cognition*, *4*, 29-35.

Fragaszy DM, Visalberghi E, Fedigan LM. (2004). *The Complete Capuchin: The Biology of the Genus* Cebus. Cambridge: Cambridge University Press.

Gouzoules, H., & Gouzoules, S. (2002). Primate communication: by nature honest, or by experience wise? *International Journal of Primatology*, *23*, 821-848.

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

Hanson, M., & Coss, R. (2001). Age differences in the response of California ground squirrels (*Spermophilus beecheyi*) to conspecific alarm calls. *Ethology*, *107*, 259-275.

Hare, J. F., & Atkins, B. A. (2001). The squirrel that cried wolf: reliability detection by juvenile Richardson's ground squirrels (*Spermophilus richardsonii*). *Behavioral Ecology and Sociobiology*, *51*, 108-112.

Hauser, M. (1996). *The Evolution of Communication*. Cambridge, Mass.: MIT 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. (1996). Toward an experimental socioecology of primates. In M. A. Norconk, A. L. Rosenberger & P. A. Garber (Eds.), *Adaptive Radiations of Neotropical Primates*. (pp.

309-325). New York: Plenum Press.

Janson, C. H. (2007a). Experimental evidence for route integration and strategic planning in wild capuchin monkeys. *Animal Cognition*, *10*, 341-356.

Janson, C. H. (2007b). Predator detection and the evolution of primate sociality: insights from experiments on a rain forest primate. *American Journal of Physical Anthropology*, *S44*, 136.

Koenig, A., & Borries, C. (2006). The predictive power of socioecological models: a reconsideration of resource characteristics, agonism, and dominance hierarchies. In G. Hohmann, M. M. Robbins & C. Boesch (Eds.), *Feeding Ecology in Apes and Other Primates: Ecological, Physical and Behavioral Aspects*. (pp. 263-284). New York: Cambridge University Press.

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

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

Ramakrishnan, U., & Coss, R. (2000). Age differences in the responses to adult and juvenile alarm calls by bonnet macaques (*Macaca radiata)*. *Ethology*, *106*, 131-144.

Randler, C. (2005). Coots *Fulica atra* reduce their vigilance under increased competition. *Behavioural Processes, 68*, 173-178.

Rendall, D., Owren, M. J., & Ryan, M. J. (2009). What do animal signals mean? *Animal Behaviour, 78,* 233-240.

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.

Zuberbühler, K., Cheney, D.L., & Seyfarth, R.M. (1999). Conceptual semantics in a nonhuman primate. *Journal of Comparative Psychology*, *113*, 33-42.

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.

