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

Donna E. Kean[a,b,*] , Barbara Tiddi[c,d], Martin Fahy[e], Michael Heistermann[f], Gabriele Schino[g], Brandon C. Wheeler[a,c]

[a] School of Anthropology & Conservation, University of Kent, Canterbury, United Kingdom.

[b] Behaviour and Evolution Research Group, Department of Psychology, School of Natural Sciences, University of Stirling.

[c] Cognitive Ethology Laboratory, German Primate Center, Göttingen, Germany.

[d] Department of Behavioral Ecology, Johann-Friedrich-Blumenbach Institute for Zoology and Anthropology, Georg-August Universität Göttingen, Göttingen, Germany.

[e] CERCOPAN Nigeria, Calabar, Cross River State, Nigeria.

[f] Endocrinology Laboratory, German Primate Center, Göttingen, Germany.

[g] Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche, Rome, Italy.

* Corresponding author: Donna Kean, email: donna.e.kean@gmail.com, postal address: Psychology, Faculty of Natural Sciences, Cottrell Building, University of Stirling, Stirling, FK9 4LA, UK

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Abstract

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 vocalisations 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. 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.

Keywords: Affect, Alarm calls, Anxiety, Emotions, Deceptive behaviour, Primates, Scratching, Self-directed behaviours, Vocalisations, Within group contest competition

Vocal production and usage in most non-human terrestrial mammals and other non-vocal learning taxa is thought to be underpinned by largely emotional mechanisms (Hammerschmidt & Fischer, 2008). In contrast to linguistic utterances, but similar to human emotional vocalisations 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 particular 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 an individual produces 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 feeding on contestable foods than in other contexts, and do so more often when food is more clumped and therefore more easily monopolised by high-ranking group members. Listeners sometimes respond to these calls with anti-predator 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 non-volitionally elicited by particular 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 which 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 based on additional factors other than emotional states (*ibid.*).

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; Maestripieri, Shino, Aureli, & Troisi, 1992; Troisi, 2002) through experiments which show that pharmacological inhibition of anxiety results in a decrease of these behaviours (e.g. Barros, Boere, Huston, & Tomaz, 2000; Schino, Perretta, Taglioni, 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 et al., 1986) in non-human 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 aims 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 if self-scratching and GCs are in fact 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 vs natural conditions; 2b: clumped vs 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.

METHODS

Study Sites and Subjects

To test the relationship between GCs and self-scratching and Predictions 1, 2a and 2b (those related to the effects of feeding competition on SDBs), we collected data from wild black capuchin monkeys (*Sapajus nigritus*; taxonomically synonymous with *Cebus apella nigritus*) in Iguazú National Park, Argentina (25°40’S, 54°30’W) from June to August 2011. Prediction 2c (that SDBs and spontaneous alarm production would be temporally related) was tested with a captive population of tufted capuchins (*Sapajus* spp.; taxonomically synonymous with *Cebus apella*) housed at the Institute of Cognitive Sciences and Technologies (ISTC-CNR), in Rome, Italy (Lucarelli et al., in press). Tufted capuchins are medium-sized New World monkeys that are highly arboreal and feed primarily on fruits and insects in the wild (Fleagle, 2013). They typically live in multi-male, multi-female groups of

7-45 individuals characterized by female philopatry and male dispersal (Janson, Baldovino, & Di Bitetti, 2012). Groups show mixed-sex linear dominance hierarchies, including a highly despotic alpha male, with dominant individuals having priority of access to preferred (central) spatial positions and contestable food resources (Di Bitetti & Janson, 2001; Janson, 1996; Janson et al., 2012). Further information on the behaviour, ecology, and social system of the study population can be found in Janson et al. (2012).

Iguazú National Park is part of the Upper Paraná Atlantic Forest and is characterized by a humid, subtropical climate with seasonal variation in temperature (Janson et al., 2012). Data were collected during the austral winter when fruits and insects, the preferred foods of capuchins, are relatively scarce (Brown & Zunino, 1990), allowing us to experimentally manipulate the contestability of preferred foods (Janson, 1996). Data for this study came from one wild group (the Rita group) in Iguazú comprising 18 individuals including four adult males (plus one additional male that joined a neighbouring group at the beginning of the study and is not included in any analyses), five adult females, four juvenile males, and five infants. The group was well habituated to both the presence of human observers and to the experimental setup described below (Janson et al., 2012; Wheeler et al., 2014).

The portion of the study conducted with captive capuchins included ten subjects split evenly between two groups that were housed in separate adjacent enclosures. Both enclosures consisted of two adjoining indoor areas (approx. $24.5m^3$) and a single outdoor area (group 1 = 106.5 m^3, group 2 = 127.4 m^3). The outdoor areas were equipped with environmental enrichment in the form of ropes, platforms, slides, tree trunks and wood chip flooring, while the indoor areas included slides and platforms. The subjects were fed a mixture of fruit, vegetables, and carbohydrates once daily, and water was provided *ad libitum*. The observations did not interfere with any of the subjects' eating, drinking or activity regimes. Group 1 included three adult males, and two adult females. Group 2 included one adult male, three adult females, and one juvenile male. Although the group sizes were small compared to wild groups, there was a clear alpha male, and there were no apparent changes in the dominance hierarchy during or in the eleven months prior to the study period (Schino, pers. obs).

Experimental Manipulation of Food Contestability

To determine whether self-scratching varies based on competitive contexts and caller type, we conducted observations on the wild subjects in Iguazú in experimental contexts in which contest competition over food was elicited through controlled provisioning. Provisioning experiments used a high-value food (eight bananas cut into approximately 2-3 cm pieces) placed in wooden platforms measuring ca. 1 m x 1 m that were suspended from tree branches by a system of ropes and pulleys at a height of 3 – 10 m above the ground. Platforms were anchored to the ground for stability, and most subjects were accustomed (or quickly habituated) to feeding on these substrates due to long-term research at the site using similar methods (Janson et al., 2012); it is thus unlikely that the use of platforms itself induced anxiety.

Five experimental sites (artificial food patches) were set up within the study group's home range at the beginning of the study period, with each site being separated from the others by at least 250 m (see Janson, 1998 for an example map). Within each site, we set up four platforms placed 10 to 20 m apart in order to both maintain group cohesion and ensure that a single individual could not monopolize more than a single platform at a given time (see Janson, 1996). Bananas were provided at each of the five sites only once per day, with baited platforms being raised as the group approached a site; in cases in which a small subgroup approached a site without the majority of the group, we waited until the majority approached to raise the platforms.

