1   # Call concatenation in wild meerkats

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4   Repertoire size, frequently determined by the number of discrete call types, has been used as

5   a means to assess vocal complexity in animals. However, species can also increase their

6   communicative complexity by using graded signals or by combining individual calls together.

7   Animal call sequences can be divided into two main categories, each subdivided into two

8   classes: repetitions, with either an unlimited or finite number of iterations of the same call

9   type, and mixed call combinations, composed of two or more graded or discrete call types.

10 Social contexts involve a wide range of behaviours and, unlike predation contexts, can be

11 associated with both positive and negative emotions. Therefore, interactions linked to social

12 contexts may place additional demands on an animal's communicative system and lead to the

13 use of call combinations. We systematically documented call combinations produced by wild

14 meerkats (*Suricata suricatta*), a highly social carnivore, in social contexts in their natural

15 habitat. We observed twelve distinct call combinations belonging to all four different classes

16 of combination, emitted in all of the observed behavioural contexts. Four combinations were

17 each produced in a specific context whereas the remaining eight were produced in several

18 contexts, albeit in different proportions. The broad use of combinations suggests that they

19 represent a non-negligible part of meerkat social communication and that they can be used in

20 flexible ways across various behavioural contexts. Comparison with combinations produced

21 in predation contexts indicated that social call combinations are more varied in number of

22 classes and structural complexity than the former, perhaps due to the greater variety of social

23 contexts. However, in meerkats, combinations of functionally referential calls have been

24 documented in predation but not social contexts, suggesting that both social and predation

25 pressures may play a role in the evolution of combinatoriality in animal communication.

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30 Communicative complexity related to signal diversity can be measured in two main ways:

31 through assessing the number of distinct signals produced or by calculating the bits of

32 information contained in the system (Freeberg, Dunbar, & Ord, 2012). To date, acoustic

33 communicative complexity has mostly been assessed using vocal repertoire size (Oller &

34 Griebel, 2008). However, most vocal repertoires only list the acoustically discrete call types

35 the species produce and, for the majority of species, the number of these call types is

36 physically constrained, limiting the size of their repertoire (Fitch, 2000). To achieve a higher

37 communicative flexibility despite this limitation, some animal species produce intermediate

38 call types, leading to a graded call system (Marler, 1976). An additional way to increase

39 communicative flexibility is to combine individual calls (Arnold & Zuberbühler, 2006;

40 Engesser, Crane, Savage, Russell, & Townsend, 2015). Combining calls has frequently been

41 argued to be a more efficient way of conveying new messages than creating new calls

42 (Jackendoff, 1999; Nowak, Plotkin, & Jansen, 2000) and may reduce the risk of perception

43 errors from the receiver's side (Nowak & Krakauer, 1999; Nowak, Krakauer, & Dress, 1999).

44 Through dividing call combinations described in the literature into categories based on the

45 number of component call types, we can identify two main groups: repetitions and mixed call

46 combinations. Repetitions are combinations composed of only one call type and can be

47 subdivided into two classes: unlimited and finite. Unlimited repetitions are combinations that

48 are not characterised by the number of times the call is repeated. Examples of such

49 combinations are corncrakes' (*Crex crex*) aggression calls (Ręk, 2013), and alarm calls

50 emitted repeatedly in many species (non- primate mammals: Blumstein & Armitage, 1997;

51 Manser, 2001; non-human primates: Macedonia, 1990; Lemasson, Ouattara, Bouchet, &

52 Zuberbühler, 2010; Schel, Candiotti, & Zuberbühler, 2010). On the contrary, finite repetitions

53 are always composed of the same number of calls, for example the Bulwer's petrel's

54 (*Bulweria bulwerii*) double calls are always composed of two calls (James & Robertson,

55 1985).

56 Here we define mixed call combinations as sequences that include at least two different call

57 types and can be either graded or discrete or both. Graded call combinations are sequences of

58 calls that grade along a structural or temporal continuum between two discrete call types

59 (Keenan, Lemasson, & Zuberbühler, 2013). Gradation can occur in the frequency parameters

60 (e.g. peak frequency, frequency range), amplitude, or duration of the call. Examples of such

61 combinations can be found in diverse taxa from amphibians to non-human primates (hereafter

62 primates). One case of such a graded sequence is the Blanchard's cricket frog's (*Acris*

63 *crepitans blanchardi*) aggression calls that become more aggressive with the approach of a

64 simulated intruder (Wagner Jr, 1989), as expressed in the calls by an increase in length and

65 number of pulses. In another case, the Senegal bushbaby (*Galago senegalensis senegalensis*)

66 produces sequences of calls when excited that grade from one call type to another as the

67 caller gets more aroused (Zimmermann, 1985). Moreover, combinations may contain graded

68 calls that are not graded into each other during the sequence, as seen in banded mongoose

69 (*Mungos mungo*) lost sequences that contain both close calls and lost calls, which are two

70 distinct graded calls (Jansen, 2013). Discrete mixed call combinations are composed of

71 several discrete call types with no intermediate forms. For example, male Túngara frogs

72 (*Physalaemus pustulosus*) produce calls composed of two distinct components, a whine

73 followed by up to six chucks to attract females (Ryan, 1980). In primates, female Diana

74 monkeys (*Cercopithecus diana*) produce several social calls, used to communicate over short

75 distances with other group members in non-predatory contexts, in combinations integrating

76 two distinct call types (Candiotti, Zuberbühler, & Lemasson, 2012). Examples of discrete

77 mixed call combinations include the assembly of functionally referential acoustic units

78 resulting in a new or related meaning, as seen in the alarm call systems of some forest guenon

79 species (putty-nosed monkeys, *Cercopithecus nictitans*: Arnold & Zuberbühler, 2006;

80 Campbell monkeys, *Cercopithecus campbelli*: Ouattara, Lemasson, & Zuberbühler, 2009).

81 Recent attention has focused on call combination production in non vocal-learning species.

82 Unlike vocal learning species such as songbirds, hummingbirds, and parrots in birds, and

83 humans, some marine mammals, and bats in mammals (Slater & Janik, 2010), non vocal-

84 learners cannot expand their vocal repertoire by learning to produce new sounds. Hence non

85 vocal-learning species could be expected to use call combinations as a means to increase their

86 communicative output (Nowak & Krakauer, 1999; Nowak et al., 1999). Many studies on call

87 combinations in animal communication systems have focused on non-human primates, in

88 particular their alarm or long calls (black-fronted titi monkeys, *Callicebus nigrifrons*: Cäsar,

89 Byrne, Young, & Zuberbühler, 2012; Bornean orang-utans, *Pongo pygmaeus wurmbii*:

90 Spillmann et al., 2010; Campbell monkeys: Ouattara et al., 2009; putty-nosed monkeys:

91 Arnold & Zuberbühler, 2006; white-handed gibbons, *Hylobates lar*: Clarke, Reichard, &

92 Zuberbühler, 2006). However, an emerging body of data suggests quieter social calls may

93 represent a suite of calls also open to combinatorial operations (chimpanzees, *Pan*

94 *troglodytes*: Crockford & Boesch, 2005; bonobos, *Pan paniscus*: Clay & Zuberbühler, 2009;

95 red-capped mangabeys, *Cercocebus torquatus*: Bouchet, Pellier, Blois-Heulin, & Lemasson,

96 2010; Diana monkeys: Candiotti et al., 2012).

