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# Call concatenation in wild meerkats

1  
2  
3  
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.

26

27 Key Words: call combination - meerkat – natural observations – social context – vocal  
28 communication

29

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 (Rek, 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 *troglydytes*: 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](http://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 ( $\pm$ SE)  
212 silence duration between two calls within a combination was  $0.05\pm 0.003$ sec (min=0,  
213 max=0.36), whereas the mean duration of a silence between two individual calls was  
214  $9.6\pm 0.6$ sec (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 ( $\kappa=0.74$  and  $\kappa=0.80$ ) (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<sub>46</sub> 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,  $\chi^2_{5}=19$ ,  $P=0.002$ ,  $P_{adj}=0.005$ ), sc.4 (GLMM,  $\chi^2_{2}=11$ ,  $P=0.003$ ,  
332  $P_{adj}=0.006$ ), di-drrr calls (GLMM,  $\chi^2_{5}=19$ ,  $P=0.002$ ,  $P_{adj}=0.005$ ) and long sequences (GLMM,  
333  $\chi^2_{3}=17$ ,  $P=0.001$ ,  $P_{adj}=0.005$ ) (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

339 *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 ( $10\pm 0.6$ ) and the fewest calls when produced in babysitting contexts ( $5.3\pm 0.6$ ). We  
351 found no significant difference in number of calls in the long sequences between sunning  
352 ( $7.9\pm 1.4$ ) and vigilance ( $6.6\pm 0.9$ ) 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  $P_{\text{adj}}=0.02$ ). 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:  $\chi^2_3=4$ ,  $P=0.4$ ,  $p_{\text{adj}}=0.3$ ; lead calls:  $\chi^2_2=2$ ,  $P=0.4$ ,  $P_{\text{adj}}=0.4$ ;  
361 moving calls:  $\chi^2_3=4$ ,  $P=0.3$ ,  $P_{\text{adj}}=0.4$ ; qc:  $\chi^2_3=4$ ,  $P=0.2$ ,  $P_{\text{adj}}=0.4$ ).



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

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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

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

581 Significance: \*:  $P < 0.05$ ; \*\*\*:  $P < 0.001$ .

582

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

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

585

586

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

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

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

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

591

592

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

594 contexts. Boxplot shows the median, interquartiles and range.

595

596

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

598 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 wheel 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
<i>Binomial GLMMs testing proportion of combinations in relation to context</i>				
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
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