While use of the provisioning platforms to create artificial food patches generally incites higher levels of contest competition than typically occurs in natural, non-provisioning contexts (see Wheeler et al., 2014), we elicited higher and lower levels of contest by varying the number of platforms in which food was provided. In the clumped (high contest) condition, the banana pieces were distributed across one or two platforms, while four platforms were used in the dispersed (low contest) condition. In order to accommodate the testing of additional hypotheses (see Wheeler et al., 2014), the same condition (e.g. clumped) was used at all five sites for several consecutive days (normally 10 days), followed by several days without provisioning, which was in turn followed by a period with the alternate provisioning condition (e.g. dispersed) relative to the previous one used. Observational data (see next section) were collected during the clumped condition over three such periods (one 7-day, one 9-day, and one 10-day period), and for the dispersed condition over two periods (both 10-day periods). These were interspersed with four periods without provisioning (one 9-day period and three 10-day periods).

Observational Methods

Continuous focal recording (Martin & Bateson, 2007) was used to collect data on self-directed scratching in both wild (by BCW, BT & MF) and captive (by DK) subjects. In all cases, self-directed scratching was defined as “the repeated movement of the hand or foot during which the fingertips [or toe tips] are drawn across the individual’s fur” (Schino et al., 1996, p. 187). In cases in which one or more scratch was produced within ten seconds of the last, these were considered as a single bout of scratching (see Polizzi di Sorrentino, Schino, Tiddi, & Aureli, 2012).

Data on self-scratching in the wild subjects were collected in non-provisioning contexts during 660 five-minute continuous focal animal samples totalling 47.1 h of focal observation (mean of 3.62 h/subject; range = 1.18 - 6.51 h). Focal animals were chosen opportunistically. In this context, an animal could be chosen as a focal only if it had not been sampled within the previous 1 h period, and if it was not within 3 m proximity to the previous focal animal during the preceding sample. Cases in which the duration of the focal sample was less than 1.5 min (due to the focal animal going out of sight) were discarded.

Data on self-scratching in the experimental provisioning contexts with the wild subjects were collected during 122 focal samples across 107 different provisioning trials, totalling 11.3 hours of focal observation (mean of 0.87 h/subject; range = 0.28 – 1.56 h). Focal animals were selected opportunistically after platforms were raised and continued until all banana pieces had been removed from all platforms at the site. Focal samples that were less than 1.5 min (due to going out of sight or the removal of the final banana piece less than 1.5 min after the initiation of the focal sample) were discarded. Most focal samples (72%) were between 3 and 10 min in length, but ranged from 1.6 min to 18.3 min.

In order to quantify the extent to which adult and juvenile subjects gave deceptive false alarms, all-occurrence sampling was undertaken by one observer (BW) during 16.4 h of platform experiments to note all cases in which ‘high-urgency’ hiccup alarm calls were spontaneously produced and, whenever possible, identified the caller (see Wheeler, 2009, 2010; Wheeler et al., 2014). We considered a call to be spontaneously produced if no eliciting stimulus (including conspecific aggression or any actual or perceived heterospecific threats) could be identified, and if the caller did not employ any additional anti-predator behaviours (including escape reactions or vigilance beyond the immediate substrate). For each subject, we calculated the rate of production of deceptive false alarms as the number of times they were observed to produce a spontaneous false alarm in each condition divided by the observation time in that condition; no individuals were observed to produce spontaneous false alarms in non-provisioning conditions during the study period. Both adults and juveniles as well as males and females were among each of the calling and non-calling individuals, although there was a tendency for juveniles (and adult females) to be more likely to be callers than adults (3 of 4 juveniles versus 5 of 9 adults; 4 of 5 adult females versus 1 of 4 adult males); this seems to result from the fact the benefits of calling are limited to relatively low-ranking individuals (Wheeler, 2009), and that juveniles and adult females tend to be lower ranking than adult males. In addition, because dominance rank may contribute to inter-individual differences in anxiety levels, we recorded all observed decided, dyadic agonistic interactions in the wild subjects in order to construct a dominance hierarchy (see details in Analytical Methods below).

To determine if spontaneous alarm production is temporally associated with increased levels of self-directed scratching (Prediction 2c), a single observer (DK) conducted 260 continuous focal samples of 10 min duration on all individuals in both captive groups. Prior to conducting observations, DK was trained by BW to recognize hiccups, a discrete call type in the tufted capuchin repertoire (Di Bitetti & Wheeler, n.d.), based on field recordings (see Wheeler & Hammerschmidt, 2013). Observations were conducted from approximately 0945 to 1400 h daily over the course of four weeks (June 2015). In addition to noting all instances of scratching by the focal animal as described above, the total number of spontaneous hiccups produced by the focal were also noted (see above for definitions). The order of focal subjects was randomised, and we selected each individual approximately the same number of times (range: 25-29 focal observation periods per individual). We sampled each individual at least once but no more than three times per day, and left at least 30 minutes between samples of the same individual. Focal samples that were less than 8 min in length (due to the focal animal going out of view) were discarded. A total of 42.8 hrs of focal observation was conducted (mean 4.3 h/subject; range = 3.9 – 4.8 h). Prior to the observation period (January 2014 to March 2015), data on aggressive behaviour (threats, chases and physical assaults) were collected *ad libitum* in order to calculate dominance ranks for all subjects (see details in Analytical Methods below).

Assessment of Glucocorticoid Output

To test whether high levels of anxiety-related behaviours are associated with high levels of GC production, we collected faecal samples from identified individuals in our wild study group to non-invasively measure hormonal states. The long time lag that characterizes the excretion of faecal hormone metabolites in most taxa makes it difficult or impossible to match a particular faecal hormone sample to a particular event, which is more typically accomplished in the field using urinary hormone metabolites due to their shorter timeframe of excretion (Surbeck, Deschner, Weltring, & Hohmann, 2012; Wittig, Crockford, Weltring, Deschner, & Zuberbühler, 2015). Tufted capuchin monkeys, however, demonstrate an extremely short time lag in faecal glucocorticoid metabolite excretion (fGCM; ca. 2 hrs from stressor to peak GC levels with baseline levels returning by 8 hrs) that is the typical time lag of urinary hormone metabolites (Wheeler, Tiddi, Kalbitzer, Visalberghi, & Heistermann, 2013; see also Carosi, Heistermann, & Visalberghi, 1999); fGCM levels in samples collected between two and five hours after a focal sample can thus be reliably paired with that behavioural observation (Wheeler et al., 2014). Because other events occurring in the two to five hour window prior to excretion but outside the focal observation will also affect fGCM levels in that sample, we excluded cases in which the animal experienced a likely stressor (including intense aggression, intergroup encounters, and actual or perceived predator encounters) in that time window prior to defecation. A total of 73 fGCM samples from 13 subjects met these criteria for inclusion in the analysis (mean number of samples per individual: 5.5; range: 1-15).

