



## Feeling anxious? The mechanisms of vocal deception in tufted capuchin monkeys



Donna Kean <sup>a, b, \*</sup>, Barbara Tiddi <sup>c, d</sup>, Martin Fahy <sup>e</sup>, Michael Heistermann <sup>f</sup>,  
Gabriele Schino <sup>g</sup>, Brandon C. Wheeler <sup>a, c</sup>

<sup>a</sup> School of Anthropology & Conservation, University of Kent, Canterbury, U.K.

<sup>b</sup> Behaviour and Evolution Research Group, Department of Psychology, School of Natural Sciences, University of Stirling, Stirling, U.K.

<sup>c</sup> Cognitive Ethology Laboratory, German Primate Center, Göttingen, Germany

<sup>d</sup> Department of Behavioral Ecology, Johann-Friedrich-Blumenbach Institute for Zoology and Anthropology, Georg-August Universität Göttingen, Göttingen, Germany

<sup>e</sup> CERCOPAN Nigeria, Calabar, Cross River State, Nigeria

<sup>f</sup> Endocrinology Laboratory, German Primate Center, Göttingen, Germany

<sup>g</sup> Istituto di Scienze e Tecnologie Della Cognizione, Consiglio Nazionale Delle Ricerche, Rome, Italy

### ARTICLE INFO

#### Article history:

Received 25 October 2016

Initial acceptance 21 November 2016

Final acceptance 12 May 2017

MS. number: 16-00935R

#### Keywords:

affect  
alarm calls  
anxiety  
deceptive behaviour  
emotions  
primates  
scratching  
self-directed behaviours  
vocalizations  
within-group contest competition

An ability to deceive conspecifics is thought to have favoured the evolution of large brains in social animals, but evidence that such behaviours require cognitive complexity is lacking. Tufted capuchin monkeys (*Sapajus* spp.) have been documented to use false alarm calls during feeding in a manner that functions to deceive competitors. However, comparative evidence suggests that the production of vocalizations by nonhuman primates is largely underpinned by emotional mechanisms, calling into question more cognitive interpretations of this behaviour. To determine whether emotional states are plausibly necessary and sufficient to proximately explain deceptive alarm call production, we examined the association between self-directed behaviours (SDBs), as a proxy for anxiety, and the production of spontaneous false alarm calls among tufted capuchins. Specifically, we predicted that if anxiety is necessary for the production of false alarms, then individuals that produce spontaneous false alarms should exhibit more SDBs in those contexts in which they call. If anxiety is also sufficient to explain the false alarm call production, then we predicted that individuals that call more in a given context would show higher rates of SDBs in that context, and that high rates of calling would be temporally associated with high rates of SDBs. Our results support the contention that states of anxiety are necessary for an individual to spontaneously produce false alarms, but that such states are not sufficient to explain patterns of calling. The link between anxiety and deceptive calling thus appears complex, and cognitively based decision-making processes may play some role in call production.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Vocal production and usage in most nonhuman terrestrial mammals and other nonvocal learning taxa is thought to be underpinned by largely emotional mechanisms (Hammerschmidt & Fischer, 2008). In contrast to linguistic utterances, but similar to human emotional vocalizations such as spontaneous laughter and crying, the production of specific call types in these taxa apparently cannot be decoupled from their associated affective states (Bryant & Aktipis, 2014; Fitch & Zuberbühler, 2013; Owren, Amoss, & Rendall, 2011; Wheeler & Fischer, 2012). This

contention is supported by neurobiological evidence (Hammerschmidt & Fischer, 2008) and the fact that not only vocal repertoires but also the general contexts of call usage appear to be largely hardwired and species-specific in these species (Seyfarth & Cheney, 2010; Wheeler & Fischer, 2012). Despite the apparent biological constraints that limit an individual's ability to choose in which context to produce a particular call type, some neurobiological and behavioural evidence suggests that nonhuman primates may have, in at least certain cases, some degree of voluntary control over whether or not to produce a call when in the associated state (Hammerschmidt & Fischer, 2008; Seyfarth & Cheney, 2010; Townsend, Rasmussen, Clutton-Brock, & Manser, 2012; Wheeler & Fischer, 2012). Based on this evidence, it seems that certain

\* Correspondence: D. Kean, Psychology, Faculty of Natural Sciences, Cottrell Building, University of Stirling, Stirling FK9 4LA, U.K.