97   It has been hypothesized that, unlike most predation contexts where an immediate change in

98   behaviour in response to a call is adaptive, in the majority of social situations, latency to

99   respond is not necessarily crucial for survival. Therefore both the caller and the receiver

100 should have more time to produce and process longer strings of acoustic units in social

101 contexts (Collier, Bickel, van Schaik, Manser, & Townsend, 2014). Moreover, social contexts

102 can involve a highly variable range of behaviours and, unlike predation contexts, they can be

103 associated with both positive and negative emotions. Thus, interactions during social contexts

104 may place additional demands on the communication system that could promote

105 combinatoriality. Data from primates seem to support this (Bouchet et al., 2010; Candiotti et

106 al., 2012; Clay & Zuberbühler, 2009; Crockford & Boesch, 2005), and some non-primate

107 species have also been described as producing call combinations in non-predation contexts

108 (banded mongooses: Jansen, Cant, & Manser, 2012; corncrakes: Ręk, 2013; chestnut-

109 crowned babblers, *Pomatostomus ruficeps*: Engesser et al., 2015). However, a systematic

110 documentation of the presence and extent of combinatorial communication within a species

111 repertoire is rarely undertaken (but see Crockford & Boesch, 2005 for a study on wild

112 chimpanzees and Bouchet et al., 2010 for a study on captive red-capped mangabeys).

113 Quantifying the extent and use of combinations within a species' communication system is

114 key to understanding both the diversity of combinations produced in animal communication,

115 and the extent to which they result from different combinatorial production mechanisms.

116 Furthermore, elucidating the variance in distribution of combination types between social and

117 predation contexts in different species could shed light on interspecies differences and

118 subsequently on the contexts promoting communicative complexity. This could ultimately

119 lead to a better understanding of the factors influencing the evolution of combinatoriality

120 more generally.

121   Some animal calls have been termed functionally referential due to their high context

122   specificity and link to an external object or event (Macedonia & Evans, 1993), while other

123   calls seem to mainly reflect the animal's internal state and are referred to as

124   motivational/emotional calls (Darwin, 1872; Morton, 1977). An animal's internal state

125   includes both motivation, which is the behavioural state the animal experiences adjusted to its

126   external environment and internal physiological state, and emotion, a short but intense

127   affective reaction to a stimulus which can be measured along two dimensions: arousal (high

128   or low) and valence (positive or negative) (Briefer, 2012). It is now recognised that the same

129   call can encode both types of information, functional reference and internal state (Manser,

130   Seyfarth, & Cheney, 2002). Given that call combinations are built from several different

131   calls, the combinations themselves have the potential to carry similar types of information,

132   pertaining to the internal state or external event experienced by the signaller. Furthermore, as

133   they comprise several calls, combinations could also inform receivers on mixed

134   motivations/emotions, more than one external event, or even combine the two types of

135   information expressing both the caller's internal state and an external event.

136   Here, we aimed to test the hypothesis that social contexts promote the production of call

137   combinations in animal communication through investigating the combinatorial vocal

138   behaviour of meerkats. In line with previous work in primates showing broad usage of call

139   combinations in social situations, we expected call combinations to be widely used in social

140   situations. Furthermore, if social contexts represent an additional relevant pressure favourable

141   to the production of call combinations, we would expect meerkats to produce at least the

142   same combinatorial structures with the same relative frequency, in social as in predation

143   contexts.

144   Meerkats (*Suricata suricatta*) are a highly social species of cooperative breeding mongoose,

145   living in groups of 3 to 50 individuals (Clutton-Brock et al., 2006), with a well-studied vocal

146 repertoire, making them an ideal species in which to explore the extent of call combination

147 production and usage. They possess a rich vocal repertoire consisting of more than 30

148 discrete and graded call types (see supplementary material; Manser, 1998; Manser et al.,

149 2014). Meerkat call combinations have already been documented in predation contexts

150 (Manser, 2001; Manser, 2009). They produce unlimited repetitions of the same alarm call

151 type such as barks (Manser et al., 2014; Townsend, Charlton, & Manser, 2014). Meerkats

152 also produce graded mixed call combinations in which the aerial or terrestrial alarm calls

153 grade in urgency (Manser, Bell, & Fletcher, 2001). Finally, they emit discrete mixed call

154 combinations consisting of terrestrial predator alarm calls and 'animal moving' alarm calls

155 (Manser, 2009; Manser et al., 2014). However, little is known about meerkats' social call

156 combinations. We therefore established a repertoire of meerkat call combinations produced

157 specifically in social contexts. We analysed in which behavioural contexts call combination

158 types were produced and how context specific they were. Furthermore, to assess if there were

159 systematic differences in composition of the structurally more variable call combinations

160 between contexts, we noted what type the first call was, the proportions of their different

161 component call types and their context specificity.

162

163 MATERIAL & METHODS

164 *Study Site and Animals*

165 Long term observational data from the Kalahari Meerkat Project (KMP) collected between

166 1995 and 2014 has been the basis for identifying the different types of vocal combinations in

167 meerkats. An observer (KC) collected systematic data for this study between December 2013

168 and February 2014. The KMP is located in the South African Kalahari near Van Zylsrus

169 (26°58'S, 21°49'E) (for more details about the habitat and climate of the study site see

170 Clutton-Brock et al., 1998). All meerkats were habituated to human observers to the extent

171 that they allowed detailed observations and recordings within 0.5-3m. All individuals were

172 tagged with subcutaneous transponders as part of the long term data collection of the KMP

173 and marked with a unique combination of dye-marks for identification in the field (Jordan,

174 Cherry, & Manser, 2007).

175

176 *Recordings and Combination Analysis*

177 We systematically recorded the vocal combinations produced by 47 adult meerkats over one

178 year of age (17 females, 30 males) residing in eight different groups. Ten minute focal

