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

3

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24

25

26 **Abstract**

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

46

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

49 Vocal production and usage in most non-human terrestrial mammals and other non-vocal
50 learning taxa is thought to be underpinned by largely emotional mechanisms
51 (Hammerschmidt & Fischer, 2008). In contrast to linguistic utterances, but similar to human
52 emotional vocalisations such as spontaneous laughter and crying, the production of specific
53 call-types in these taxa apparently cannot be decoupled from their associated affective states
54 (Bryant & Aktipis, 2014; Fitch & Zuberbühler, 2013; Owren, Amoss, & Rendall, 2011;
55 Wheeler & Fischer, 2012). This contention is supported by neurobiological evidence
56 (Hammerschmidt & Fischer, 2008) and the fact that not only vocal repertoires but also the
57 general contexts of call usage appear to be largely hardwired and species-specific in these
58 species (Seyfarth & Cheney, 2010; Wheeler & Fischer, 2012). Despite the apparent
59 biological constraints that limit an individual's ability to choose in which context to produce
60 a particular call type, some neurobiological and behavioural evidence suggests that
61 nonhuman primates may have, in at least certain cases, some degree of voluntary control over
62 whether or not to produce a call when in the associated state (Hammerschmidt & Fischer,
63 2008; Seyfarth & Cheney, 2010; Townsend, Rasmussen, Clutton-Brock, & Manser, 2012;
64 Wheeler & Fischer, 2012). Based on this evidence, it seems that particular emotional states
65 are *necessary* for a given call to be produced, but it is less clear when such states are (or are
66 not) also *sufficient* to explain whether an individual produces that call in a given situation.

67

68 A number of recent behavioural studies, however, have demonstrated that vocal production
69 and usage in primates and some other terrestrial mammals is more flexible than previously
70 appreciated (e.g. with evidence for learning of appropriate call usage or complex audience
71 effects; Chow, Mitchell, & Miller, 2015; Crockford, Wittig, Mundry, & Zuberbühler, 2012),
72 leading some authors to argue that call production may not in fact be as closely linked with
73 current emotional states as the evidence above suggests (Mazzini, Townsend, Virányi, &

74 Range, 2013; Schel, Machanda, Townsend, Zuberbühler, & Slocombe, 2013; Watson et al.,
75 2015b). Even in these cases of apparent flexibility, however, it remains plausible that
76 particular emotional mechanisms are necessary and indeed even sufficient for individuals to
77 engage in the observed behaviour (e.g. Fischer, Wheeler, & Higham, 2015), although a lack
78 of evidence indicative of the emotional states of signallers makes it difficult to determine
79 how likely such explanations are (Watson et al., 2015a).

80

81 One example of vocal communication in a nonhuman primate that may be indicative of
82 flexible production and a lack of strict association with concurrent affective states is the use
83 of terrestrial predator-associated alarm calls (“hiccups”; see Wheeler, 2010) by tufted
84 capuchin monkeys (*Sapajus nigritus*) outside of predatory contexts (Wheeler, 2009). Here,
85 lower-ranking capuchins give false alarm calls far more often when feeding on contestable
86 foods than in other contexts, and do so more often when food is more clumped and therefore
87 more easily monopolised by high-ranking group members. Listeners sometimes respond to
88 these calls with anti-predator escape reactions, thereby increasing the caller’s opportunity to
89 access the contested resource. This vocal behaviour is thus consistent with an interpretation
90 of functional or tactical deception (hereafter “deception”; Hauser, 1996; Whiten & Byrne,
91 1988). Such behaviours are predicted by the Machiavellian intelligence hypothesis, which
92 argues that an ability to outwit group-mates in competitive interactions favoured increased
93 encephalization in primate evolution (Whiten & Byrne, 1988). However, to be described as
94 “Machiavellian” would seem to require that deceptive calling is intentional insofar as
95 individuals performing the behaviour have the goal to change at least the behaviour (if not the
96 beliefs) of receivers (Dennett, 1983; Shettleworth, 2010; see also Liebal, Waller, Slocombe,
97 & Burrows, 2013 for a recent review of intentionality in communication, including suggested
98 criteria for diagnosing intentionality). Whether deceptive calling in this case is indeed

99 intentional or is instead an unintentional behaviour that is non-volitionally elicited by
100 particular emotional states is not clear. A plausible alternative explanation to intentional
101 production is that relatively low-ranking individuals involved in direct competition with high-
102 ranking conspecifics experience an emotional state which spontaneously elicits hiccup alarm
103 calls. Indeed, it has been shown that elevated physiological stress is associated with increased
104 hiccup production in captive capuchins (Boinski, Gross, & Davis, 1999), although a previous
105 attempt to test whether stress may underpin deceptive false alarm production found no
106 support for the prediction that calling is associated with higher glucocorticoid (GC) hormone
107 levels (Wheeler, Tiddi, & Heistermann, 2014). While the latter study apparently rules out the
108 possibility that GCs play a causal role in the production of deceptive false alarms, it is
109 possible that the discrepancy between the studies stems from the fact that GC levels vary
110 based on additional factors other than emotional states (*ibid.*).