E-mail address: [donna.e.kean@gmail.com](mailto:donna.e.kean@gmail.com) (D. Kean).

emotional states are necessary for a given call to be produced, but it is less clear when such states are (or are not) also sufficient to explain whether individuals produce that call in a given situation.

A number of recent behavioural studies, however, have demonstrated that vocal production and usage in primates and some other terrestrial mammals is more flexible than previously appreciated (e.g. with evidence for learning of appropriate call usage or complex audience effects; Chow, Mitchell, & Miller, 2015; Crockford, Wittig, Mundry, & Zuberbühler, 2012), leading some authors to argue that call production may not in fact be as closely linked with current emotional states as the evidence above suggests (Mazzini, Townsend, Virányi, & Range, 2013; Schel, Machanda, Townsend, Zuberbühler, & Slocombe, 2013; Watson et al., 2015b). Even in these cases of apparent flexibility, however, it remains plausible that particular emotional mechanisms are necessary and indeed even sufficient for individuals to engage in the observed behaviour (e.g. Fischer, Wheeler, & Higham, 2015), although a lack of evidence indicative of the emotional states of signallers makes it difficult to determine how likely such explanations are (Watson et al., 2015a).

One example of vocal communication in a nonhuman primate that may be indicative of flexible production and a lack of strict association with concurrent affective states is the use of terrestrial predator-associated alarm calls ('hiccups'; see Wheeler, 2010) by tufted capuchin monkeys, *Sapajus nigritus*, outside of predatory contexts (Wheeler, 2009). Here, lower-ranking capuchins give false alarm calls far more often when contestable foods are experimentally presented than in other contexts, and do so more often when food is more clumped and therefore more easily monopolized by high-ranking group members. Listeners sometimes respond to these calls with antipredator escape reactions, thereby increasing the caller's opportunity to access the contested resource. This vocal behaviour is thus consistent with an interpretation of functional or tactical deception (hereafter 'deception'; Hauser, 1996; Whiten & Byrne, 1988). Such behaviours are predicted by the Machiavellian intelligence hypothesis, which argues that an ability to outwit group-mates in competitive interactions favoured increased encephalization in primate evolution (Whiten & Byrne, 1988). However, to be described as 'Machiavellian' would seem to require that deceptive calling is intentional insofar as individuals performing the behaviour have the goal to change at least the behaviour (if not the beliefs) of receivers (Dennett, 1983; Shettleworth, 2010; see also Liebal, Waller, Slocombe, & Burrows, 2013 for a recent review of intentionality in communication, including suggested criteria for diagnosing intentionality). Whether deceptive calling in this case is indeed intentional or is instead an unintentional behaviour that is nonvolitionally elicited by certain emotional states is not clear. A plausible alternative explanation to intentional production is that relatively low-ranking individuals involved in direct competition with high-ranking conspecifics experience an emotional state that spontaneously elicits hiccup alarm calls. Indeed, it has been shown that elevated physiological stress is associated with increased hiccup production in captive capuchins (Boinski, Gross, & Davis, 1999), although a previous attempt to test whether stress may underpin deceptive false alarm production found no support for the prediction that calling is associated with higher glucocorticoid (GC) hormone levels (Wheeler, Tiddi, & Heistermann, 2014). While the latter study apparently rules out the possibility that GCs play a causal role in the production of deceptive false alarms, it is possible that the discrepancy between the studies stems from the fact that GC levels vary with factors other than emotional states (Wheeler et al., 2014).