179 recordings (Altmann, 1974) were made using a portable recorder (Roland R-26, Roland

180 Corporation, Hamamatsu, Japan) attached to a directional microphone (Sennheiser ME66/K6,

181 Sennheiser Electronic Corp., Old Lyme, CT, USA) (sampling frequency 44.1 kHz, 16 bits).

182 Comments on the meerkats' behaviour were recorded simultaneously onto the second

183 channel. The focal recordings took place in the morning, between the times when meerkats

184 emerged from the sleeping burrow and when they started to rest during the hottest part of the

185 day and again in the afternoon, from when they resumed foraging until they went back into

186 their sleeping burrow in the evening. These were the periods of the day when the meerkats

187 were the most active, socially and vocally. On average 60 minutes of usable recordings were

188 obtained each day (range: 10 – 130min). The subject's behaviour was classed as belonging to

189 one of eight categories which include the majority of behaviours meerkats perform on a daily

190 basis: relaxed, sunning, babysitting, digging, moving, vigilance, aggression or submission

191 (for definitions see Table 1).

192 In an attempt to document all meerkats' social call combinations, we included 'food

193 aggression call sequences' in our descriptions of meerkat call combinations, despite not

194 recording any during the two month focal observation period. This absence of food

195 aggression call sequences was potentially due to the high rainfall, and therefore high food

196 availability, during this short study period. Descriptions of this combination were based on

197 spectrograms from our long term recording database. In particular, we used food aggression

198 sequences elicited through food presentation experiments where a focal meerkat was fed a

199 scorpion and its vocalisations were recorded from a close distance. These calls were,

200 however, only used in a descriptive way and were not included in the quantitative analysis.

201 Praat software (www.praat.org) was used to visualise and categorise the call combinations

202 recorded. Systematically and objectively defining call combinations in animal

203 communication is problematic and many previous studies lack a quantitative approach

204 (Kershenbaum et al., 2014). In line with Crockford and Boesch (2005), who documented the

205 repertoire of social call combinations in chimpanzees, we defined a call combination as a

206 series of two or more calls that was clearly separated from the preceding and following calls

207 by a longer silence than those separating the calls within the combination. These

208 combinations could easily be distinguished by ear and the time separating two calls within a

209 combination was never longer than 1sec and often, depending on the length of the discrete

210 call types comprising the combination, much shorter, in the order of 0.01sec. Based on a

211 randomly selected subset of recordings (amounting to 4.5 hours of recording), mean (±SE)

212 silence duration between two calls within a combination was 0.05±0.003sec (min=0,

213 max=0.36), whereas the mean duration of a silence between two individual calls was

214 9.6±0.6sec (min=0.03, max=328) (Appendix Figure A1). Contrary to Crockford and Boesch

215 (2005), however, we also included sequences of the same call type as call combinations as we

216 aimed to document all combinations, including repetitions. The combinations and their

217 individual component calls were identified by visual and audio inspection of the

218 corresponding spectrograms. Additionally, two naïve observers independently classified a

219 randomly selected subset of the call combinations (N=560 combinations, 10% of total

220 dataset). Observer reliability was calculated using Cohen's Kappa coefficients, which

221 indicated substantial agreement (κ=0.74 and κ=0.80) (Landis & Koch, 1977). Combinations

222 were then classified according to their component calls: for example, combinations composed

223 of only one call type were identified as repetitions whereas combinations containing several

224 different call types were categorised as mixed combinations. The context of emission of a

225 combination was determined by the behaviour of the caller at that time. To control for a

226 potentially varying number of combinations emitted in each context, we then looked at the

227 proportions of each combination for each behavioural context. For combinations of three or

228 more calls comprising at least two call types, named 'long sequences', the length of the

229 combination in number of calls and the proportions of the different call types in each

230 combination were noted. Given that the first call-type of a sequence may encode initial

231 information or function to alert the receiver, as seems to be the case in certain guenon

232 species where the first call of a sequence functions as an attention getter (putty-nosed

233 monkey: Arnold & Zuberbühler, 2012), we also specifically noted the first call of the

234 sequence.

235

236 *Statistical Analysis*

237 All statistical analyses were carried out using R version 3.2.1 (R Core Team, 2015) and the

238 packages lme4 (Bates, Maechler, Bolker & Walker, 2015) and asbio (Aho, 2016). We

239 compared the production rate of call combinations in different continuous behavioural

240 contexts (babysitting, digging, sentinel and sunning) using a Mack-Skillings test. The Mack-

241 Skillings test is a Friedman-type statistic that can be used for block designs with missing data

242 (Chatfield & Mander, 2009). When a significant result was found, we carried out pairwise

243   Wilcoxon tests and corrected *P*-values for multiple testing using false discovery rate

244   (Benjamini & Hochberg, 1995).

245   In order to determine if the proportions of each combination type varied in relation to

246   behavioural context we ran a Generalized Linear Mixed Model (GLMM; Baayen, 2008) with

247   a binomial family and a logit link function for each combination type produced in more than

248   one context (8 GLMMs, data obtained from 45 individuals belonging to 8 groups). Context

249   was fitted as fixed effect and individual nested within group as random effect to control for

250   potential group or individual differences. Random slopes for context (Schielzeth &

251   Forstmeier, 2009) were specified for both random effects: group and individual. Additionally,

252   as we had several recordings from the same individual in the same context, we controlled for

253   pseudo-replication by fitting an observation level random term as random effect. This random

254   effect also controlled for over-dispersion (Harrison, 2014) which is sometimes an issue with

255   such models. We verified the dispersion of the models using overdisp_fun from glmm_funs.R

256   (Bolker et al., 2009). *P*-values close to 1 indicated that models were not over-dispersed. A

257   GLMM of the same format was run for each call type produced in a long sequence (5

258   GLMMs, *N* individuals=28, *N* groups=7) to analyse the proportions of the different call types

259   within the long sequences, again depending on context. Random intercept GLMMs were run

260   for each call type initiating long sequences (4 GLMMs, *N* individuals=28, *N* groups=7), to

261   determine if call type initiating long sequences varied with context.

262   A GLMM (*N* individuals=28, *N* groups=7) with a Poisson family and a log link function was

263   used to analyse the number of calls in the long sequence. Context was fitted as fixed effect

264   with random slopes and individual nested within group as random effect. We controlled for

265   over-dispersion of the data by creating an observation level random term that was fitted as

266   random effect (Harrison, 2014).