111

112 Of particular relevance for the relationship between GCs, emotions, and deceptive
113 vocalizations may be the relationship between anxiety and the physiological stress response.
114 The mammalian stress response consists of two distinct components (Sapolsky, 2002). First,
115 the sympathetic nervous system triggers secretion of catecholamines (e.g. adrenaline) almost
116 instantaneously after perception of the stressor. Second, the peripheral stress response
117 involving the hypothalamus, pituitary, and adrenal gland results in secretion of GCs within
118 minutes. However, these two stages of the stress response do not necessarily need to co-occur
119 (Frankenhaeuser & Lundberg, 1985), as attempts to actively cope with a stressor potentially
120 increase catecholamine production and suppress that of GCs. It has been suggested that one
121 way in which individuals attempt to cope with stressors is through displacement activities
122 (e.g. Pico-Alfonso et al., 2007), such as self-scratching and other self-directed behaviours
123 (SDBs). Indeed, the relationship between SDBs and anxiety has been convincingly

124 documented (see Coleman & Pierre, 2014; Maestriperi, Shino, Aureli, & Troisi, 1992;
125 Troisi, 2002) through experiments which show that pharmacological inhibition of anxiety
126 results in a decrease of these behaviours (e.g. Barros, Boere, Huston, & Tomaz, 2000;
127 Schino, Perretta, Taglioni, Monaco, & Troisi, 1996), supplemented by numerous studies
128 showing that SDBs increase in situations in which individuals can reasonably be inferred to
129 be experiencing anxiety (e.g. Aureli, 1992; Kutsukake, 2003; Manson & Perry, 2000).
130 Evidence that this may be a coping strategy comes from studies showing that displacement
131 activities are associated with a reduced peripheral stress response (Hennessy & Foy, 1987;
132 Levine, Coe, & Wiener, 1989; Watson, Ward, Davis, & Stavisky, 1999) and increased
133 endorphin production (Cronin et al., 1986) in non-human mammals (see also Berridge,
134 Mitton, Clark, & Roth, 1999; Mohiyeddini & Semple, 2013; Pico-Alfonso et al., 2007). For
135 this reason, measurement of GCs may be a poor indicator of the emotional state of anxiety
136 (see also Higham, MacLarnon, Heistermann, Ross, & Semple, 2009; Tkaczynski,
137 MacLarnon, & Ross, 2014; Ulyan et al., 2006), which is instead better measured by SDBs.

138

139 This study aims to determine whether states of anxiety, as measured by self-scratching
140 behaviour, are plausibly necessary and sufficient to explain patterns of spontaneous false
141 alarm call production in tufted capuchins. Because a previous study indicated no relationship
142 between GCs and the production of deceptive false alarms (Wheeler et al., 2014), we initially
143 tested if self-scratching and GCs are in fact unrelated in our wild population before moving
144 on to our two main questions. First, if anxiety is *necessary* for the production of spontaneous
145 false alarms, then anxiety should be elevated in those contexts in which such calls are given,
146 relative to baseline levels. Specifically, we predicted that (1) among those individuals in the
147 wild population observed to give deceptive false alarms, levels of self-scratching will be
148 higher in association with experimental contexts in which resources are presented in

149 contestable patches relative to natural conditions wherein the potential for contest
150 competition is reduced. Second, if anxiety is also *sufficient* to explain spontaneous false
151 alarm production, then variation in calling within and between individuals should be matched
152 with similar variation in anxiety. We thus predicted that, across all wild subjects, those
153 individuals with a greater propensity to produce false alarms in a given condition (2a:
154 experimental vs natural conditions; 2b: clumped vs dispersed conditions) would tend to show
155 greater increases in self-scratching in those conditions relative to those that showed little or
156 no difference in calling behaviour across conditions. Finally, we predicted that (2c) higher
157 rates of spontaneous call production would be temporally associated with higher rates of self-
158 scratching in the captive subjects if anxiety is both necessary and sufficient to explain false
159 alarm production. Investigating these relationships is key to ascertaining the proximate
160 factors underlying deceptive alarm calling among tufted capuchins.

161

162 **METHODS**

163 *Study Sites and Subjects*

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

174 7-45 individuals characterized by female philopatry and male dispersal (Janson, Baldovino,
175 & Di Bitetti, 2012). Groups show mixed-sex linear dominance hierarchies, including a highly
176 despotic alpha male, with dominant individuals having priority of access to preferred
177 (central) spatial positions and contestable food resources (Di Bitetti & Janson, 2001; Janson,
178 1996; Janson et al., 2012). Further information on the behaviour, ecology, and social system
179 of the study population can be found in Janson et al. (2012).

180

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

191

192 The portion of the study conducted with captive capuchins included ten subjects split evenly
193 between two groups that were housed in separate adjacent enclosures. Both enclosures
194 consisted of two adjoining indoor areas (approx. 24.5m³) and a single outdoor area (group 1 =
195 106.5 m³, group 2 = 127.4 m³). The outdoor areas were equipped with environmental
196 enrichment in the form of ropes, platforms, slides, tree trunks and wood chip flooring, while
197 the indoor areas included slides and platforms. The subjects were fed a mixture of fruit,
198 vegetables, and carbohydrates once daily, and water was provided *ad libitum*. The

199 observations did not interfere with any of the subjects' eating, drinking or activity regimes.
200 Group 1 included three adult males, and two adult females. Group 2 included one adult male,
201 three adult females, and one juvenile male. Although the group sizes were small compared to
202 wild groups, there was a clear alpha male, and there were no apparent changes in the
203 dominance hierarchy during or in the eleven months prior to the study period (Schino, pers.
204 obs).