Of particular relevance for the relationship between GCs, emotions and deceptive vocalizations may be the relationship between

anxiety and the physiological stress response. The mammalian stress response consists of two distinct components (Sapolsky, 2002). First, the sympathetic nervous system triggers secretion of catecholamines (e.g. adrenaline) almost instantaneously after perception of the stressor. Second, the peripheral stress response involving the hypothalamus, pituitary and adrenal gland results in secretion of GCs within minutes. However, these two stages of the stress response do not necessarily need to co-occur (Frankenhaeuser & Lundberg, 1985), as attempts to actively cope with a stressor potentially increase catecholamine production and suppress that of GCs. It has been suggested that one way in which individuals attempt to cope with stressors is through displacement activities (e.g. Pico-Alfonso et al., 2007), such as self-scratching and other self-directed behaviours (SDBs). Indeed, the relationship between SDBs and anxiety has been convincingly documented (see Coleman & Pierre, 2014; Maestriperi, Shino, Aureli, & Troisi, 1992; Troisi, 2002) through experiments that show that pharmacological inhibition of anxiety results in a decrease in these behaviours (e.g. Barros, Boere, Huston, & Tomaz, 2000; Schino, Perretta, Tagliani, Monaco, & Troisi, 1996), supplemented by numerous studies showing that SDBs increase in situations in which individuals can reasonably be inferred to be experiencing anxiety (e.g. Aureli, 1992; Kutsukake, 2003; Manson & Perry, 2000). Evidence that this may be a coping strategy comes from studies showing that displacement activities are associated with a reduced peripheral stress response (Hennessy & Foy, 1987; Levine, Coe, & Wiener, 1989; Watson, Ward, Davis, & Stavisky, 1999) and increased endorphin production (Cronin, Wiepkema, & Van Ree, 1986) in nonhuman mammals (see also Berridge, Mitton, Clark, & Roth, 1999; Mohiyeddini & Semple, 2013; Pico-Alfonso et al., 2007). For this reason, measurement of GCs may be a poor indicator of the emotional state of anxiety (see also Higham, MacLarnon, Heistermann, Ross, & Semple, 2009; Tkaczynski, MacLarnon, & Ross, 2014; Ulyan et al., 2006), which is instead better measured by SDBs.

This study aimed to determine whether states of anxiety, as measured by self-scratching behaviour, are plausibly necessary and sufficient to explain patterns of spontaneous false alarm call production in tufted capuchins. Because a previous study indicated no relationship between GCs and the production of deceptive false alarms (Wheeler et al., 2014), we initially tested whether self-scratching and GCs are unrelated in our wild population, before moving on to our two main questions. First, if anxiety is necessary for the production of spontaneous false alarms, then anxiety should be elevated in those contexts in which such calls are given, relative to baseline levels. Specifically, we predicted that (1) among those individuals in the wild population observed to give deceptive false alarms, levels of self-scratching will be higher in association with experimental contexts in which resources are presented in contestable patches relative to natural conditions wherein the potential for contest competition is reduced. Second, if anxiety is also sufficient to explain spontaneous false alarm production, then variation in calling within and between individuals should be matched with similar variation in anxiety. We thus predicted that, across all wild subjects, those individuals with a greater propensity to produce false alarms in a given condition (2a: experimental versus natural conditions; 2b: clumped versus dispersed conditions) would tend to show greater increases in self-scratching in those conditions relative to those that showed little or no difference in calling behaviour across conditions. Finally, we predicted that (2c) higher rates of spontaneous call production would be temporally associated with higher rates of self-scratching in the captive subjects if anxiety is both necessary and sufficient to explain false alarm production. Investigating these relationships is key to ascertaining the proximate factors underlying deceptive alarm calling among tufted capuchins.

Download English Version:

<https://daneshyari.com/en/article/5538404>

Download Persian Version:

<https://daneshyari.com/article/5538404>

[Daneshyari.com](https://daneshyari.com)