Details on sample collection, storage, extraction and fGCM assay can be found in Heistermann, Palme, & Ganswidt (2006), Tiddi, Wheeler, & Heistermann (2015), and Wheeler et al. (2014). Briefly, samples were collected within 30 min of defecation and stored in a cold pack until frozen at the field station. Samples were later thawed and hormone metabolites extracted from wet faeces by vortexing with 80% ethanol. Faecal sample extracts were then transported to the Endocrinology Laboratory at the German Primate Center, where fGCM concentrations were measured on microtitre plates with a corticosterone (CCST) enzyme immunoassay previously validated for assessing adrenocortical activity in our study species (see Wheeler et al., 2013). Intra-assay coefficients of variation (CVs) of high- and low-value quality controls were respectively 6.3% and 7.9%; interassay CVs were 10.6% and 11.7%, respectively (as in Wheeler et al., 2014).

Analytical Methods

To test whether anxiety-related behaviours and fGCMs are associated, we conducted a mixed-effects linear regression wherein the log transformed CCST concentration was the dependent variable and the rate of scratching (number of scratch bouts divided by the length of the focal observation) was the independent variable. In addition, because dominance rank, the time of defecation and provisioning condition (i.e. whether or not provisioning had occurred that day) are all known to affect fGCM levels (Wheeler et al., 2014), these potentially confounding factors were included among the independent variables. Because data were collected by multiple observers, we also included observer ID as a fixed effect (which was significant in some models, indicating that it is indeed important to control for this effect). Finally, because most subjects contributed multiple observations to the analysis, we included individual ID as a random effect in the model.

To test Prediction 1, that levels of self-scratching among individuals that produce deceptive false alarms will be higher in the experimental provisioning conditions relative to baseline (natural) conditions, we conducted a conditional within-subject negative binomial regression in which the number of self-directed scratch bouts in each focal observation (N=525 focal observations) was the dependent variable, and provisioning condition (i.e. provisioning versus natural) was the independent. We chose the negative binomial regression because data were zero-inflated, owing to the large number of observations with no observed bouts of scratching. The duration of the focal observation was entered as the exposure variable to control for variation in the length of focal observations. Because data were collected by multiple observers, this model also included observer ID as a fixed effect. We did not include factors that only vary between subjects (i.e. rank, age, or sex) due to the fact that this analysis tested only within-subject effects (Allison, 2009).

To test Predictions 2a and 2b, that anxiety levels will increase with an increasing strength of contest competition to a greater extent in those individuals observed to give spontaneous false alarms more often, we conducted two mixed-effects negative binomial regressions with the number of self-directed scratch bouts in a focal observation as the dependent variable, while the independent variables were the interaction between propensity to call and provisioning condition (provisioning versus no provisioning for Prediction 2a; clumped versus dispersed for Prediction 2b) as well as the main effects of these two variables. For Prediction 2a, an individual's propensity to call was calculated simply as the observed number of spontaneous false alarm bouts given in both provisioning conditions (as no individuals were observed to produce such bouts in natural contexts). For prediction 2b, this was calculated as the difference in their rate of calling between the clumped and dispersed conditions; rate of calling was calculated as the number of observed call bouts in each of the clumped and dispersed conditions divided by the respective observation time in that condition. In addition, to control for the potentially confounding effects of age, sex, and dominance rank, we included these variables among the independent variables in both models; Pearson correlations suggest that no independent variables were correlated at the level in which multicollinearity is considered to be problematic ($r > 0.7$; Dormann et al., 2013), with only one set of variables showing $r > 0.5$ (rate of calling during provisioning and sex: $r = 0.58$; others: $0.07 \leq |r| \leq 0.48$). Dominance rank was determined by entering all observed decided dyadic agonistic interactions among identified individuals into a matrix to generate a linear dominance hierarchy with MatMan (De Vries, Netto, & Hanegraaf, 1993; Noldus Information Technology, Wageningen, The Netherlands). The duration of the focal observation was entered as the exposure variable. Because an individual's typical rate of self-directed scratching may not be well-represented by any one single focal observation, and because five subjects were observed during fewer than 3 focal observations in either the clumped or dispersed condition, we ran an additional model for the test of Prediction 2b that was limited to the eight individuals sampled at least three times in each of the clumped and dispersed conditions to determine if these limited observations affected the results.

Finally, to test Prediction 2c, that higher rates of call production will be temporally associated with greater levels of SDBs in the captive subjects, we conducted a mixed-effects negative binomial regression with the number of spontaneous hiccups during the focal observation as the dependent variable, and the number of scratch bouts as the independent variable. The duration of the focal observation was entered as the exposure variable. Because the captive subjects came from two groups, and because this analysis tested for a relationship between self-scratching and hiccup production both within and between subjects, we included as random effects individual ID nested in Group ID, and controlled for the potentially confounding effects of age, sex, and dominance rank (the latter calculated using David's scores based on aggressive behaviours; De Vries, Stevens, & Vervaecke, 2006) by including these variables among the independent variables. Because this analysis was based on observations of a single observer, we did not include observer ID as a potentially confounding factor in this model.

All statistical analyses were conducted with Stata 13.0 (Stata-Corp LP, College Station, TX, U.S.A).

Ethical Note

Permission to conduct the research in Argentina was provided by the Centro de Investigaciones Ecológicas Subtropicales and the Delegación Tecnica Regional NEA of the Argentine Administration of National Parks (permit no. NEA 142). The Animal Welfare Officer at the German Primate Center provided ethical approval for the portion of the study conducted in the field, while the Ethics Committee of the School of Anthropology and Conservation at the University of Kent provided approval for the captive study. This research complied with the legal requirements of Italy and Argentina. To minimise any potential adverse effects resulting from observations at the ISTC-CNR, we avoided contact with the subjects and minimised the observer's movements and sounds.

RESULTS

Anxious Behaviour and Glucocorticoids

Prior to testing the main predictions, we first tested whether self-directed scratching predicted fGCM output, and thus whether GC levels provide a reliable measure of anxiety. Although the association between the two variables was positive, rates of self-scratching during a given focal sample were not a significant predictor of fGCM levels in samples excreted in the 2 to 5 h window following the focal sample (mixed-effects linear regression: z =1.00, *N* = 73 observations from 13 subjects, *P* = 0.318; Fig. 1, Table 1).

Is Anxiety Necessary for Production of False Alarms?