205

206 *Experimental Manipulation of Food Contestability*

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

217

218 Five experimental sites (artificial food patches) were set up within the study group's home
219 range at the beginning of the study period, with each site being separated from the others by
220 at least 250 m (see Janson, 1998 for an example map). Within each site, we set up four
221 platforms placed 10 to 20 m apart in order to both maintain group cohesion and ensure that a
222 single individual could not monopolize more than a single platform at a given time (see
223 Janson, 1996). Bananas were provided at each of the five sites only once per day, with baited

224 platforms being raised as the group approached a site; in cases in which a small subgroup
225 approached a site without the majority of the group, we waited until the majority approached
226 to raise the platforms.

227

228 While use of the provisioning platforms to create artificial food patches generally incites
229 higher levels of contest competition than typically occurs in natural, non-provisioning
230 contexts (see Wheeler et al., 2014), we elicited higher and lower levels of contest by varying
231 the number of platforms in which food was provided. In the clumped (high contest)
232 condition, the banana pieces were distributed across one or two platforms, while four
233 platforms were used in the dispersed (low contest) condition. In order to accommodate the
234 testing of additional hypotheses (see Wheeler et al., 2014), the same condition (e.g. clumped)
235 was used at all five sites for several consecutive days (normally 10 days), followed by several
236 days without provisioning, which was in turn followed by a period with the alternate
237 provisioning condition (e.g. dispersed) relative to the previous one used. Observational data
238 (see next section) were collected during the clumped condition over three such periods (one
239 7-day, one 9-day, and one 10-day period), and for the dispersed condition over two periods
240 (both 10-day periods). These were interspersed with four periods without provisioning (one
241 9-day period and three 10-day periods).

242

243 *Observational Methods*

244 Continuous focal recording (Martin & Bateson, 2007) was used to collect data on self-
245 directed scratching in both wild (by BCW, BT & MF) and captive (by DK) subjects. In all
246 cases, self-directed scratching was defined as “the repeated movement of the hand or foot
247 during which the fingertips [or toe tips] are drawn across the individual’s fur” (Schino et al.,
248 1996, p. 187). In cases in which one or more scratch was produced within ten seconds of the

249 last, these were considered as a single bout of scratching (see Polizzi di Sorrentino, Schino,
250 Tiddi, & Aureli, 2012).

251

252 Data on self-scratching in the wild subjects were collected in non-provisioning contexts
253 during 660 five-minute continuous focal animal samples totalling 47.1 h of focal observation
254 (mean of 3.62 h/subject; range = 1.18 - 6.51 h). Focal animals were chosen opportunistically.
255 In this context, an animal could be chosen as a focal only if it had not been sampled within
256 the previous 1 h period, and if it was not within 3 m proximity to the previous focal animal
257 during the preceding sample. Cases in which the duration of the focal sample was less than
258 1.5 min (due to the focal animal going out of sight) were discarded.

259

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

268

269 In order to quantify the extent to which adult and juvenile subjects gave deceptive false
270 alarms, all-occurrence sampling was undertaken by one observer (BW) during 16.4 h of
271 platform experiments to note all cases in which ‘high-urgency’ hiccup alarm calls were
272 spontaneously produced and, whenever possible, identified the caller (see Wheeler, 2009,
273 2010; Wheeler et al., 2014). We considered a call to be spontaneously produced if no

274 eliciting stimulus (including conspecific aggression or any actual or perceived heterospecific
275 threats) could be identified, and if the caller did not employ any additional anti-predator
276 behaviours (including escape reactions or vigilance beyond the immediate substrate). For
277 each subject, we calculated the rate of production of deceptive false alarms as the number of
278 times they were observed to produce a spontaneous false alarm in each condition divided by
279 the observation time in that condition; no individuals were observed to produce spontaneous
280 false alarms in non-provisioning conditions during the study period. Both adults and juveniles
281 as well as males and females were among each of the calling and non-calling individuals,
282 although there was a tendency for juveniles (and adult females) to be more likely to be callers
283 than adults (3 of 4 juveniles versus 5 of 9 adults; 4 of 5 adult females versus 1 of 4 adult
284 males); this seems to result from the fact the benefits of calling are limited to relatively low-
285 ranking individuals (Wheeler, 2009), and that juveniles and adult females tend to be lower
286 ranking than adult males. In addition, because dominance rank may contribute to inter-
287 individual differences in anxiety levels, we recorded all observed decided, dyadic agonistic
288 interactions in the wild subjects in order to construct a dominance hierarchy (see details in
289 Analytical Methods below).