267   For all models overall *P*-values were obtained using likelihood ratio tests, in which the full

268   model was compared to a null model containing only the random factors, slopes and

269   intercept. For pairwise comparisons of contexts, *P*-values were obtained from the coefficients

270   of the model summary. GLMMs were relevelled to obtain *P*-values for all pairwise

271   comparisons. When multiple GLMMs were carried out on the same dataset, *P*-values were

272   adjusted to correct for multiple testing using false discovery rate (Benjamini & Hochberg,

273   1995).

274   In order to check whether any one individual strongly affected our results, we re-ran each

275   model, removing sequentially each individual from the dataset, and compared the coefficients

276   to those obtained from the model with the full dataset (Hedwig, Mundry, Robbins, & Boesch,

277   2014). Where our findings were significant, we observed little variation in the coefficients of

278   the models when an individual was removed from the model. However, there were some

279   appreciable differences in coefficients related to some of our non-significant results,

280   indicating that effects could be stronger than suggested by our models (Hedwig et al., 2014).

281

282   *Ethical Note*

283   All data collection adhered to ASAB guidelines. This study was purely observational, with no

284   invasive or experimental procedures conducted as part of it. The study population was

285   habituated to observers following them at a close distance all day and to microphones. Care

286   was taken not to disturb the meerkats' daily routine during observations. All research was

287   conducted under the permission of the ethical committee of Pretoria University and the

288   Northern Cape Conservation Service, South Africa (Permit number: EC011-10).

289

290   RESULTS

291   Over a period of two months we obtained more than 2700 minutes (around forty five hours)

292   of focal recordings (mean±SE=57±4 (range 10 to 117) minutes of observation per meerkat).

293   Forty-five out of the forty-seven meerkats produced call combinations (122±20 (range 2 to

294   571) combinations recorded per meerkat). On average the meerkats that combined calls

295   emitted 2.6±0.7 (range 0.1 to 10.2) combinations per minute of recording. Rate of production

296   of call combinations varied between the different continuous behavioural contexts that

297   typically last more than a few seconds (Mack-Skillings, MS_{46} test statistic=87, $P<0.001$;

298   Figure 2). Subjects produced call combinations at lower rates while digging (0.2±0.1

299   combinations/min) than while sunning (3.6±0.8 combinations/min), babysitting (5.0±1.4

300   combinations/min.) or while on sentinel (7.0±1.2 combinations/min) (pairwise Wilcoxon test,

301   respectively $P<0.001$, $P<0.001$ and $P<0.001$). They also produced combinations at

302   significantly lower rates while sunning than during sentinel behaviour (Wilcoxon test,

303    $P=0.04$). There were no significant differences in combination production rates between

304   sunning and babysitting, and between babysitting and sentinel behaviour (Wilcoxon test,

305   respectively $P=0.33$ and $P=0.34$).

306

307   *Meerkat Call Combination Types and Contexts of Production*

308   Based on our long-term adlib vocal data and focal recordings over the two-month study

309   period, meerkats produced twelve different types of combinations from seven discrete call

310   types (see Figure 1). All four classes, belonging to both categories of combination were

311   represented: unlimited and finite repetitions and graded and discrete mixed call combinations

312   (see Table 2). The call combinations differed in how frequently they were recorded during

313   the two-month focal observation period, with 'two short calls' (hereafter sc.2) being recorded

314   the most often (3361 times) whereas 'chatter call sequences' were recorded the least (9

315   times), and no food aggression call sequences were recorded during the same period (see

316   supplementary material). The discrete call types that were recorded as part of a call

317   combination are described in Figure 3.

318   Focal subjects produced call combinations in all eight of the predefined contexts: aggression,

319   babysitting, digging, moving, relaxed, submission, sunning and vigilance (see Table 1). Four

320   call combinations, composed of context-specific calls, were produced exclusively in one

321   behavioural context. 'Moving call sequences' were only emitted in the moving context,

322   chatter call sequences were emitted only in the aggression context and 'submission call

323   sequences' only in the submission context. Additionally, food aggression call sequences were

324   only obtained during food competition events.

325   The eight other call combination types were produced in more than one behavioural context.

326   Whilst longer 'short call sequences' (sc.>4), 'mixed short call sequences' (sc+) and 'quasi-

327   combinations' (qc) were never produced in the digging context the remaining call

328   combinations (sc.2, 'three short calls' (sc.3), 'four short calls' (sc.4), long sequences and 'di-

329   drrr calls') were produced in all contexts. The proportions of specific call combinations

330   emitted in relation to the total number of call combinations produced varied with context: this

331   was the case for sc.2 (GLMM, χ^2_5=19, P=0.002, P_{adj}=0.005), sc.4 (GLMM, χ^2_2=11, P=0.003,

332   P_{adj}=0.006), di-drrr calls (GLMM, χ^2_5=19, P=0.002, P_{adj}=0.005) and long sequences (GLMM,

333   χ^2_3=17, P=0.001, P_{adj}=0.005) (see Table 3 and Figure 4). Meerkats produced a lower

334   proportion of sc.2 and a higher proportion of long sequences in the moving context than in

335   any other context (see Table 3). Sc.2, the most frequently produced combination, was given

336   in higher proportions in the vigilance and sunning contexts. Di-drrr combinations were

337   produced in the lowest proportions in the vigilance contexts.

338

Long Sequences

340   Long sequences, whose component calls include 'short calls' (sc), qc, di-drrr calls, 'lead

341   calls' and 'moving calls', were produced by meerkats in six out of the eight contexts, with the

342   majority produced in the moving context (131/194). Of the 194 long sequences produced,

343   few were emitted in the digging and relaxed contexts (recorded 2 and 5 times respectively)

344   and so these contexts were excluded from the analysis. Five other sequences were not of

345   sufficient quality to identify the calls composing them. In total 182 long sequences were of

346   high enough quality to include in the analysis. No long sequences were produced in the

347   aggression and submission contexts

348   The length (number of calls) of long sequences varied with the context (GLMM, $\chi^2_3=9$,

349   $P=0.035$) (see Figure 5). Long sequences contained the most calls when produced in moving

350   contexts (10 ± 0.6) and the fewest calls when produced in babysitting contexts (5.3 ± 0.6). We

351   found no significant difference in number of calls in the long sequences between sunning

352   (7.9 ± 1.4) and vigilance (6.6 ± 0.9) contexts.