Among the 13 subjects, 8 were observed to give spontaneous false alarms at least once in experimental feeding conditions, while 5 were never observed to do so (see Table 2 for summary statistics for each subject). Among the 8 individuals observed to spontaneously produce false alarms in the experimental provisioning conditions, self-directed scratching occurred at a rate of 0.45 ± 0.65 bouts/min (mean ± SD), and 0.26 ± 0.35 bouts/min during baseline observations in natural conditions. With 7 of 8 callers showing this higher rate of self-scratching in the provisioning condition relative to baseline conditions, this contextual difference was statistically significant (conditional within-subject negative binomial regression: z = 2.33, *P* = 0.020, *N* = 525 focal observations on 8 subjects; Fig. 2, Table 3).

Is Anxiety Sufficient to Explain False Alarm Production?

The effect of provisioning condition on scratch rates among individuals that were never observed to produce a spontaneous false alarm (0.42 ± 0.63 bouts/min; non-provisioning condition: 0.32 ± 0.37 bouts/min) was slightly weaker than that seen among callers (see descriptive statistics above), but the interaction between false alarm call rate and provisioning condition (provisioning vs natural) was not a significant predictor of rates of self-directed scratching (z = 1.02, $P = 0.305$, $N = 13$ subjects) when controlling for potentially confounding variables (Fig. 2; Table 4).

When considering only observations conducted in provisioning contexts, six of the eight individuals observed to call did so more often in the clumped than in the dispersed condition. Self-directed scratching across all individuals occurred at a rate of 0.56 ± 0.69 bouts/min when food was clumped (and the potential for contest competition was highest), and at a rate of 0.21 ± 0.51 bouts/min when food was dispersed (and potential for contest was thus relatively lower). However, this trend of higher rates of scratching in the clumped than in the dispersed condition was not consistent across all classes of deceptive callers; the six individuals observed to call more often in the clumped than in the dispersed condition actually tended to scratch more in the dispersed than the clumped context (clumped: 0.43 ± 0.32 bouts/min; dispersed: 0.59 ± 0.62 bouts/min). This was in the opposite direction to the trends seen in the two individuals who called more in the dispersed condition (clumped: 0.58 ± 0.25 bouts/min; dispersed: 0.07 ± 0.01 bouts/min), or in those who did not call in either condition (clumped: 0.69 ± 0.38 bouts/min; dispersed: 0.31 ± 0.20 bouts/min). Despite these varying trends across groups (which did not match predictions), the interaction between call propensity (i.e., the difference in call rates between the two conditions) and condition (clumped vs dispersed) was not significant (z = 0.52, $P = 0.602$ $N = 122$ focal observations among 13 subjects) when controlling for potentially confounding effects (Fig. 3; Table 5). This result was largely unchanged in a more conservative model that included only the 8 individuals observed at least 3 times in both the clumped and dispersed contexts (z = 0.50, *P* = 0.619, *N* = 93 focal observations among 8 subjects).

Finally, the number of bouts of self-directed scratching in a focal sample was found to significantly predict the number of spontaneous false alarms produced among captive subjects (mixed-effects negative binomial regression: z = 2.10, *P* = 0.035, *N* = 261 focal observations among 10 subjects), although the trend was not consistent across all subjects (Fig. 4; Table 6).

DISCUSSION

Our results support the hypothesis that being in a state of anxiety is necessary for the production of spontaneous false alarm calls in tufted capuchin monkeys, but suggest that such states are not sufficient to explain patterns of calling. They also provide further evidence that glucocorticoid (GC) output is not necessarily a good proxy for emotional states, given the lack of an association between self-directed behaviours (SDBs) and GC metabolite levels. The hypothesis that experiencing anxiety is a necessary pre-requisite for the production of these calls is supported by the fact that, among individuals that spontaneously produce false alarms in both captivity and the wild, callers show evidence of higher anxiety in those contexts in which they call relative to baseline conditions. In contrast, although high rates of calling tended to be temporally associated with higher rates of SDBs in captive individuals, suggesting that elevated anxiety may in some cases be both necessary and sufficient to explain patterns of calling, the fact that non-calling individuals also demonstrated increases in self-scratching behaviours in the contexts characterized by relatively intense contest competition compared to those with more relaxed contest competition suggests that elevated anxiety alone is generally insufficient to explain why some individuals give spontaneous false alarms and some do not. While it is possible that the general lack of support for our predictions regarding whether anxiety is sufficient to explain false alarm calling is due to the fact that our relatively small sample size limits the power of our analyses, the lack of consistent trends in our non-significant analyses make a Type II error unlikely. Indeed, that anxiety is not sufficient to explain patterns of calling is further suggested by the fact that, although most individuals typically experienced elevated anxiety in competitive feeding contexts, spontaneous false alarms were given only in a subset of trials. More generally, these results are in accordance with the hypothesis that call production in nonhuman primates cannot occur in the absence of a particular emotional state (see Goodall, 1986; Tomasello, 2010), but also that cognitive factors, such as associative learning, may play a role in affecting whether or not individuals produce a call in a given situation (Fitch & Zuberbühler, 2013; Schel et al., 2013; Townsend et al., 2012). As such, it leaves open the possibility that deceptive alarm calling is underpinned by at least the first-order intention to change the behaviour of call receivers (see Dennett, 1983; Shettleworth, 2010), which would provide some support for the Machiavellian intelligence hypothesis (Whiten & Byrne, 1988), even if individuals would lack the flexibility (see Liebal et al., 2013) to produce false alarms when not experiencing elevated anxiety.

That alarm calling in capuchins is more generally associated with anxiety is suggested by previous research in our wild study population which suggests that individuals experience increases in anxiety in contexts in which predation risk is high (Polizzi di Sorrentino et al., 2012; see also Palagi & Norscia, 2011; but see Manson & Perry, 2000) (although it should be noted that an emotional basis to calling does not necessarily imply that only a single emotional state must elicit a given call type across multiple contexts). However, neither this fact nor the correlations documented in the current study are themselves necessarily indicative of a causal link between anxiety and production of spontaneous false alarms. The body of evidence that, among terrestrial mammals, experiencing a particular emotional state is a necessary precondition for producing a particular call type (Fitch, 2006; Hammerschmidt & Fischer, 2008) suggests the plausibility of a similar link in the current case, although further experimental evidence (e.g., based on pharmacological induction or suppression of anxiety; Schino et al., 1996) would be needed to demonstrate this conclusively.