290

291 To determine if spontaneous alarm production is temporally associated with increased levels
292 of self-directed scratching (Prediction 2c), a single observer (DK) conducted 260 continuous
293 focal samples of 10 min duration on all individuals in both captive groups. Prior to
294 conducting observations, DK was trained by BW to recognize hiccups, a discrete call type in
295 the tufted capuchin repertoire (Di Bitetti & Wheeler, n.d.), based on field recordings (see
296 Wheeler & Hammerschmidt, 2013). Observations were conducted from approximately 0945
297 to 1400 h daily over the course of four weeks (June 2015). In addition to noting all instances
298 of scratching by the focal animal as described above, the total number of spontaneous hiccups

299 produced by the focal were also noted (see above for definitions). The order of focal subjects
300 was randomised, and we selected each individual approximately the same number of times
301 (range: 25-29 focal observation periods per individual). We sampled each individual at least
302 once but no more than three times per day, and left at least 30 minutes between samples of
303 the same individual. Focal samples that were less than 8 min in length (due to the focal
304 animal going out of view) were discarded. A total of 42.8 hrs of focal observation was
305 conducted (mean 4.3 h/subject; range = 3.9 – 4.8 h). Prior to the observation period (January
306 2014 to March 2015), data on aggressive behaviour (threats, chases and physical assaults)
307 were collected *ad libitum* in order to calculate dominance ranks for all subjects (see details in
308 Analytical Methods below).

309

310 *Assessment of Glucocorticoid Output*

311 To test whether high levels of anxiety-related behaviours are associated with high levels of
312 GC production, we collected faecal samples from identified individuals in our wild study
313 group to non-invasively measure hormonal states. The long time lag that characterizes the
314 excretion of faecal hormone metabolites in most taxa makes it difficult or impossible to
315 match a particular faecal hormone sample to a particular event, which is more typically
316 accomplished in the field using urinary hormone metabolites due to their shorter timeframe of
317 excretion (Surbeck, Deschner, Weltring, & Hohmann, 2012; Wittig, Crockford, Weltring,
318 Deschner, & Zuberbühler, 2015). Tufted capuchin monkeys, however, demonstrate an
319 extremely short time lag in faecal glucocorticoid metabolite excretion (fGCM; ca. 2 hrs from
320 stressor to peak GC levels with baseline levels returning by 8 hrs) that is the typical time lag
321 of urinary hormone metabolites (Wheeler, Tididi, Kalbitzer, Visalberghi, & Heistermann,
322 2013; see also Carosi, Heistermann, & Visalberghi, 1999); fGCM levels in samples collected
323 between two and five hours after a focal sample can thus be reliably paired with that

324 behavioural observation (Wheeler et al., 2014). Because other events occurring in the two to
325 five hour window prior to excretion but outside the focal observation will also affect fGCM
326 levels in that sample, we excluded cases in which the animal experienced a likely stressor
327 (including intense aggression, intergroup encounters, and actual or perceived predator
328 encounters) in that time window prior to defecation. A total of 73 fGCM samples from 13
329 subjects met these criteria for inclusion in the analysis (mean number of samples per
330 individual: 5.5; range: 1-15).

331

332 Details on sample collection, storage, extraction and fGCM assay can be found in
333 Heistermann, Palme, & Ganswidt (2006), Tididi, Wheeler, & Heistermann (2015), and
334 Wheeler et al. (2014). Briefly, samples were collected within 30 min of defecation and stored
335 in a cold pack until frozen at the field station. Samples were later thawed and hormone
336 metabolites extracted from wet faeces by vortexing with 80% ethanol. Faecal sample extracts
337 were then transported to the Endocrinology Laboratory at the German Primate Center, where
338 fGCM concentrations were measured on microtitre plates with a corticosterone (CCST)
339 enzyme immunoassay previously validated for assessing adrenocortical activity in our study
340 species (see Wheeler et al., 2013). Intra-assay coefficients of variation (CVs) of high- and
341 low-value quality controls were respectively 6.3% and 7.9%; interassay CVs were 10.6% and
342 11.7%, respectively (as in Wheeler et al., 2014).

343

344 *Analytical Methods*

345 To test whether anxiety-related behaviours and fGCMs are associated, we conducted a
346 mixed-effects linear regression wherein the log transformed CCST concentration was the
347 dependent variable and the rate of scratching (number of scratch bouts divided by the length
348 of the focal observation) was the independent variable. In addition, because dominance rank,

349 the time of defecation and provisioning condition (i.e. whether or not provisioning had
350 occurred that day) are all known to affect fGCM levels (Wheeler et al., 2014), these
351 potentially confounding factors were included among the independent variables. Because
352 data were collected by multiple observers, we also included observer ID as a fixed effect
353 (which was significant in some models, indicating that it is indeed important to control for
354 this effect). Finally, because most subjects contributed multiple observations to the analysis,
355 we included individual ID as a random effect in the model.

