



## Competition-induced stress does not explain deceptive alarm calling in tufted capuchin monkeys



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Tactical deception has long attracted interest because it is often assumed to entail complex cognitive mechanisms. However, systematic evidence of tactical deception is rare and no study has attempted to determine whether such behaviours may be underpinned by relatively simple mechanisms. This study examined whether deceptive alarm calling among wild tufted capuchin monkeys, *Cebus apella nigrinus*, feeding on contestable food resources can be potentially explained by a physiological mechanism, namely increased activation in the adrenocortex and the resulting production of glucocorticoids (GCs; 'stress hormones'). This was tested experimentally in Iguazú National Park, Argentina, by manipulating the potential for contest competition over food and noninvasively monitoring GC production through analysis of faecal hormone metabolites. If deceptive false alarms are indeed associated with adrenocortical activity, it was predicted that the patterns of production of these calls would match the patterns of GC output, generally being higher in callers than noncallers in cases in which food is most contestable, and specifically being higher in callers on those occasions when a deceptive false alarm was produced. This hypothesis was not supported, as (1) GC output was significantly lower in association with the experimental introduction of contestable resources than in natural contexts wherein the potential for contest is lower, (2) within experimental contexts, there was a nonsignificant tendency for noncallers to show higher GC output than callers when food was most contestable, and (3) individuals did not show higher GC levels in cases in which they produced deceptive alarms relative to cases in which they did not. A learned association between the production of alarms and increased access to food may be the most likely cognitive explanation for this case of tactical deception, although unexplored physiological mechanisms also remain possible.

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The well-documented relationship between social group size and the size of the brain generally and the neocortex specifically has lent widespread support for the so-called social brain hypothesis (Dunbar & Shultz, 2007; Dunbar, 1998; but see Barton, 2012). While there are a number of reasons why individuals with larger brains may be favoured in highly social environments, the Machiavellian intelligence hypothesis (MIH) posits that larger brains are advantageous for social animals specifically because increased cognitive abilities allow individuals to outwit their groupmates in the competitive interactions that are a near-

universal result of group living (Byrne & Whiten, 1988). In particular, the MIH predicts tactical deception, that is 'acts from the normal repertoire of the agent, deployed such that another individual is likely to misinterpret what the acts signify, to the advantage of the agent' (Byrne & Whiten, 1990, p. 3), to be common among large-brained, social taxa, especially primates.

In support of the MIH, there have been many anecdotal observations of apparent tactical deception in a wide range of anthropoid primates (Byrne & Whiten, 1990), with more such anecdotal observations reported for taxa with a larger neocortex ratio (Byrne & Corp, 2004). Unfortunately, the anecdotal nature of these observations has hampered systematic investigation into the proximate mechanisms underpinning the behaviours. It is thus unclear whether these observations of tactical deception are examples of flexibly deployed behaviours underpinned by an intention to

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change the targets' behaviour or beliefs (and thus involving, respectively, first- or second-order intentionality; see Shettleworth, 2010) as the MIH would predict. Alternatively, such apparently complex behaviours may involve zero-order intentionality (i.e. nonintentional; see Shettleworth, 2010) and be better explained as rather inflexible and innate responses to external stimuli mediated, for example, by hormonal states (e.g. see Bshary et al., 2011).

Systematic examination of the proximate mechanisms underlying tactical deception has been complicated by the rarity of such behaviours, a consequence of the fact that tactical deception deployed too frequently is likely to be ignored, reducing its effectiveness (Johnstone & Grafen, 1993; Maynard Smith & Harper, 2003). Antipredator communication systems, however, are vulnerable to high rates of functionally deceptive signalling because the cost of ignoring a signal that honestly indicates the presence of a predator is potentially death, outweighing the costs of responding to deceptive false alarms (Searcy & Nowicki, 2005). Indeed, an increasing number of studies across a range of taxa, including passerine birds, ungulates, sciurid rodents and primates, have provided systematic evidence that false alarm signals given in competitive feeding and mating contexts function to provide the signaller with a tactical advantage by eliciting unnecessary antipredator behaviours in receivers (Bro-Jørgensen & Pangle, 2010; Flower, 2011; Møller, 1988; Munn, 1986; Tamura, 1995; Wheeler, 2009). However, while these studies show that functionally deceptive antipredator signals can occur frequently enough to be examined systematically, no study to date has attempted to directly examine the underlying proximate mechanisms.