Even if experiencing anxiety is a prerequisite for calling, it remains unclear which additional factors proximately trigger call production once an individual has reached the threshold level of anxiety. It is possible that these include additional emotional mechanisms that we were unable to measure, or cognitive mechanisms associated with a decision of whether to produce or inhibit the call given additional contextual factors (e.g. Crockford et al., 2012), which in turn may relate to the costs and benefits of call production versus inhibition (Lee, Rushworth, Walton, Watanabe, & Sakagami, 2007). For example, because there is little benefit for individuals to produce false alarms in terms of increased access to food if they are not in the immediate vicinity of a platform (see Wheeler, 2009), it is possible that some low ranking individuals, because they tend to sit on the group periphery during periods of intense contest competition (a behaviour that has been documented in the wild study population to reduce aggression over food; see Di Bitetti & Janson, 2001; Janson et al., 2012), suppress call production despite experiencing a high state of anxiety because there would be little benefit in calling. Alternatively, or in addition, reinforcement learning theory could account for individual differences in this propensity (Camerer, 2003; Lee et al., 2007) whereby an individual's perceived utility of calling has been shaped by its previous experience in which spontaneous alarm call production under a state of competition-induced anxiety resulted in a food reward (see also Flower, 2011). Thus it is plausible that conditioning plays a role in triggering call production, but that producing an alarm call with the intention of gaining access to food is nonetheless limited to occasions in which the individual is in a heightened state of anxiety.

Finally, the finding that SDBs and GCs are not significantly correlated adds to evidence that glucocorticoids are not necessarily a good proxy for emotional states, possibly because such behaviours serve as a coping mechanism that limits GC output when in states of anxiety (Higham et al., 2009; Mohiyeddini & Semple, 2013). We thus urge caution when drawing such links. For example, a previous study on wolves (*Canis lupus*) that found no relationship between the production of howls and GC levels may have falsely discounted the role of emotions in the production of these vocalisations based on this evidence (Mazzini et al., 2013). Rather than using GCs as a proxy, a more sound approach may be to use species-specific behavioural indicators of anxiety or other emotional states (e.g. Schwartz, 2003). Additionally, the possibility that catecholamine hormones may be a better indicator of anxiety than are GCs (see Higham et al., 2009) requires further investigation.

In conclusion, the results of this study are consistent with the hypothesis that vocal deception in tufted capuchin monkeys is underpinned, at least in part, by anxiety-related affective states. However, while being in such an emotional state may be a necessary precondition for calling, such states alone are insufficient to explain the observed patterns of call production. An interplay between emotional state and an accounting of extrinsic factors that affect the likely costs and benefits of call production versus inhibition may better explain the observed patterns. This leaves open the possibility that deceptive false alarms are produced with at least first-order intentionality (see Dennett, 1983). Further study is needed to confirm whether this is in fact the case, and thus whether deceptive alarm calling behaviour in tufted capuchins provides evidence in favour of the Machiavellian intelligence hypothesis (Whiten & Byrne, 1988).

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Table 1. Results of the mixed-effects linear regression testing whether self-directed scratching predicted faecal glucocorticoid metabolite levels (N=73 observations among 13 individuals).

Variable	Coefficient	SE	95% CI		z	*P*
Scratch rate	0.095	0.095	-0.091	0.281	1.00	0.318
Provisioning condition*	-0.306	0.130	-0.561	-0.051	-2.35	0.019
Time of day	-0.065	0.030	-0.124	-0.005	-2.12	0.034
Observer ID	-0.039	0.047	-0.131	0.054	-0.82	0.413
Constant	3.5604	0.434	2.754	4.455	8.31	<0.001

*Provisioning versus no provisioning

Table 2. Summary statistics for each of the 13 subjects included in this study.

Sub	Age	Sex	Rank	Call rate (bouts/hr)			Mean ± SD scratch rate (N)			
				Prov*	Clumped	Disp'd	Natural	Prov*	Clumped	Disp'd
BRD	A	M	3	0	0	0	0.30 ± 0.34 (39)	0.47 ± 0.54 (7)	0.69 ± 0.98 (2)	0.39 ± 0.40 (5)
DAV	J	M	7	0	0	0	0.35 ± 0.38 (18)	0.79 ± 0.67 (5)	1.05 ± 0.50 (2)	0.61 ± 0.81 (3)
ELE	A	F	13	0.47	0.46	0.48	0.25 ± 0.30 (71)	0.53 ± 0.57 (15)	0.76 ± 0.57 (10)	0.08 ± 0.15 (5)
GUE	A	F	5	0.41	0.34	0.48	0.22 ± 0.37 (90)	0.26 ± 0.53 (12)	0.40 ± 0.67 (7)	0.06 ± 0.11 (5)
HOR	J	M	8.5	0.18	0.23	0.12	0.32 ± 0.29 (17)	0.55 ± 0.87 (6)	0.05 ± 0.09 (4)	1.56 ± 0.83 (2)
JAC	J	M	8.5	0.41	0.46	0.36	0.27 ± 0.42 (35)	0.64 ± 0.99 (8)	0.23 ± 0.30 (4)	1.05 ± 1.33 (4)
LIL	A	F	10	0.29	0.46	0.12	0.28 ± 0.34 (73)	0.57 ± 0.76 (9)	0.85 ± 0.79 (6)	0.00 ± 0.00 (3)
MAR	A	M	1	0	0	0	0.28 ± 0.34 (52)	0.08 ± 0.19 (15)	0.06 ± 0.16 (6)	0.09 ± 0.21 (9)
MAY	A	F	6	0	0	0	0.36 ± 0.42 (61)	0.51 ± 0.78 (15)	0.79 ± 1.01 (7)	0.27 ± 0.45 (8)
MER	A	M	11	0.06	0.11	0.00	0.24 ± 0.34 (28)	0.47 ± 0.43 (6)	0.71 ± 0.48 (3)	0.22 ± 0.20 (3)
RIT	A	F	4	0.59	1.03	0.12	0.26 ± 0.37 (93)	0.35 ± 0.67 (13)	0.55 ± 0.81 (8)	0.03 ± 0.06 (5)
SEA	J	M	12	0.29	0.34	0.24	0.31 ± 0.38 (44)	0.27 ± 0.38 (5)	0.18 ± 0.36 (4)	0.65 (1)
VEL	A	M	2	0	0	0	0.37 ± 0.29 (39)	0.65 ± 0.81 (6)	0.88 ± 0.92 (4)	0.21 ± 0.29 (2)

Sub = subject ID; Prov = provisioning condition; Disp’d = dispersed food condition; N is the number of focal observations for each subject in each condition which were used to calculate the descriptive statistics for self-scratch rates. *The “Provisioning” condition includes both the “clumped” and “dispersed” conditions.

Table 3. Results of the within-subjects negative binomial regression comparing the occurrence of self-directed scratching (dependent variable) between contexts with and without provisioning among individuals observed to give spontaneous false alarms in the former context (N=525 focal observations among 8 subjects).