353   Investigating the call types that initiated long sequences, we found that only the proportion of

354   long sequences starting with a di-drrr call varied with context (GLMM, $\chi^2_2=11$, $P=0.004$,

355   $P_{adj}=0.02$). Specifically, there was a higher proportion of long sequences initiated by a di-drrr

356   call in the babysitting context (14/28) than in the other contexts. A lower proportion of long

357   sequences started with a di-drrr call in the moving and vigilance contexts (respectively

358   24/126 and 1/18), and no long sequences started with a di-drrr call in the sunning context

359   (0/10). The proportion of long sequences starting with the other call types did not vary

360   between contexts (GLMM, sc: $\chi^2_3=4$, $P=0.4$, $p_{adj}=0.3$; lead calls: $\chi^2_2=2$, $P=0.4$, $P_{adj}=0.4$;

361   moving calls: $\chi^2_3=4$, $P=0.3$, $P_{adj}=0.4$; qc: $\chi^2_3=4$, $P=0.2$, $P_{adj}=0.4$).

362   There was a trend for the proportions of lead calls within a long sequence to vary with

363   context (GLMM, $\chi^2_2=8$, $P=0.014$, $P_{adj}=0.070$) (see Figure 6). Long sequences produced in the

364   moving context consisted of a lower proportion of sc than the sunning contexts. We found no

365   significant difference in the proportion of the other call types in long sequences between

366   contexts (GLMM, di-drrr: $\chi^2_3=6$, $P=0.12$, $P_{adj}=0.20$; sc: $\chi^2_3=6$, $P=0.09$, $P_{adj}=0.20$; moving

367   calls: $\chi^2_3=1$, $P=0.70$, $P_{adj}=0.70$; qc: $\chi^2_3=3$, $P=0.45$, $P_{adj}=0.57$).

368

369   DISCUSSION

370   In this study we quantified the production of call combinations by wild meerkats in social

371   contexts in order to test the prediction that call combinations should be widespread in such

372   contexts. We first discuss call combinations as part of social communication. Secondly, we

373   consider possible mechanisms underlying call combination production. Thirdly, we compare

374   call combination use in social and predation contexts. Finally, we discuss potential

375   implications of this study for research into human language evolution.

376

377   *Call Combinations as part of Social Communication*

378   In this study, we have shown that meerkats produce twelve different types of call

379   combinations from seven discrete call types and these call combinations were emitted across

380   all of the eight main social contexts. This frequent and broad occurrence implies that call

381   combinations represent a non-negligible part of social communication for this species. These

382   results fall in line with previous research in some primate species for which high rates of call

383   combination production overall were also shown. For example 49% of chimpanzee calls

384   (Crockford & Boesch, 2005) and 38% of wedge-capped capuchin (*Cebus olivaceus*) calls

385   were produced in combinations (Robinson, 1984).

386 We identified call combinations produced in social contexts that fitted the definitions of the

387 two main categories of combination: repetitions of the same call type and mixed call

388 combinations, comprising several discrete call types. Repetitions, containing only one call

389 type, differed from one another either in terms of the call type repeated (e.g. chatter calls vs

390 short calls) or by the number of repetitions (e.g. within short call sequences: sc.2 vs sc.3).

391 Mixed call combinations likewise differed in component call types (for example, di-drrr calls

392 comprised two distinct call types, a short call and a wheek call whereas call sequences in the

393 context of food competition comprised various gradations of aggression calls). Mixed call

394 combinations also showed more variation within a combination type, for example individual

395 long sequences differed in component calls, number of calls and call order. Additionally,

396 some long sequences seemed to have a higher structural complexity with combinations

397 embedded inside other combinations, such as long sequences including di-drrr calls, which

398 are themselves mixed combinations (see above).

399 Structurally complex combinations that include other combinations have been observed in the

400 closely related banded mongoose. Specifically, banded mongooses can combine their close

401 calls with distinct, additional calls producing new combinations in three contexts: leading the

402 group, lost from the group or in excitement at rain or wet ground (Jansen, 2013). The close

403 calls themselves are composed of two acoustic segments, an initial noisy segment and a

404 second harmonic segment. Acoustic analysis has shown that the initial noisy part carries

405 information about the caller's identity whereas the second harmonic part carries information

406 about the caller's activity (Jansen et al., 2012). Hence, in these combinations, banded

407 mongoose could potentially indicate the caller's identity, its activity and an external event

408 such as the beginning of rain. However, so far it has not been tested what information

409 receivers actually extract from such a combination. In line with this, we have yet to

410 investigate what information receivers extract from call combinations, and in particular from

411   long sequences, in meerkats. One possibility is that more complex combinatorial structures

412   encode a greater variety of information. However, in some cases, the variation in complexity

413   itself may carry information, regarding, for example, the caller's quality, as is the case in

414   European starling (*Sturnus vulgaris*) song (Mountjoy & Lemon, 1991).

415   The fact that combinations of similar structural complexity are found in two closely related

416   mongoose species could indicate that combinatorial tendency per se is a shared trait inherited

417   through common descent. However, these species also share similarities in their social

418   structure, both being group living, cooperative breeders, albeit with meerkats having a more

419   despotic hierarchy (Manser et al., 2014). This social structure may have favoured the

420   production of call combinations in these species given that it has been hypothesized that new

421   inferential processes evolve when communication is driven by more cooperative motives

422   (Vygotsky, 1980 cited by Pika & Bugnyar, 2011). Comparative analyses of the

423   communication systems of species from different taxa and/or social systems are needed to

424   shed light on the evolution of communicative complexity and combinatoriality which could

425   in turn help disentangle these two alternative possibilities.

426

427   *Mechanisms of Call Combination Production*

428   Through systematically documenting the structural variance underlying sequences of calls,

429   our work suggests there may be two primary combinatorial operations that guide meerkat call

430   combination production. The first is where each individual call within the combination is

431   associated with the caller's internal state and the caller emits these calls sequentially as the

432   situation unfolds. The resulting call combinations could therefore reflect the persistence of a

433   single internal state of the caller, as is probably the case for unlimited repetitions such as

434   meerkat submission or chatter call sequences. Alternatively, the call combinations could

435 reflect the caller's changing internal states, potentially induced by changes in external events

436 (e.g. approach of a rival), which can emerge in two ways. Firstly, the change in internal state

437 could be due to variations in emotion, in particular arousal. For example, in graded food

438 aggression call sequences, the individual calls can reflect varying levels of aggression, where

439 the motivation stays the same, but the arousal changes. Secondly, the change in internal state

440 leading to the production of a call combination could be linked to varying motivations. In

441 meerkats, long sequences may be an example of such a combination with the different

442 component calls reflecting different motivations, though this remains to be tested. The

443 production of combinations linked to differing motivations has been reported in several

444 primate species (Cleveland & Snowdon, 1982; Robinson, 1984; Crockford & Boesch, 2005;

445 Rothacher, 2013) where combinations are produced in contexts intermediate to those of the

446 individual component calls. The production of such call combinations that might depend on

447 internal state could be argued to rely on relatively simple proximate mechanisms and our

448 work suggests that changes in arousal could lead to the use of graded mixed call

449 combinations whereas changes in motivation can lead to the use of discrete mixed call

450 combinations.