356

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

369

370 To test Predictions 2a and 2b, that anxiety levels will increase with an increasing strength of
371 contest competition to a greater extent in those individuals observed to give spontaneous false
372 alarms more often, we conducted two mixed-effects negative binomial regressions with the
373 number of self-directed scratch bouts in a focal observation as the dependent variable, while

374 the independent variables were the interaction between propensity to call and provisioning
375 condition (provisioning versus no provisioning for Prediction 2a; clumped versus dispersed
376 for Prediction 2b) as well as the main effects of these two variables. For Prediction 2a, an
377 individual's propensity to call was calculated simply as the observed number of spontaneous
378 false alarm bouts given in both provisioning conditions (as no individuals were observed to
379 produce such bouts in natural contexts). For prediction 2b, this was calculated as the
380 difference in their rate of calling between the clumped and dispersed conditions; rate of
381 calling was calculated as the number of observed call bouts in each of the clumped and
382 dispersed conditions divided by the respective observation time in that condition. In addition,
383 to control for the potentially confounding effects of age, sex, and dominance rank, we
384 included these variables among the independent variables in both models; Pearson
385 correlations suggest that no independent variables were correlated at the level in which
386 multicollinearity is considered to be problematic ($r > 0.7$; Dormann et al., 2013), with only
387 one set of variables showing $r > 0.5$ (rate of calling during provisioning and sex: $r = 0.58$;
388 others: $0.07 \leq |r| \leq 0.48$). Dominance rank was determined by entering all observed decided
389 dyadic agonistic interactions among identified individuals into a matrix to generate a linear
390 dominance hierarchy with MatMan (De Vries, Netto, & Hanegraaf, 1993; Noldus
391 Information Technology, Wageningen, The Netherlands). The duration of the focal
392 observation was entered as the exposure variable. Because an individual's typical rate of self-
393 directed scratching may not be well-represented by any one single focal observation, and
394 because five subjects were observed during fewer than 3 focal observations in either the
395 clumped or dispersed condition, we ran an additional model for the test of Prediction 2b that
396 was limited to the eight individuals sampled at least three times in each of the clumped and
397 dispersed conditions to determine if these limited observations affected the results.
398

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

412

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

415

416 *Ethical Note*

417 Permission to conduct the research in Argentina was provided by the Centro de
418 Investigaciones Ecológicas Subtropicales and the Delegación Técnica Regional NEA of the
419 Argentine Administration of National Parks (permit no. NEA 142). The Animal Welfare
420 Officer at the German Primate Center provided ethical approval for the portion of the study
421 conducted in the field, while the Ethics Committee of the School of Anthropology and
422 Conservation at the University of Kent provided approval for the captive study. This research
423 complied with the legal requirements of Italy and Argentina. To minimise any potential

424 adverse effects resulting from observations at the ISTC-CNR, we avoided contact with the
425 subjects and minimised the observer's movements and sounds.

426

427 **RESULTS**

428 *Anxious Behaviour and Glucocorticoids*

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

435

436 *Is Anxiety Necessary for Production of False Alarms?*

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

446

447 *Is Anxiety Sufficient to Explain False Alarm Production?*

448 The effect of provisioning condition on scratch rates among individuals that were never

449 observed to produce a spontaneous false alarm (0.42 ± 0.63 bouts/min; non-provisioning
450 condition: 0.32 ± 0.37 bouts/min) was slightly weaker than that seen among callers (see
451 descriptive statistics above), but the interaction between false alarm call rate and provisioning
452 condition (provisioning vs natural) was not a significant predictor of rates of self-directed
453 scratching ($z = 1.02$, $P = 0.305$, $N = 13$ subjects) when controlling for potentially
454 confounding variables (Fig. 2; Table 4).

455

456 When considering only observations conducted in provisioning contexts, six of the eight
457 individuals observed to call did so more often in the clumped than in the dispersed condition.
458 Self-directed scratching across all individuals occurred at a rate of 0.56 ± 0.69 bouts/min
459 when food was clumped (and the potential for contest competition was highest), and at a rate
460 of 0.21 ± 0.51 bouts/min when food was dispersed (and potential for contest was thus
461 relatively lower). However, this trend of higher rates of scratching in the clumped than in the
462 dispersed condition was not consistent across all classes of deceptive callers; the six
463 individuals observed to call more often in the clumped than in the dispersed condition
464 actually tended to scratch more in the dispersed than the clumped context (clumped: $0.43 \pm$
465 0.32 bouts/min; dispersed: 0.59 ± 0.62 bouts/min). This was in the opposite direction to the
466 trends seen in the two individuals who called more in the dispersed condition (clumped: 0.58
467 ± 0.25 bouts/min; dispersed: 0.07 ± 0.01 bouts/min), or in those who did not call in either
468 condition (clumped: 0.69 ± 0.38 bouts/min; dispersed: 0.31 ± 0.20 bouts/min). Despite these
469 varying trends across groups (which did not match predictions), the interaction between call
470 propensity (i.e., the difference in call rates between the two conditions) and condition
471 (clumped vs dispersed) was not significant ($z = 0.52$, $P = 0.602$ $N = 122$ focal observations
472 among 13 subjects) when controlling for potentially confounding effects (Fig. 3; Table 5).
473 This result was largely unchanged in a more conservative model that included only the 8

474 individuals observed at least 3 times in both the clumped and dispersed contexts ($z = 0.50$, P
475 $= 0.619$, $N = 93$ focal observations among 8 subjects).