Variable	Coefficient	SE	95% CI		z	*P*
Provisioning condition*	0.330	0.142	0.053	0.608	2.33	0.020
Observer ID	0.114	0.042	0.031	0.197	2.72	0.007
Constant	-2.027	0.165	-2.351	-1.703	-12.26	<0.001

* Provisioning versus no provisioning

Table 4. Results of the mixed-effects negative binomial regression comparing the occurrence of self-directed scratching (dependent variable) between contexts with and without provisioning (N=782 focal observations among 13 subjects).

Variable	Coefficient	SE	95% CI		z	*P*
Provisioning condition*[†]	0.069	0.168	-0.261	0.399	0.41	0.682
Call freq[†]	-0.047	0.019	-0.083	-0.011	-2.53	0.011
Interaction**	0.030	0.029	-0.028	0.088	1.02	0.305
Rank	0.029	0.013	0.002	0.055	2.14	0.032
Sex	0.097	0.151	-0.198	0.392	0.065	0.518
Age	0.064	0.182	-0.294	0.421	0.35	0.728
Observer ID	0.118	0.035	0.050	0.186	3.40	0.001
Constant	-2.062	0.393	-2.833	-1.292	-5.25	<0.001

* Provisioning versus no provisioning

** Interaction between call rate and the provisioning condition

† Although these main effects are included in the model, their significance or non-significance may be driven by the inclusion of the interaction term

Table 5. Results of the mixed-effects negative binomial regression comparing the occurrence of self-directed scratching (dependent variable) between the clumped and dispersed conditions (N=93 focal observations among 8 subjects).

Variable	Coefficient	SE	95% CI		z	*P*
Provisioning condition*†	0.673	0.262	0.160	1.187	2.57	0.010
Call rate diff**†	-0.314	0.861	-2.001	1.373	-0.37	0.715
Interaction***	0.511	0.979	-1.407	2.429	0.52	0.602
Rank	0.089	0.030	0.030	0.148	2.95	0.003
Sex	-0.295	0.278	-0.840	0.251	-1.06	0.290
Age	0.700	0.397	-0.078	1.479	1.76	0.078
Observer ID	0.013	0.096	-0.175	0.201	0.14	0.891

*Clumped versus dispersed conditions

**Difference in call rate between clumped and dispersed conditions

***Interaction between call rate and the provisioning condition

† Although these main effects are included in the model, their significance or non-significance may be driven by the inclusion of the interaction term

Table 6. Results of the mixed-effects negative binomial regression examining the relationship between the number of spontaneous hiccups (dependent variable) and the number of bouts of self-directed scratching during a focal observation, controlling for the potentially confounding factors of subject rank and sex (N=281 focal observations among 10 subjects).

Variable	Coefficient	SE	95% CI		z	*P*
Scratch bouts	0.127	0.060	0.009	0.246	2.10	0.035
Rank	-0.030	0.151	-0.327	0.266	-0.20	0.841
Sex	0.717	0.406	-0.078	1.513	1.77	0.077
Constant	-2.027	0.165	-2.351	-1.703	-12.26	<0.001

Figure legends

Figure 1. The non-significant relationship between self-scratching behaviour and faecal glucocorticoid metabolites (fGCM) excreted in the two- to five-hour window after the behavioural observation. N = 73 matched fGCM/focal observations from 13 subjects.

Figure 2. Matched comparisons of mean rates of self-scratching between contexts with and without provisioning among 13 individuals with different propensities to produce spontaneous false alarms in the former context. Dashed lines represent the 5 non-callers (i.e. individuals that were never observed to produce spontaneous false alarms). Solid lines represent the 8 individuals observed to produce spontaneous false alarms in the provisioning condition, with darker and thicker lines indicating individuals that were observed to call more often. Note that the test of Prediction 1, which is based only on the 8 calling individuals represented by solid lines and does not consider variation in rate of calling, shows a significant effect of provisioning condition (N = 525 focal observations among 8 subjects), while the test of Prediction 2a is based on all individuals, does consider variation in rate of calling, and shows a non-significant effect of the interaction between call rate and provisioning condition (N = 782 focal observations among 13 subjects). The individual showing the marked decrease in self-scratching in the provisioning context is the alpha male.

Figure 3. Matched comparisons of mean rates of self-scratching between the clumped and dispersed provisioning conditions among 13 individuals with different propensities to produce spontaneous false alarms each context (Prediction 2b). Dashed lines represent the 5 non-callers (i.e. individuals that were never observed to produce spontaneous false alarms). Dotted lines represent the 2 individuals that called more often in the dispersed than the

clumped condition. Solid lines represent the 6 individuals that called more often in the clumped than the dispersed condition. Across all individuals, increasing darkness and thickness of lines indicates an increasing propensity to call in the clumped relative to the dispersed condition. Stars indicate cases in which means are based on fewer than three focal observations. The effect of the interaction of increased calling propensity and provisioning condition is not significant. N = 93 focal observations among 8 subjects. The individual showing low levels of scratching in both conditions is the alpha male. The three individuals showing sharp decreases in scratching in the clumped compared to the dispersed condition are juvenile males. The observations on these individuals in the dispersed condition were largely conducted while they were in proximity to a platform being monopolized by the alpha male, but did not co-feed with the alpha male, while in the clumped condition tolerated co-feeding with the alpha male occurred in several focal observations of these individuals.

Figure 4. Rates of self-scratching during focal observations in captive subjects against rates of spontaneous alarms in the focal observation period; each point represents a single focal observation. Although relatively weak, the positive relationship between the occurrence of self-scratching and spontaneous alarm production was significant (N = 261 focal observations among 10 subjects).