451 The second combinatorial operation by which other call combinations seem to be produced is

452 less flexible. In these combinations the component calls cannot be freely combined, they

453 always appear in a stereotyped order and/or number of occurrences. One example of such a

454 combination from our data set would be the di-drrr calls which always consisted of a short

455 call followed by a wheek call, with call order and call number remaining unchanged for all of

456 the 530 exemplars recorded. Such call combinations do not seem to be the result of changing

457 or conflicting internal states but may reflect a particular consistent internal state or external

458 event.

459   To determine which of these two mechanisms is used for the production of a combination,

460   callers could be observed in situations leading either to i) varying levels of arousal or to ii)

461   several motivations. One could then record if the individual component calls reflect the

462   immediate arousal or the motivational state of the caller or, rather, if they are always emitted

463   in a stereotyped order. Documenting the proximate mechanisms by which calls come to be

464   associated with other calls is particularly important as it will lead to a better understanding of

465   the evolutionary scenario accompanying the emergence of combinatoriality in general.

466

467   *Social vs Predation Contexts*

468   When analysing social call combinations, we noticed certain similarities with call

469   combinations produced in predatory contexts. Specifically, meerkats emit three of the

470   combination classes in both contexts: unlimited repetitions, graded and discrete mixed call

471   combinations. Unlimited repetitions in social contexts, such as submission or chatter call

472   sequences, seem to have the same function as those produced in predation contexts, such as

473   bark call sequences (Manser et al., 2014; Townsend et al., 2014): to indicate the persistence

474   of a state either internal or external of the signaller. In the case of graded mixed call

475   combinations, graded alarm call sequences seem to be produced in a similar way to food

476   aggression call sequences with the variation in structure of the calls reflecting a change in the

477   caller's arousal, here in terms of alertness or aggressiveness respectively. However, the

478   discrete mixed call combinations in the social and predation situations seem to present some

479   differences. This type of combination in social contexts seems to either be produced as a

480   single unit such as the di-drrr call or perhaps, in the case of the long sequences, may reflect

481   the caller's multiple or conflicted motivations. On the other hand, in the terrestrial-animal

482   moving sequence meerkats produce sequences of terrestrial alarm calls and animal moving

483   calls, normally given to moving animals regardless of whether they are dangerous or not, in

484   response to moving terrestrial predators (Manser, 2009; Manser et al., 2014). This sequence

485   combines two functionally referential calls to produce a new meaning derived from the

486   meaning of the component calls. It is possible to compare this combination with a simple

487   two-expression package akin to those seen in early developing languages or when children

488   initiate their syntactic development (Hurford, 2011). This sequence could therefore be

489   considered as a more syntax-like combination, where syntax is the level of combinatoriality

490   in which meaningful morphemes or words are combined into larger structures such as

491   sentences in human language (de Boer, Sandler, & Kirby, 2012). Lastly, finite repetitions

492   seem to be a class of combinations specific to social contexts in meerkats as they are not

493   found in predation contexts (Manser et al., 2014). Thus, whilst meerkats do seem to produce

494   more classes of combinations in social contexts as opposed to predation contexts, at present,

495   they do not seem to produce meaningful syntax-like combinations in the former.

496   Meerkat call combinations in the social context could be argued to surpass those in predatory

497   contexts in variety, both in classes and complexity. This would seem to support the

498   hypothesis that social contexts are important in selecting for combinations because of the

499   variety of behaviours and interactions they involve that are coordinated by vocalisations

500   (Collier et al., 2014). In line with this, previous modelling work has indicated that when

501   behaviours and interactions outweigh the number of discrete vocalisations in the species

502   vocal repertoire one solution to this pressure involves the concatenation of calls (Nowak et

503   al., 2000). The extent to which social and ecological pressures contribute to promoting

504   combinatoriality requires further work, though comparisons with other species, particularly in

505   terms of the forms sequences take in social and ecological contexts, is one valuable way to do

506   this.

507   Despite apparent differences in terms of types and complexity of call combinations emitted in

508   social and predation contexts, meerkats seem to produce an arguably more syntax-like

509   combination in the predation but not social context. Other well-known examples of syntax-

510   like call combinations, such as Campbell monkey alarm calls (Ouattara et al., 2009), are also

511   produced in a predation context. It therefore appears that certain combinations in predation

512   contexts seem to be, at least on the surface level, more similar to human forms of

513   combinatoriality than those produced in social situations. Given the survival benefits

514   associated with efficiently transferring more specific information in dangerous contexts, it

515   could be hypothesised that alarm contexts may select for less ambiguous (and hence

516   referential) sequences. Deconstructing the meaning of the combination as a function of the

517   meaning of the individual calls may then be easier compared to combinations composed of

518   non-referential calls which could, in turn, lead to a bias in identifying syntax-like

519   combinations in predation as opposed to social contexts. Whilst these considerations should

520   be taken into account when investigating the form and function of animal call combinations,

521   our data indicates that both social and predation pressures play important roles in the

522   emergence of cognitive abilities facilitating the production and perception of call

523   combinations.

524

525   *Human Language Evolution*

526   Comparative studies looking at call combinations in animal communication systems are one

527   method of exploring the evolution of language and in particular its combinatorial layers,

528   phonology and syntax. These forms of articulation have received renewed empirical interest

529   over the years given that they are fundamental in facilitating the creation of a large lexicon

530   out of relatively few sounds: a central feature of human language (Hockett, 1960; Hurford,

531   2008; Hurford, 2011). An increased focus on call combinations, particularly in social

532   contexts may reveal combinations to be more widespread in animal vocal communication

533   than previously documented. However, in meerkats it is worth noting that the production of at

534   least some of these combinations seem to result from simple mechanisms far removed from

535   the complexity of human syntax. Whilst in meerkats, combinations in predation contexts

536   might be more syntax-like and therefore afford better opportunities for comparative research,

537   studying more "primitive" social combinations could also help better understand, at the

538   proximate level, how combinations emerge in the first place.

539

540   *Conclusion*

541   In conclusion, meerkats frequently use call combinations across a wide variety of social

542   contexts. Although several classes of combination are found in both social and predation

543   contexts, there seems to be more classes of combinations, some of which present a higher

544   complexity, in the social situations. Whilst animal call combinations have been often

545   described in alarm contexts, our study on meerkats indicates that social contexts are at least

546   as important for the study of call combinations in animal communication as predation

547   contexts. Future research needs to complement our findings by investigating exactly how

548   receivers perceive social call combinations in meerkats in order to fully identify the function

549   of call combinations in animal communication.