Tufted capuchin monkeys, *Cebus apella nigrinus* (synonymous with *Sapajus nigrinus*), have been shown to produce terrestrial predator-associated alarm calls ('hiccups') in competitive feeding contexts, but in the absence of predators, in a manner that is consistent with an interpretation of tactical deception (Wheeler, 2009). Specifically, these alarm calls, which are acoustically indistinguishable from alarms elicited by predatory stimuli (Wheeler & Hammerschmidt, 2013), are given far more often in experimental feeding contexts wherein high-value foods are presented in discrete, contestable patches than they are in natural contexts (Wheeler, 2010a). The interpretation of these as tactical deception is supported by the fact that listeners commonly run higher into the canopy and out of the food patch, while callers do not show such predator evasion behaviours, but instead move into the food patch (Wheeler, 2009). Furthermore, these spontaneously produced alarm calls tend to be given by relatively low-ranking individuals sitting in the immediate vicinity of the food patch, and they occur most often when food is highly clumped, and therefore easily contested and monopolized by dominants (Janson, 1996; Wheeler, 2009). These systematic observations indicate that false alarm calls function to deceive more dominant competitors, and suggest this as an ideal system to examine the proximate mechanisms underpinning the behaviour.

While at least superficially providing support for the MIH, functionally deceptive alarm calling among capuchins might be better explained as a relatively inflexible behaviour mediated by emotional mechanisms and their hormonal correlates than by the more cognitively complex mechanisms (e.g. reasoning or learning) necessary for first- or second-order intentionality. Such a 'simple' explanation in fact appears likely in this case given that vocal production in nonhuman primates (and most other terrestrial mammals) is generally rather inflexible in terms of the contexts in which a given call can be produced, resulting from an innate relationship between a particular call type and underlying internal states (e.g. Hammerschmidt & Fischer, 2008; Owren, Dieter, Seyfarth, & Cheney, 1992; Seyfarth & Cheney, 2010; Wheeler & Fischer, 2012). Encounters with predators are known to cause

activation of the adrenocortex and an associated increase in the production of glucocorticoids (GCs; 'stress hormones') in many prey taxa (e.g. Arlet & Isbell, 2009; Clinchy, Sheriff, & Zanette, 2013; Cockrem & Silverin, 2002; Mateo, 2010; Monclús, Rödel, Palme, Von Holst, & de Miguel, 2006). Likewise, several studies of primates and other mammals, including capuchins, have demonstrated a positive relationship between circulating GC levels and rates of production of vocalizations associated with terrestrial predators (Blumstein, Patton, & Saltzman, 2006; Boinski, Gross, & Davis, 1999; Cross & Rogers, 2006; see also Fichtel & Kappeler, 2002; Mateo, 2010), with one such study suggesting a causal relationship in macaques (Bercovitch, Hauser, & Jones, 1995). Furthermore, a study of captive bonobos, *Pan paniscus*, has shown that adrenocortical activity can also be affected by food distribution, with higher GC levels seen when food is clumped relative to when it is dispersed (Hohmann, Mundry, & Deschner, 2009). Given that the intensity of contest competition (i.e. dominance rank-based skew in energy gain) is well documented to increase with food clumpiness in social foragers (reviewed in Koenig, 2002; Wheeler, Scarry, & Koenig, 2013), competition for clumped foods might be expected to elicit a stronger stress response in relatively lower-ranking individuals (Foerster & Monfort, 2010; see also Abbott et al., 2003). It is thus plausible that the use of deceptive false alarms in capuchins and other animals (e.g. Bro-Jørgensen & Pangle, 2010; Møller, 1988; Munn, 1986) results from an underlying relationship between GCs and the propensity to produce predator-associated calls.

This study aimed to test whether variation in GC production indeed provides a plausible proximate explanation for the documented deceptive alarm-calling behaviour of tufted capuchin monkeys. If this is the case, then the patterns of GC production should match the patterns of false alarm production, with individuals that produce more false alarm calls in particular contexts showing higher GC levels in those contexts than individuals that produce fewer deceptive calls. We thus predicted that, relative to individuals who do not produce deceptive false alarms, individuals with a higher propensity to give deceptive calls should show higher GC output in association with (1) experimental contexts in which resources are presented in contestable patches than in natural contexts wherein the potential for contest competition is reduced, and (2) experimental contexts in which food is highly clumped (and contestable) than in experimental contexts in which food is relatively dispersed (and therefore less contestable). Last, we predicted that (3) on those specific occasions in which individuals produced deceptive false alarms, GC levels would be higher than on occasions in which no alarms were given. Although support for these predictions would not necessarily indicate a causal relationship between the production of GCs and deceptive false alarms, nor rule out the possibility that the production of false alarms is a result of physiological stress working in conjunction with cognitive mechanisms (see Mateo, 2008; Soares et al., 2010), a lack of support would in effect rule out the possibility that high GC levels are a necessary precondition for the production of these calls. Direct tests of the relationship between GC levels and deceptive false alarm call production are thus an important first step in narrowing down the possible proximate explanations for this example of tactical deception.

## METHODS

### *Study Site and Subjects*

Data were collected from June to August 2010 and June to August 2011 in Iguazú National Park in northeastern Argentina (25°40'S, 54°30'W). The site is part of the South American Atlantic

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