476

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

482

483 **DISCUSSION**

484 Our results support the hypothesis that being in a state of anxiety is necessary for the
485 production of spontaneous false alarm calls in tufted capuchin monkeys, but suggest that such
486 states are not sufficient to explain patterns of calling. They also provide further evidence that
487 glucocorticoid (GC) output is not necessarily a good proxy for emotional states, given the
488 lack of an association between self-directed behaviours (SDBs) and GC metabolite levels.
489 The hypothesis that experiencing anxiety is a necessary pre-requisite for the production of
490 these calls is supported by the fact that, among individuals that spontaneously produce false
491 alarms in both captivity and the wild, callers show evidence of higher anxiety in those
492 contexts in which they call relative to baseline conditions. In contrast, although high rates of
493 calling tended to be temporally associated with higher rates of SDBs in captive individuals,
494 suggesting that elevated anxiety may in some cases be both necessary and sufficient to
495 explain patterns of calling, the fact that non-calling individuals also demonstrated increases in
496 self-scratching behaviours in the contexts characterized by relatively intense contest
497 competition compared to those with more relaxed contest competition suggests that elevated
498 anxiety alone is generally insufficient to explain why some individuals give spontaneous

499 false alarms and some do not. While it is possible that the general lack of support for our
500 predictions regarding whether anxiety is sufficient to explain false alarm calling is due to the
501 fact that our relatively small sample size limits the power of our analyses, the lack of
502 consistent trends in our non-significant analyses make a Type II error unlikely. Indeed, that
503 anxiety is not sufficient to explain patterns of calling is further suggested by the fact that,
504 although most individuals typically experienced elevated anxiety in competitive feeding
505 contexts, spontaneous false alarms were given only in a subset of trials. More generally, these
506 results are in accordance with the hypothesis that call production in nonhuman primates
507 cannot occur in the absence of a particular emotional state (see Goodall, 1986; Tomasello,
508 2010), but also that cognitive factors, such as associative learning, may play a role in
509 affecting whether or not individuals produce a call in a given situation (Fitch & Zuberbühler,
510 2013; Schel et al., 2013; Townsend et al., 2012). As such, it leaves open the possibility that
511 deceptive alarm calling is underpinned by at least the first-order intention to change the
512 behaviour of call receivers (see Dennett, 1983; Shettleworth, 2010), which would provide
513 some support for the Machiavellian intelligence hypothesis (Whiten & Byrne, 1988), even if
514 individuals would lack the flexibility (see Liebal et al., 2013) to produce false alarms when
515 not experiencing elevated anxiety.

516

517 That alarm calling in capuchins is more generally associated with anxiety is suggested by
518 previous research in our wild study population which suggests that individuals experience
519 increases in anxiety in contexts in which predation risk is high (Polizzi di Sorrentino et al.,
520 2012; see also Palagi & Norscia, 2011; but see Manson & Perry, 2000) (although it should be
521 noted that an emotional basis to calling does not necessarily imply that only a single
522 emotional state must elicit a given call type across multiple contexts). However, neither this
523 fact nor the correlations documented in the current study are themselves necessarily

524 indicative of a causal link between anxiety and production of spontaneous false alarms. The
525 body of evidence that, among terrestrial mammals, experiencing a particular emotional state
526 is a necessary precondition for producing a particular call type (Fitch, 2006; Hammerschmidt
527 & Fischer, 2008) suggests the plausibility of a similar link in the current case, although
528 further experimental evidence (e.g., based on pharmacological induction or suppression of
529 anxiety; Schino et al., 1996) would be needed to demonstrate this conclusively.

530

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

549 triggering call production, but that producing an alarm call with the intention of gaining
550 access to food is nonetheless limited to occasions in which the individual is in a heightened
551 state of anxiety.

552

553 Finally, the finding that SDBs and GCs are not significantly correlated adds to evidence that
554 glucocorticoids are not necessarily a good proxy for emotional states, possibly because such
555 behaviours serve as a coping mechanism that limits GC output when in states of anxiety
556 (Higham et al., 2009; Mohiyeddini & Semple, 2013). We thus urge caution when drawing
557 such links. For example, a previous study on wolves (*Canis lupus*) that found no relationship
558 between the production of howls and GC levels may have falsely discounted the role of
559 emotions in the production of these vocalisations based on this evidence (Mazzini et al.,
560 2013). Rather than using GCs as a proxy, a more sound approach may be to use species-
561 specific behavioural indicators of anxiety or other emotional states (e.g. Schwartz, 2003).
562 Additionally, the possibility that catecholamine hormones may be a better indicator of
563 anxiety than are GCs (see Higham et al., 2009) requires further investigation.

564

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

574 capuchins provides evidence in favour of the Machiavellian intelligence hypothesis (Whiten
575 & Byrne, 1988).

576

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586

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- 782

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

Variable	Coefficient	SE	95% CI		<i>z</i>	<i>P</i>
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

786 *Provisioning versus no provisioning

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

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

788

789 Sub = subject ID; Prov = provisioning condition; Disp'd = dispersed food condition; N is the number of focal observations for each subject in
790 each condition which were used to calculate the descriptive statistics for self-scratch rates. *The "Provisioning" condition includes both the
791 "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		<i>z</i>	<i>P</i>
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		<i>z</i>	<i>P</i>
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