Figure 1

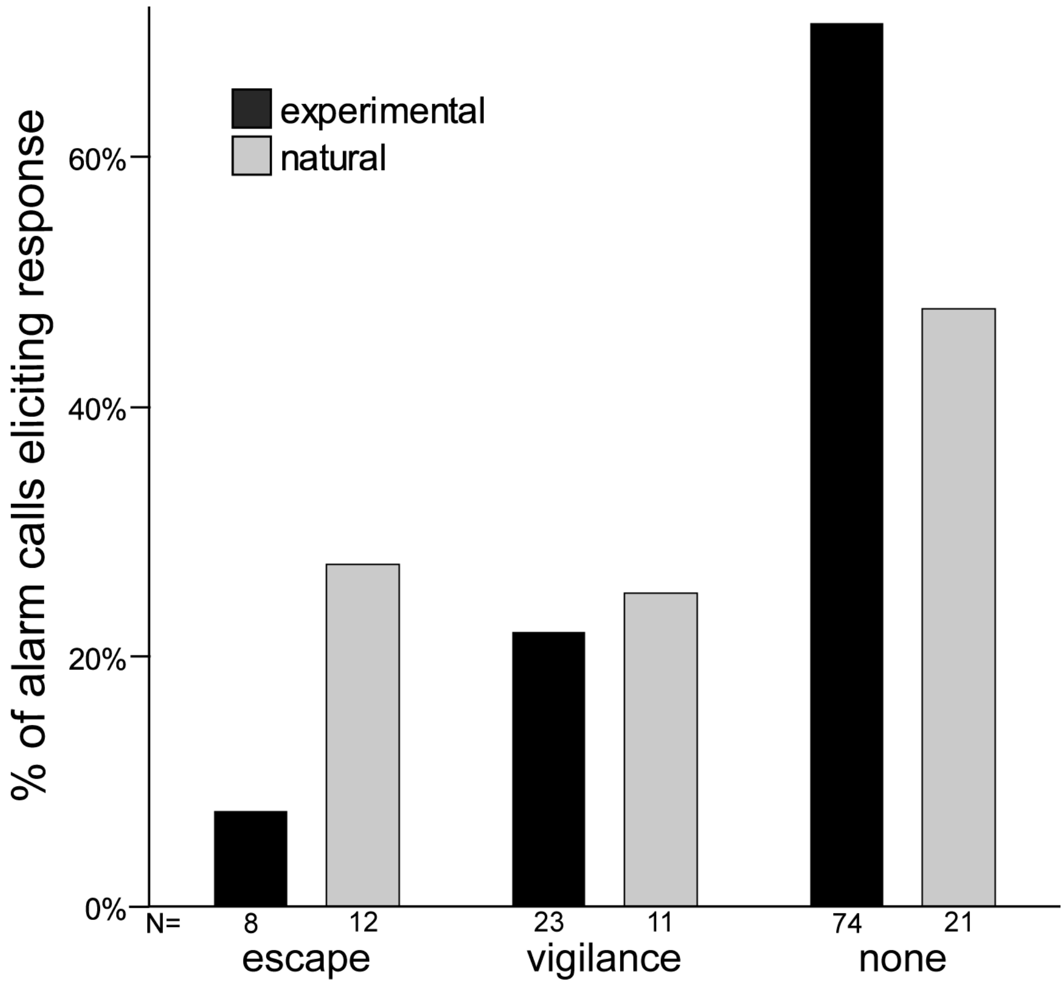
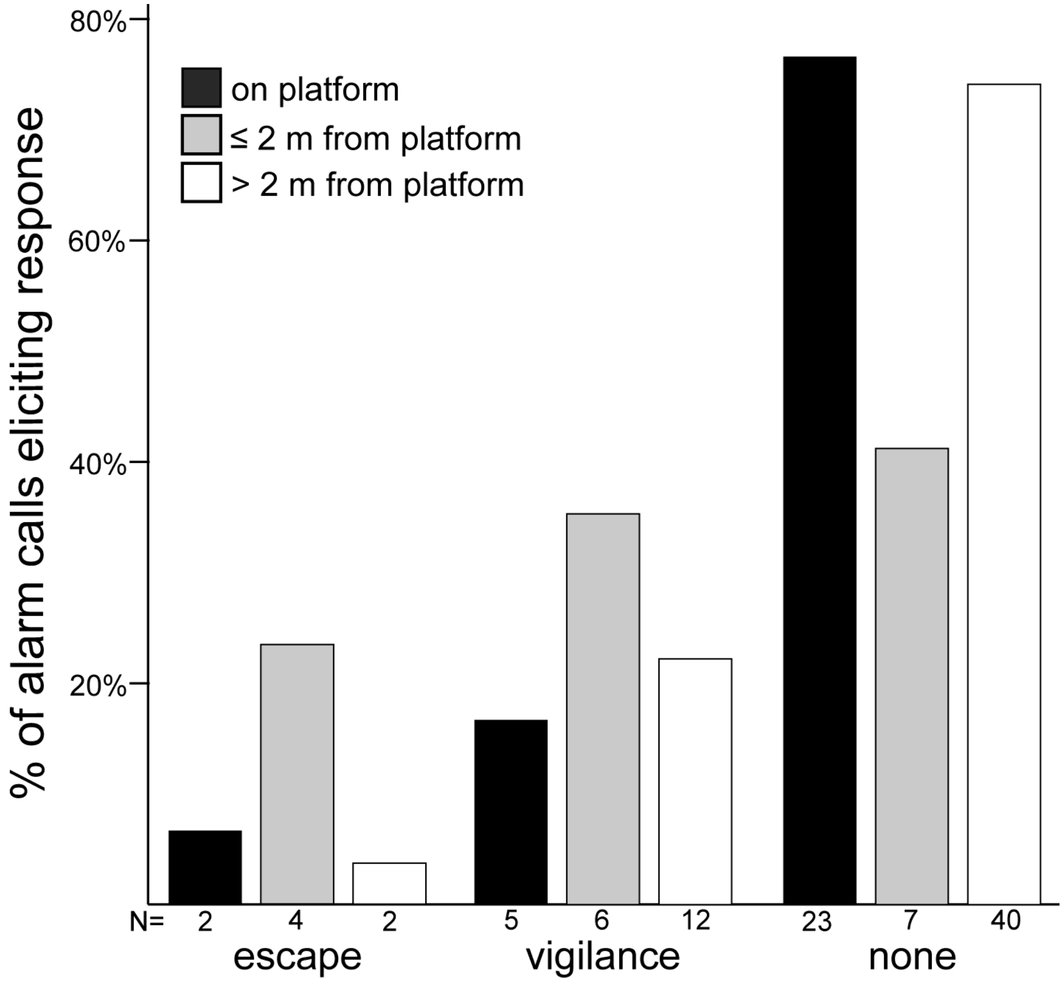

% of alarm calls eliciting response
60%
40%
20%
0%
experimental
natural
N=
8
12
23
11
74
21
escape
vigilance
none

Figure 2



% of alarm calls eliciting response
80%
60%
40%
20%
on platform
≤ 2 m from platform
> 2 m from platform
N=
2
4
2
5
6
12
23
7
40
escape
vigilance
none