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## **Effect of group size and experience on the ontogeny of sentinel calling behaviour in meerkats**

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# Effect of group size and experience on the ontogeny of sentinel calling behaviour in meerkats

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## HIGHLIGHTS

- Meerkats started acting as sentinels as subadults around 200 days of age.
- They produced all six sentinel call types when they first acted as sentinel.
- Call rate of the different sentinel call types changed with experience.
- The acoustics of the common double note calls differed between individuals.
- Meerkats showed individual distinctiveness when they first acted as sentinel.

# 1 Effect of group size and experience on the ontogeny of sentinel 2 calling behaviour in meerkats

## 3 ABSTRACT

4 Increased vulnerability to predation results in young individuals of many species  
5 experiencing higher predation pressure than adults. Consequently, the production of  
6 antipredator-related calls by young can differ from the same vocalisations given by adults.  
7 Sentinel behaviour is a coordinated vigilance behaviour, where one individual climbs on  
8 an elevated position and scans the surroundings for predators, while the rest of the group  
9 is mainly foraging. Meerkat (*Suricata suricatta*) sentinels produce six distinct sentinel call  
10 types, which inform other group members about the perceived predation risk, resulting  
11 in the adjustment of personal vigilance behaviour in foraging group members. Here, we  
12 investigated the onset of sentinel behaviour and the ontogeny of the different sentinel call  
13 types as well as the development of individual vocal signatures in meerkats. Our results  
14 demonstrate that meerkats started acting as a sentinel around 200 days of age, but this  
15 was highly dependent on group size, with individuals from smaller groups exhibiting  
16 sentinel behaviour earlier than individuals from larger groups. All six sentinel call types  
17 were already present in the repertoire upon first emergence of the behaviour, however,  
18 call rates of 'all-clear' calls increased while 'warning' calls decreased with increasing  
19 experience as sentinel. Analysis of one of the most frequent sentinel calls, the double note  
20 calls, indicated that fundamental frequency, mean amplitude, duration and entropy  
21 differed consistently between individuals, but we found no effect of age. Rather, our  
22 results provide evidence that individual signatures in this call type were already  
23 developed when young meerkats first started to act as sentinel and changed little later on  
24 in age. To conclude, we show that overall sentinel behaviour as well as its vocal  
25 coordination undergo little ontogenetic change, indicating potentially high selection  
26 pressures on antipredator behaviours, such as the sentinel system, resulting in consistent  
27 behavioural response upon first emergence.

28

29

30 Keywords: acoustic communication, individual vocal signature, ontogeny, sentinel  
31 behaviour

32

### 33 INTRODUCTION

34 As a consequence of living in groups, some animals have evolved specific coordinated  
35 antipredator defence mechanisms (Krause & Ruxton, 2002; Kruuk, 1964; Zoratto,  
36 Santucci, & Alleva, 2009), such as sentinel behaviour (Horrocks & Hunte, 1986; Manser,  
37 1999; McGowan & Woolfenden, 1989). Sentinel behaviour is a coordinated vigilance  
38 behaviour mostly seen in cooperative breeders, where one individual climbs onto an  
39 elevated position and scans the surrounding for predators while the rest of the group is  
40 foraging (Bednekoff, 2015; Clutton-Brock, O'Riain, et al., 1999; Horrocks & Hunte, 1986;  
41 McGowan & Woolfenden, 1989; Ridley & Raihani, 2006; Wright, Berg, De Kort, Khazin, &  
42 Maklakov, 2001; Zahavi, 1990). Sentinels have been demonstrated to detect predators  
43 more frequently and from greater distances than foraging group members (Manser, 1999;  
44 Wright, Berg, de Kort, Khazin, & Maklakov, 2001) and foraging group members show a  
45 higher foraging efficiency when a sentinel is on guard (Hollén, Bell, & Radford, 2008;  
46 Manser, 1999).

47 When sentinels spot a predator, they produce alarm calls, allowing group  
48 members to initiate the proper antipredator behaviour (Bednekoff, 2001; Manser, 2001;  
49 Manser, Bell, & Fletcher, 2001; McGowan & Woolfenden, 1989; Rasa, 1989). Alarm calls  
50 represent a common antipredator strategy (Caro, 2005; Sherman, 1977), and are thought  
51 to be under strong selection. However, selection pressures can vary between different  
52 group members, and are generally higher for younger individuals than adults. Thus,  
53 offspring environment, including the mobility of young to move away from the nesting  
54 site or the presence of siblings (Berg, Beissinger, & Bradbury, 2013), as well as differences  
55 in predation risk due to higher vulnerability to predation in general or a different set of  
56 predators than adults, result in selection pressures that can be very different from those  
57 of adults. Consequently, alarm calls produced by young individuals have been  
58 demonstrated to differ from calls produced by adults on three levels: i) vocal production:

59 the development of species-specific calls with a specific set of acoustic properties; ii) vocal  
60 usage: the correct choice of call types given the context; and iii) response: the  
61 development of the appropriate response to conspecific calls (Hollén & Radford, 2009;  
62 Seyfarth & Cheney, 1986). In meerkats (*Suricata suricatta*), for example, it has been  
63 shown that young produce higher pitched and longer calls (Hollén & Manser, 2007), they  
64 call more often in response to non-threatening stimuli (Hollén, Clutton-Brock, & Manser,  
65 2008) and newly emerged young show stronger responses to alarm calls which over the  
66 course of ontogeny become more and more adult-like (Hollén & Manser, 2006).