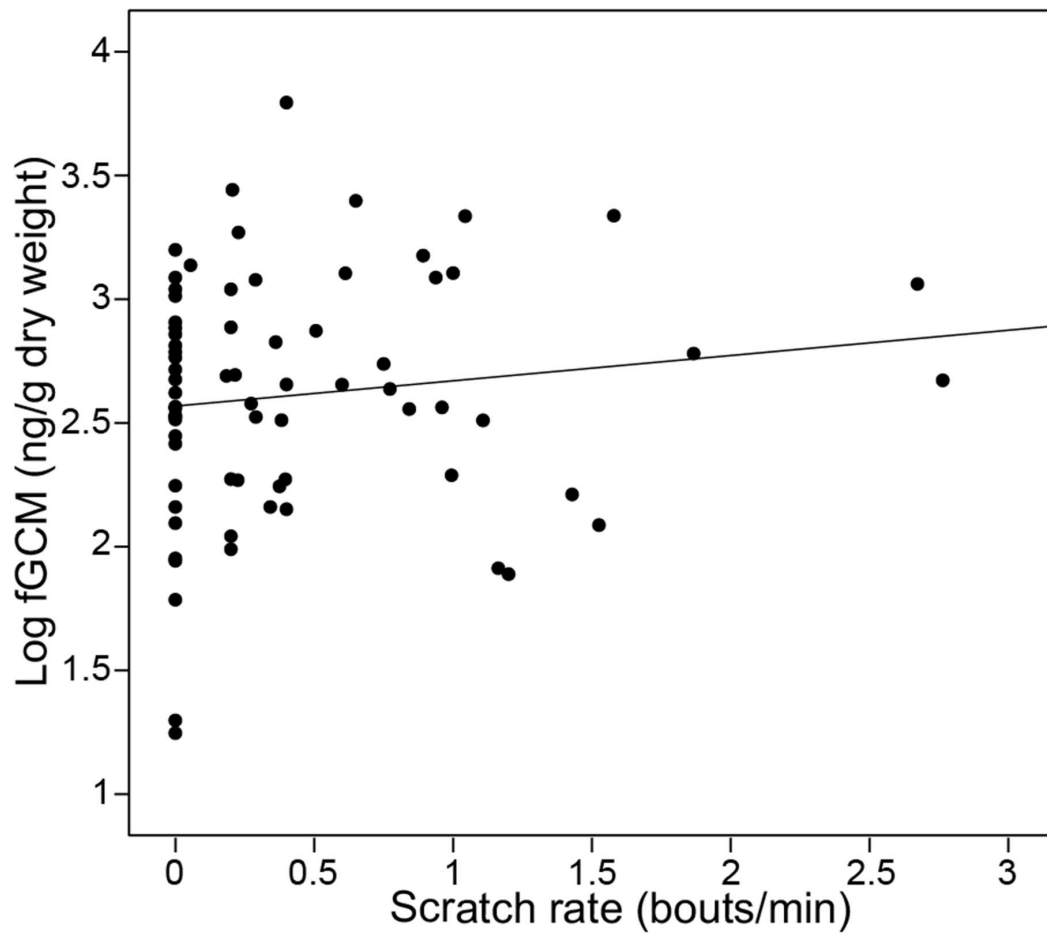


Figure 2

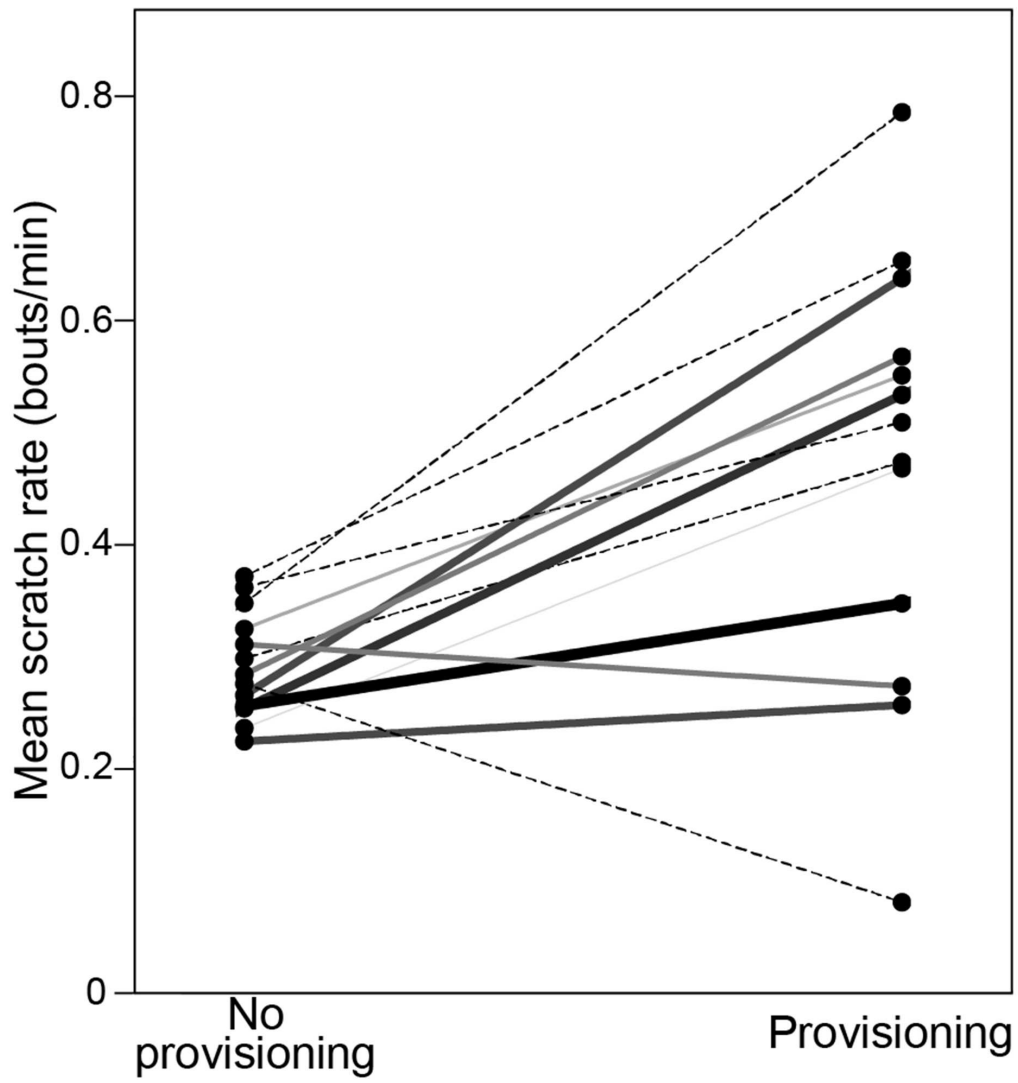