Figure 1

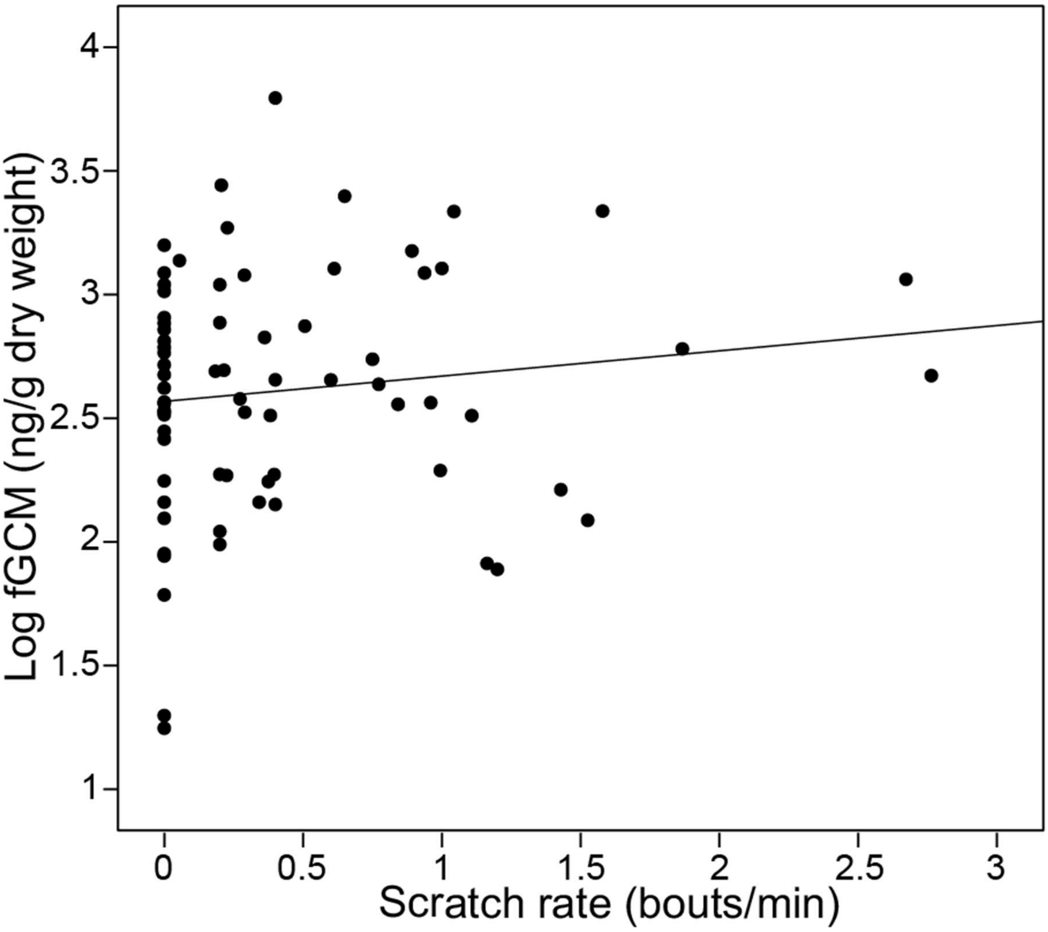
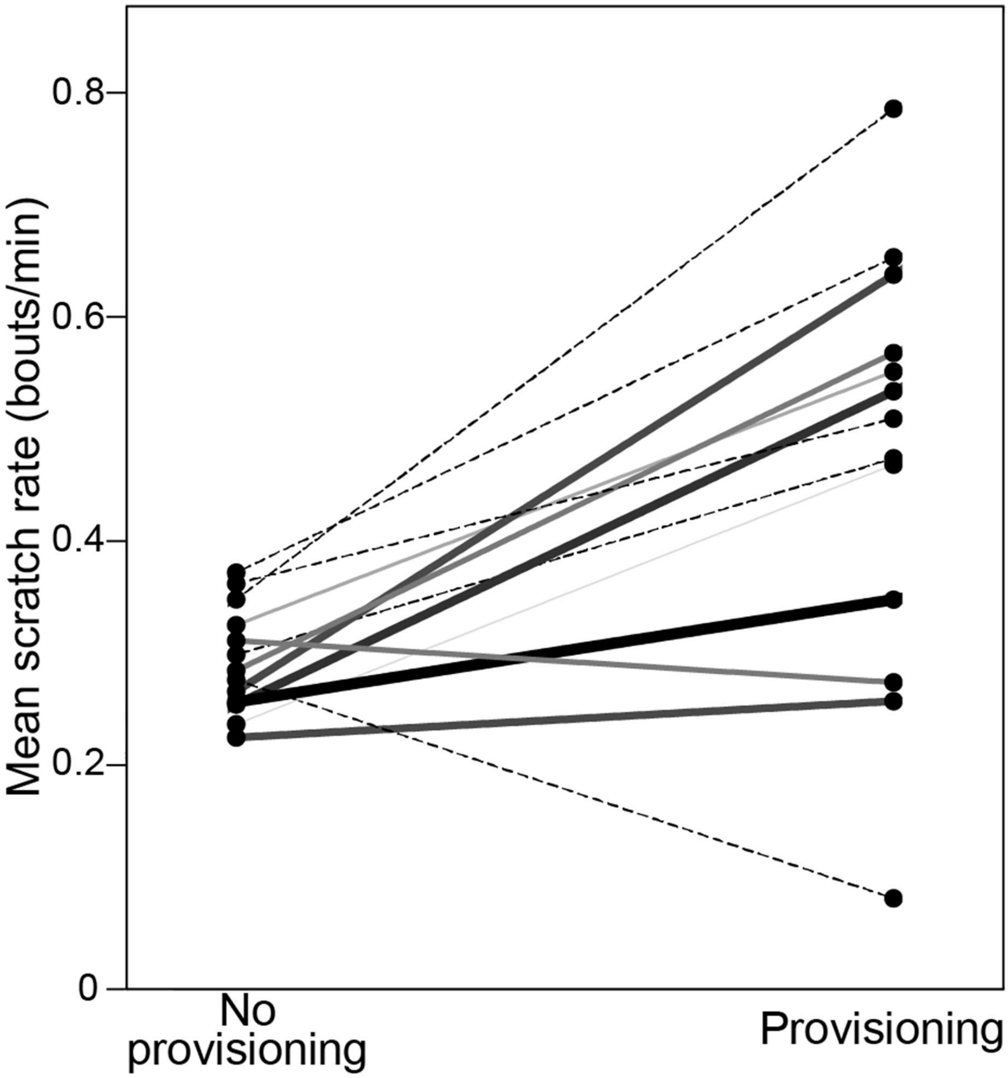

Log fGCM (ng/g dry weight)
4
3.5
3
2.5
2
1.5
1
0
0.5
1
1.5
2
2.5
3
Scratch rate (bouts/min)