550   Combinatoriality is one way by which information output can be increased in spite of a

551   limited number of signals. Despite its importance, particularly in the case of vocal

552   communication, little is known about the pressures that select for combinatoriality. Further

553   research on call combinations between and across species and contexts is necessary to shed

554   more light on how and why combinatoriality emerged.

555

572

573   Figure 1: Spectrograms of the different call combinations produced by meerkats. A: unlimited

574   repetitions, including a) submission call sequence, b) chatter call sequence, c) moving call sequence,

575   and d) short call sequence. B: finite repetitions, including e) two short calls, f) three short calls, g)

576   four short calls, and h) quasi-combination. C: graded call combinations, including i) food aggression

577   call sequence. D: discrete mixed call combinations, including j) di-drrr, k) mixed short call sequence

578   and l) long sequence. The time and frequency scales apply to all spectrograms.

579

Figure 2: Mean production rate of call combinations in relation to continuous behavioural context.

Significance: *: P<0.05; ***: P<0.001.

582

Figure 3: Description of the main call types comprising meerkat call combinations and the contexts

they are produced in. The time and frequency scales apply to all spectrograms.

585

586

Figure 4: Proportions of the eleven different call combination types collected in the two-month field

period in the eight different behavioural contexts. ls: long sequence; qc: quasi-combination; sc.>4:

short call sequence; sc.2: two short calls; sc.3: three short calls; sc.4: four short calls; sc+: mixed short

call sequence. N indicates the number of combinations recorded in a context

591

592

Figure 5: Length of long sequences, in number of component calls, produced in different behavioural

contexts. Boxplot shows the median, interquartiles and range.

595

596

Figure 6: Mean proportions of the different call types composing long sequences produced in different

behavioural contexts.

599

600

601   Figure A1: Duration of silence between calls within a combination and between
602   combinations or individual calls, measured for a randomly selected subset of sound files
603   amounting to 4.5 hours of recordings.

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Table 1: Description of the behavioural contexts in which the meerkats produced call combinations.

Context	Description
Relaxed	Includes huddling, where several meerkats gather together in a tight group; autogrooming and allogrooming (delBarco-Trillo et al., 2016); contact lying (Habicher, 2009)
Sunning (or sunbathing)	Sitting or standing on hind legs in the sun, often in close proximity to the sleeping burrow (Habicher, 2009)
Babysitting	Remaining at the sleeping burrow with pups while the rest of the group forages (Clutton-Brock et al., 1998)
Digging	Includes foraging for food (Doolan & Macdonald, 1996) and renovating sleeping burrows (Manser & Bell, 2004)
Moving	Walking or running (Habicher, 2009)
Vigilance	Includes sentinel behaviour and scanning the environment for predators while on all fours, sitting or standing on hind legs (delBarco-Trillo et al., 2016)
Aggression	Food competition, displacement and fights (delBarco-Trillo et al., 2016)
Submission	Approaching a dominant individual in a crouched position (delBarco-Trillo et al., 2016)

Table 2: The different types of combinations produced by meerkats in non-urgent contexts.

Category	Class	Combination	Description
Repetitions	Unlimited	Submission call sequence	Repetition of submission calls of undetermined length
		Chatter call sequence	Repetition of chatter calls of undetermined length
		Moving call sequence	Repetition of moving calls of undetermined length
		Short call sequence (sc.>4)	Repetition of more than 4 short calls
	Finite	2 short calls (sc.2)	Repetition of 2 short calls
		3 short calls (sc.3)	Repetition of 3 short calls
		4 short calls (sc.4)	Repetition of 4 short calls
		Quasi-combination (qc)	Repetition of 2 short calls with no silence between them
Mixed call combinations	Graded	Food aggression sequence	Two acoustically different aggression calls grading into each other with intermediate calls, likely related to low and high arousal
	Discrete	Di-drrr calls	A short call followed by a longer wheek call, potentially with modulation
		Mixed short call sequence (sc+)	Sequence containing a short call and one or two quasi-combinations or di-drrrs
		Long sequence	Sequence containing 3 or more calls and at least two different call types

Table 3: Comparison of the proportions of call combination types produced in different behavioural contexts.

		Sunning	Relaxed	Babysitting	Digging	Moving	Vigilance
Sunning	sc.2		↑ than relaxed; P<0.001	↑ than babysitting; P<0.001	↑ than digging; P<0.001	↑ than moving; P<0.001	↓ than vigilance; P<0.001
	sc.3		NS overall	NS overall	NS overall	NS overall	NS overall
	sc.4		—	NS; P=0.451	—	—	NS; P=0.294
	sc.>4		—	NS overall	—	NS overall	NS overall
	sc+		—	NS overall	—	—	NS overall
	qc		—	NS overall	—	—	NS overall
	di-drrr		NS; P=0.418	↓ than babysitting; P=0.043	↓ than digging; P<0.001	↓ than moving; P<0.001	NS; P=0.483
	ls		—	NS; P=0.198	—	↓ than moving; P<0.001	NS; P=0.198
Relaxed	sc.2	↓ than sunning; P=0.033		NS; P=0.638	NS; P=0.638	↑ than moving; P=0.001	↓ than vigilance; P=0.051
	sc.3	NS overall		NS overall	NS overall	NS overall	NS overall
	sc.4	—		—	—	—	—
	sc.>4	—		—	—	—	—
	sc+	—		—	—	—	—
	qc	—		—	—	—	—
	di-drrr	NS; P=0.418		NS; P=0.199	NS; P=0.138	NS; P=0.138	NS; P=0.330
	ls	—		—	—	—	—
Baby-sitting	sc.2	↓ than sunning; P=0.028	NS; P=0.638		NS; P=0.414	↑ than moving; P<0.001	↓ than vigilance; P=0.075
	sc.3	NS overall	NS overall		NS overall	NS overall	NS overall
	sc.4	NS; P=0.451	—		—	—	NS; P=0.294
	sc.>4	NS overall	—		—	NS overall	NS overall
	sc+	NS overall	—		—	NS overall	NS overall
	qc	NS overall	—		—	—	NS overall
	di-drrr	↑ than sunning; P=0.043	NS; P=0.199		NS; P=0.145	NS; P=0.138	NS; P=0.106
	ls	NS; P=0.207	—		—	↓ than moving; P=0.025	↑ than vigilance; P=0.046