67         Animals with individually distinct calls including some birds (Jouventin & Aubin,  
68 2002; Lefevre, Gaston, & Montgomerie, 2001; Radford & Ridley, 2008), primates  
69 (Cleveland & Snowdon, 1982; Miller & Thomas, 2012; Salmi, Hammerschmidt, & Doran-  
70 Sheehy, 2014; Snowdon & Cleveland, 1980), hyenas (Theis, Greene, Benson-Amram, &  
71 Holekamp, 2007) and social mongooses (Jansen, Cant, & Manser, 2012; Manser, 1999;  
72 Sharpe, Hill, & Cherry, 2013) provide another aspect of vocal ontogeny: the ontogenetic  
73 development of acoustic individuality. Individually distinct vocalisations allow receivers  
74 to adjust their behavioural response to the caller identity (Salmi et al., 2014). In the  
75 context of mother offspring behaviour, discrimination among individuals based on vocal  
76 signals provides the potential for reliable recognition of dependent offspring and  
77 therefore offspring survival while avoiding misdirected maternal care (Briefer &  
78 McElligott, 2011; Volodin, Lapshina, Volodina, Frey, & Soldatova, 2011). In the context of  
79 anti-predatory behaviours, group members of various species have been demonstrated  
80 to adjust the response to alarm calls depending on the identity of the caller (or some  
81 characteristics of the caller) and the associated quality and relevance of the provided  
82 information (Blumstein & Daniel, 2004; Blumstein, Verneyre, & Daniel, 2004; Hare &  
83 Atkins, 2001; Ramakrishnan & Coss, 2000). However, whether individuals already  
84 possess individually distinctive calls when they first start producing the relevant call

85 types, such as alarm calls, or whether this is something that develops during vocal  
86 ontogeny often remains unknown (but see (Schneiderova et al., 2015).

87           In addition to alarm calls, sentinels in some species continuously produce specific  
88 sentinel calls, in social mongooses also referred to as “Watchman’s song”, which allow  
89 foraging group members to obtain acoustic information about the presence of a sentinel  
90 individual (Hollén, Bell, et al., 2008; Manser, 1999; Rasa, 1986). The structure and  
91 information content of sentinel vocalisations varies greatly, with some species producing  
92 one type of sentinel call to announce their presence (pied babbler (*Turdoides bicolor*): (Hollén et al., 2011)). In contrast, others produce graded information contained in the call  
93 rate of one (dwarf mongoose (*Helogale parvula*): (Kern & Radford, 2013)) to several  
94 sentinel call types (meerkats): (Rauber, Kranstauber, & Manser, 2020; Rauber & Manser,  
95 2017)), which informs the rest of the group about temporary changes in the perceived  
96 predation risk. However, little is known about the ontogeny of sentinel behaviour  
97 (Bednekoff, 2015), and nothing about the ontogeny of sentinel vocalisations. Thus, it  
98 remains unknown at what age the different sentinel calls are exhibited and whether and  
99 how sentinel calls produced by young differ from those produced by adults.  
100

101           In this study we investigated the onset and vocal ontogeny of sentinel behaviour  
102 in meerkats. Meerkats are small, highly sociable mongoose occurring in the Kalahari  
103 Desert in southern Africa (Clutton-Brock, Gaynor, et al., 1999; Clutton-Brock & Manser,  
104 2016). They are cooperative breeders living in groups of three to 50 individuals (average  
105 17), containing one dominant breeding pair and multiple subordinate helpers, which help  
106 to rear the dominant’s offspring by providing them with food and protection (Clutton-  
107 Brock et al., 1998; Clutton-Brock, Gaynor, et al., 1999; Clutton-Brock & Manser, 2016).  
108 Although all members of a group contribute to sentinel behaviour, individual  
109 contributions vary within and between groups (Clutton-Brock, O’Riain, et al., 1999;  
110 Rauber & Manser, 2018), whereby individuals from smaller groups have a higher daily  
111 likelihood to act as sentinels (30%) compared to individuals from larger groups (10%)