Figure 2



Mean scratch rate (bouts/min)
0.8
0.6
0.4
0.2
0
No provisioning
Provisioning

Figure 3

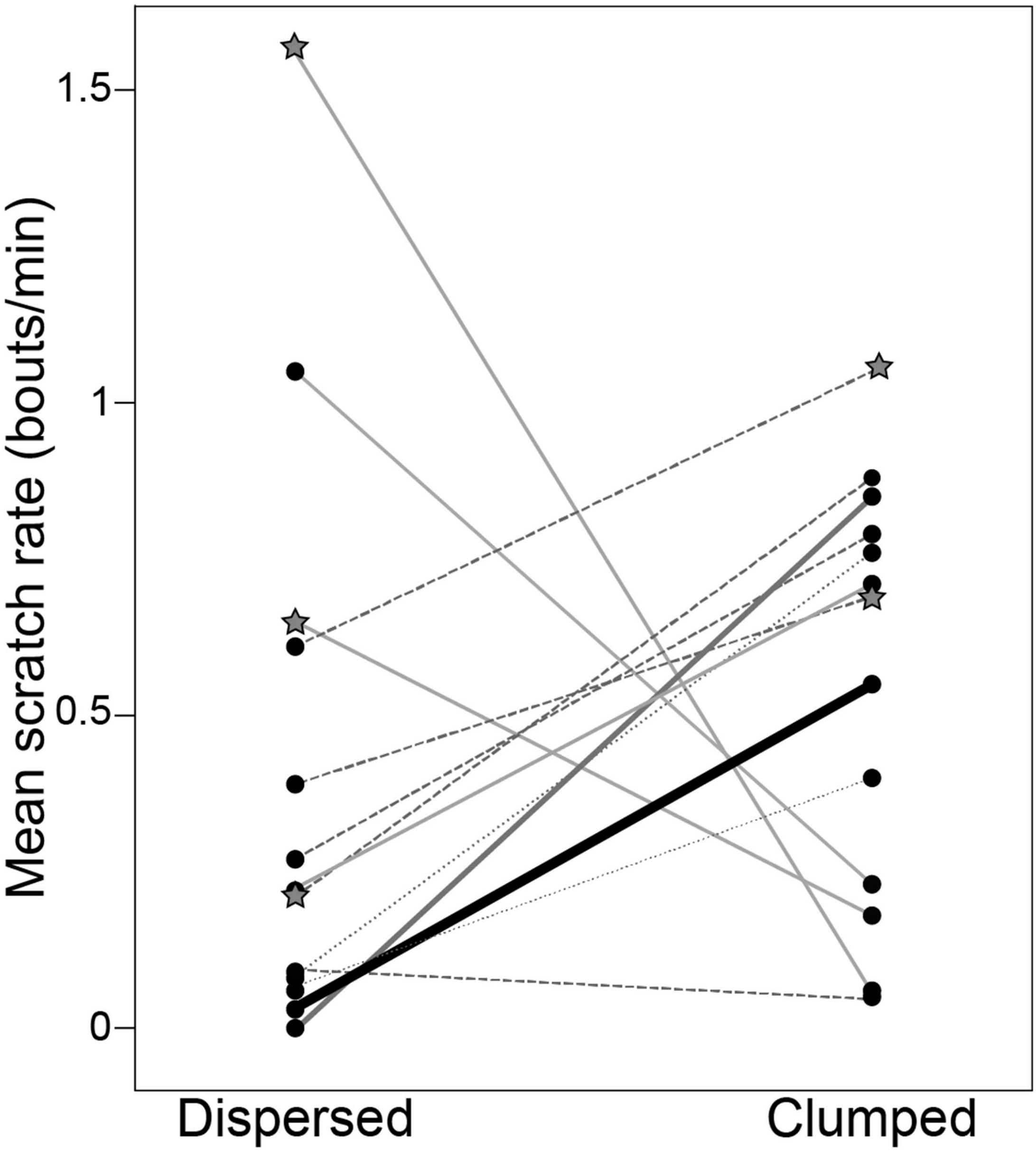
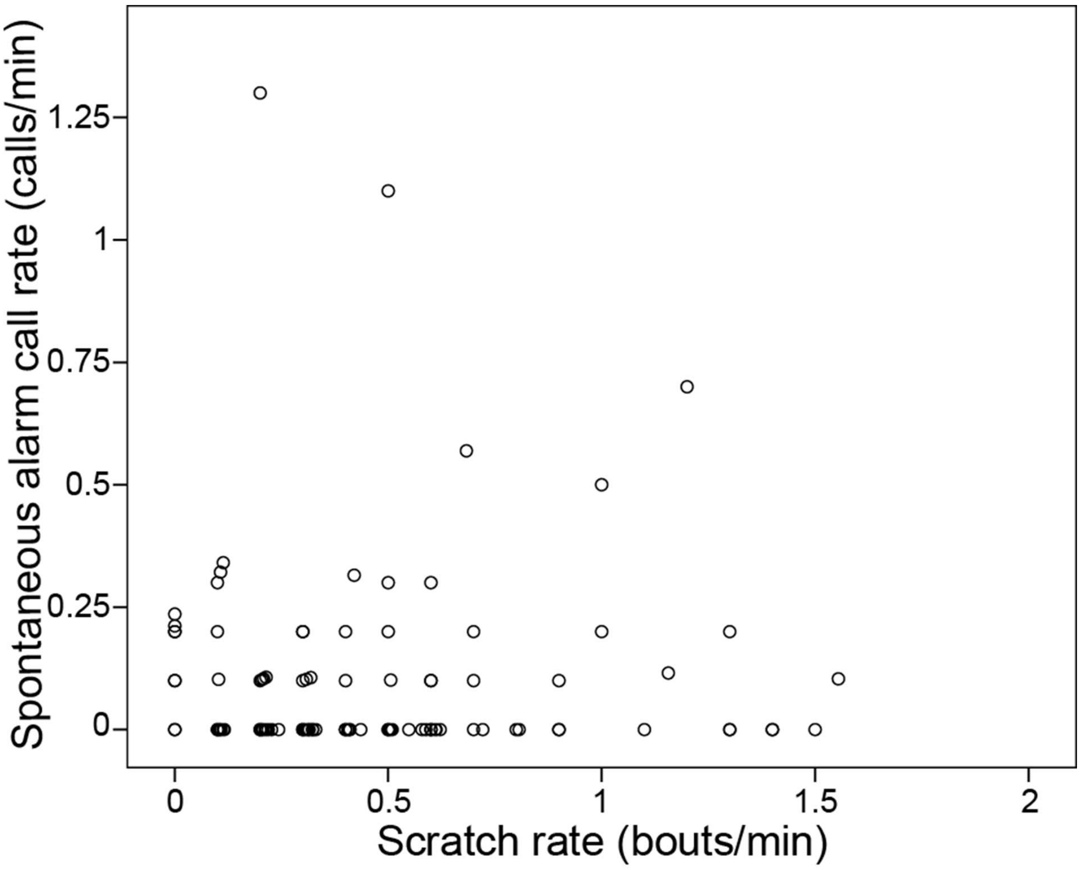


Figure 4



Spontaneous alarm call rate (calls/min)
1.25
1
0.75
0.5
0.25
0
Scratch rate (bouts/min)
0
0.5
1
1.5
2