		Sunning	Relaxed	Babysitting	Digging	Moving	Vigilance
Digging	sc.2	↓ than sunning; P=0.012	NS; P=0.563	NS; P=0.293		↑ than moving; P=0.022	↓ than vigilance; P=0.012
	sc.3	NS overall	NS overall	NS overall		NS overall	NS overall
	sc.4	—	—	—		—	—
	sc.>4	—	—	—		—	—
	sc+	—	—	—		—	—
	qc	—	—	—		—	—
	di-drrr	↑ than sunning; P<0.001	NS; P=0.138	NS; P=0.145		NS; P=0.760	↑ than vigilance; P=0.001
	ls	—	—	—		—	—
Moving	sc.2	↓ than sunning; P<0.001	↓ than relaxed; P=0.001	↓ than babysitting; P<0.001	↓ than digging; P=0.028		↓ than vigilance; P<0.001
	sc.3	NS overall	NS overall	NS overall	NS overall		NS overall
	sc.4	—	—	—	—		—
	sc.>4	NS overall	—	NS overall	—		NS overall
	sc+	—	—	—	—		—
	qc	NS overall	—	—	—		—
	di-drrr	—	NS; P=0.138	NS; P=0.139	NS; P=0.537		↑ than vigilance; P<0.001
	ls	↑ than sunning; P<0.001	—	↑ than babysitting; P=0.025	—		↑ than vigilance; P=0.001
Vigilance	sc.2	NS; P=0.945	↑ than relaxed; P=0.052	NS; P=0.193	↑ than digging; P=0.021	↑ than moving; P<0.001	
	sc.3	NS overall	NS overall	NS overall	NS overall	NS overall	
	sc.4	NS; P=0.294	—	NS; P=0.294	—	NS; P=0.746	
	sc.>4	NS overall	—	NS overall	—	NS overall	
	sc+	NS overall	—	NS overall	—	NS overall	
	qc	NS overall	—	NS overall	—	NS overall	
	di-drrr	NS; P=0.483	NS; P=0.317	NS; P=0.106	↓ than digging; P=0.001	↓ than moving; P<0.001	
	ls	NS; P=0.192	—	↓ than babysitting; P=0.046	—	↓ than moving; P=0.001	

↑: higher proportion; ↓: lower proportion; NS: Non-significant difference; —: combination type not produced in this context. *P*-values adjusted using false discovery rate.
sc.2: two short calls; sc.3: three short calls; sc.4: four short calls; sc.>4: short call sequence; sc+: mixed short call sequence; qc: quasi-combinations; ls: long sequence.

Table A1: Meerkat calls and the contexts they are produced in according to Manser (1998).

Context	Call	Single/Multiple element	Discrete/Graded
Spatial coordination	Close call	Single	Discrete
	Joining call	Multiple	Discrete
	Leading call	Single/Multiple	Graded
	Lost call	Single	Discrete
	Moving call	Single/Multiple	Graded
Social interaction	Aggression call	Single/Multiple	Graded
	Chatter call	Multiple	Discrete
	Grooming call	Single/Multiple	Discrete
	Submissive call	Multiple	Discrete
Social interaction & sentinel duty	Single note call	Single	Discrete
Sentinel duty	Di-drrr call	Multiple	Discrete
	Double note call	Multiple	Discrete
	Triple note call	Multiple	Discrete
	Multiple note call	Multiple	Discrete
	Wheek call	Single	Discrete
Alarm call	Aerial alarm call	Single/Multiple	Graded
	High pitched barking	Single/Multiple	Discrete
	Moderate alarm call	Single/Multiple	Graded
	Panic call	Single	Graded
	Recruitment call	Single/Multiple	Graded
	Rolling alarm call	Single	Graded
	Spitting call	Single/Multiple	Discrete
	Terrestrial alarm call	Single/Multiple	Graded
	Worry call	Single/Multiple	Graded
Alarm call & spatial coordination	Barking call	Single/Multiple	Discrete
Calls given by pups	Begging call (pup)	Single/Multiple	Graded
	Chatter call (pup)	Single/Multiple	Graded
	Digging call (pup)	Single	Graded
	Eating call (pup)	Single	Graded
	Excited call (pup)	Multiple	Graded
	Joining call (pup)	Multiple	Discrete
	Lost call (pup)	Single	Discrete
	Moving off call (pup)	Multiple	Discrete
	Sleeping call (pup)	Single	Discrete
	Spitting call (pup)	Single/Multiple	Discrete

Following Catchpole & Slater (2003) an element is defined as a continuous trace on a spectrograph.

Table A2: Number of times each combination type was recorded during the two-month study Period.

Combination	Occurrence
Submission call sequence	24
Chatter call sequence	9
Moving call sequence	22
sc.>4	150
sc.2	3361
sc.3	666
sc.4	178
qc	198
Di-drrr	530
Food aggression call sequence	0
sc+	149
Long sequence	195

Table A3: GLMM information.

Model	Data	Levels per fixed effect	Levels per random effect	
	Number of rows	Context	Group	Individual
Binomial GLMMs testing proportion of combinations in relation to context				
sc.2	270	Babysitting Digging Moving Relaxed Sunning Vigilance	8	45
sc.3	270	Babysitting Digging Moving Relaxed Sunning Vigilance	8	45
sc.4	135	Babysitting Sunning Vigilance	8	45
sc.>4	180	Babysitting Moving Sunning Vigilance	8	45
sc.+	135	Babysitting Sunning Vigilance	8	45
qc	135	Babysitting Sunning Vigilance	8	45
di-drrr	270	Babysitting Digging Moving Relaxed Sunning Vigilance	8	45
long sequence	180	Babysitting Moving Sunning Vigilance	8	45

Binomial GLMMs testing proportions of call types within long sequences in relation to context				
sc	182	Babysitting Moving Sunning Vigilance	7	28
qc	182	Babysitting Moving Sunning Vigilance	7	28
di-drrr	182	Babysitting Moving Sunning Vigilance	7	28
lead calls	172	Babysitting Moving Vigilance	7	28
move calls	182	Babysitting Moving Sunning Vigilance	7	28
Binomial GLMMs testing initial call type of long sequences in relation to context				
sc	112	Babysitting Moving Sunning Vigilance	7	28
qc	112	Babysitting Moving Sunning Vigilance	7	28
di-drrr	84	Babysitting Moving Vigilance	7	28
lead calls	84	Babysitting Moving Vigilance	7	28
move calls	112	Babysitting Moving Sunning Vigilance	7	28
Poisson GLMM testing long sequence length in relation to context				
Number of calls	182	Babysitting Moving Sunning Vigilance	7	28