Figure 3

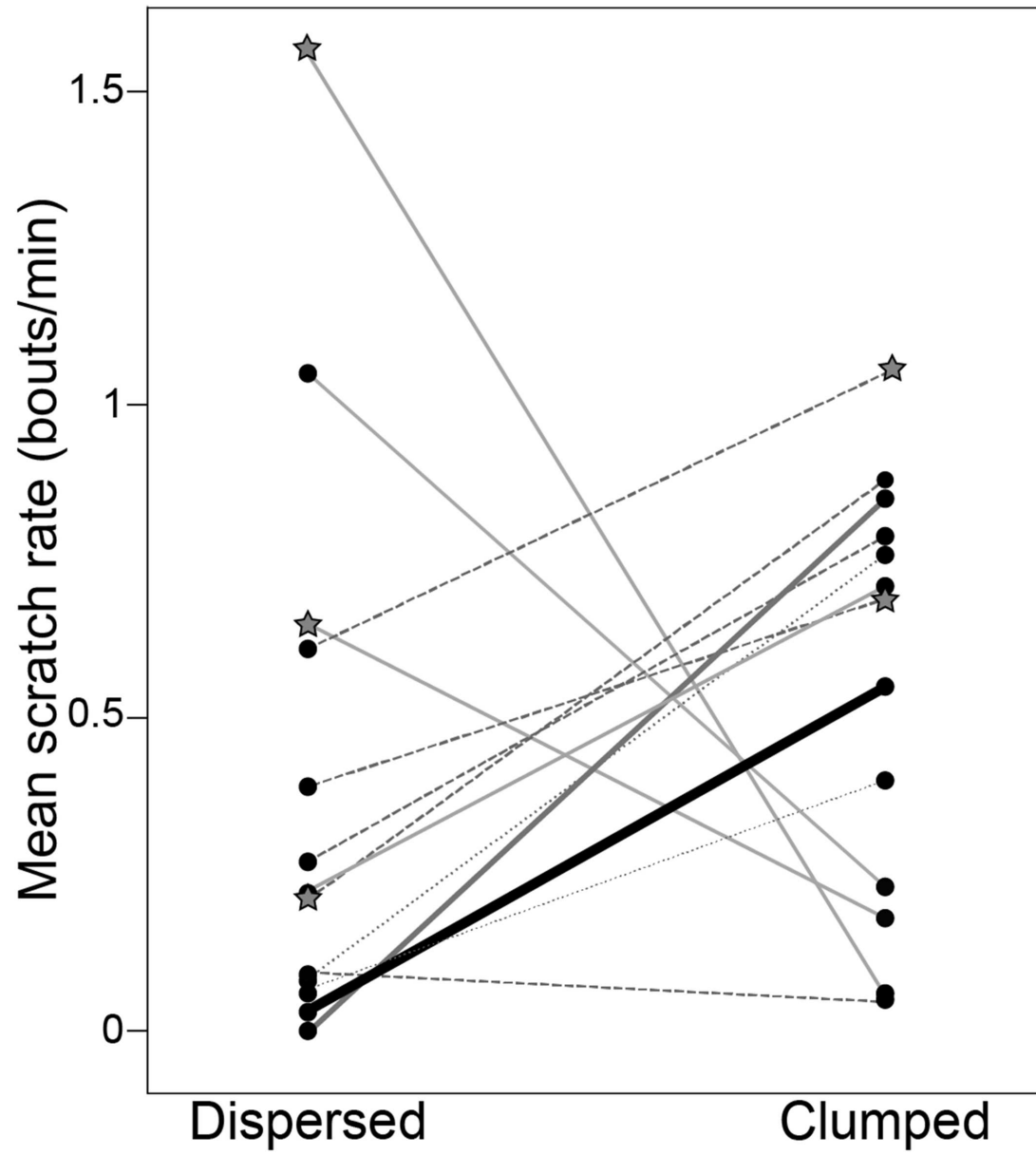


Figure 4