112 (Rauber, Clutton-Brock, & Manser, 2019). Meerkats on sentinel duty produce six different  
113 sentinel call types (Manser, 1999; Rauber & Manser, 2017) and in case a predator is  
114 detected they give functionally referential alarm calls (Manser, 1999, 2001; Manser et al.,  
115 2001). The six described, discrete sentinel call types all differ in their acoustic structure  
116 and include: single note, double note, triple note, multiple note, di-drrr and wheek calls  
117 (Fig. 1, Fig. A1.) (Manser, 1999). Previous work on the function of sentinel calls in  
118 meerkats has demonstrated that sentinel calming calls, including single- and double note  
119 calls, are produced when no predator is in sight and function as an 'all-clear' signal,  
120 leading to an increase in foraging behaviour and a decrease in vigilance behaviour by the  
121 foraging group members (Rauber & Manser, 2017). In contrast, sentinel warning calls,  
122 which contain di-drrr and wheek calls, are emitted when the sentinel individual  
123 experiences an increase in perceived risk and function as a pre-stage of alarm calls,  
124 leading to an increase in vigilance behaviour and a decrease in foraging by receivers  
125 (Rauber & Manser, 2017). Furthermore, alarm calls contain information about different  
126 urgency levels of a flight response as well as information about the predator type, i.e.  
127 terrestrial or aerial (Manser, 2001; Manser et al., 2001; Manser, Seyfarth, & Cheney,  
128 2002). Moreover, meerkat sentinel calls are individually distinct (Manser, 1999) and  
129 foraging group members adjust their behavioural response to sentinel calming calls based  
130 on the experience levels of the caller (Rauber & Manser, 2018). Having these varying  
131 levels of urgency, i.e. sentinel calming calls, sentinel warning calls, and alarm calls, all  
132 produced by the individual on sentinel guard, allows us to compare vocal ontogeny of  
133 sentinel calls with that of alarm calls regarding potential differences between subadults  
134 and adults in terms of vocal usage and development of individual signatures.

135         In this study we investigated at what age meerkats begin to act as sentinels and  
136 whether and how group size may influence the onset of this behaviour. Individual  
137 contribution to sentinel behaviour decreases with increasing group size (Clutton-Brock,  
138 O'Riain, et al., 1999). Accordingly, individuals in smaller groups might have to contribute



139 to this coordinated vigilance behaviour at a younger age than individuals from larger  
140 groups. Alternatively, it is possible that in larger groups, which have on average more  
141 often an individual on raised guard (Clutton-Brock, O'Riain, et al., 1999), individuals learn  
142 more quickly from other group members, and perform the behaviour at a younger age.  
143 Secondly, we determined the age when different sentinel call types were first produced  
144 by young meerkats and how call rates changed with increasing experience as a sentinel.  
145 Based on the different urgency levels of sentinel calming and warning calls and due to the  
146 higher vulnerability of young individuals to predation, we expected young individuals to  
147 produce more warning calls and less calming calls. Lastly, focusing on double note calls,  
148 one of the two most commonly produced sentinel call types, we examined how individual  
149 distinctiveness in this call type changed with increasing age of the signaller.

150

## 151 METHODS

### 152 *Study site and population*

153 This study was carried out between February and July 2017 at the Kalahari Meerkat  
154 Project (KMP) located at the Kuruman River Reserve in South Africa. Additionally, the  
155 analyses relied on long term data collected for the KMP between 1996 and 2017 (see next  
156 methods section: *Behavioural data from long term database*). The study site has a semi-  
157 arid climate and is characterised by perennial grasses, shrubs and trees as main  
158 vegetations (see (Clutton-Brock, Gaynor, et al., 1999; Doolan & Macdonald, 1996) for  
159 more information about the habitat and climate at the study site). All animals recorded  
160 during this study were habituated to close human observations and sound recording  
161 equipment, allowing for recording distances of less than 1m from the calling meerkat.  
162 Information about individual identity, age, as well as the frequency of sentinel behaviour  
163 was collected as part of the KMP's long-term data collection. In total, we recorded sentinel  
164 calls emitted by young meerkats from eight groups with group size varying between nine

165 and 24 individuals (mean±sd=14.1±6.25). Age classes were characterised as following:  
166 individuals younger than 3 months, i.e. pups, are for the most part dependent on food  
167 provisioning and protection from adult group members. Juveniles, 3-6 months, start to  
168 forage on their own, but still get complementary feeds from adults. Subadults, 6-12  
169 months, forage independently and show more adult like behaviours, including offspring  
170 care or burrow maintenance. Individuals over 12 months of age are sexually mature and  
171 considered adults.

172

### 173 *Behavioural data from the long-term database*

174 As part of the daily data collection at the KMP, researchers observe groups of meerkats  
175 for three hours while foraging in the morning and one to two hours in the evening  
176 conducting adlib observations whenever they see a specific behaviour. Each group is  
177 observed for four to five days a week, whereby over a whole month observation durations  
178 are equalized across all groups. We extracted the age at the first sentinel bout equal or  
179 longer than one minute for all meerkats born between 1996 and 2017, resulting in a total  
180 of 1411 individuals from 39 different groups ( $N=755$  males,  $N=656$  females). One minute  
181 was chosen to exclude individuals that were just climbing up an object and were  
182 mistakenly noted down as sentinel individual. When individuals stay in the raised  
183 position (at least 0.1m higher than the surrounding area) for a minute or longer, we can  
184 assume that this individual is acting as a sentinel and not just exploring its surroundings.  
185 To compare the onset of sentinel behaviour with the onset of the other cooperative  
186 behaviours we also extracted the age when they first participated in pup feeding and  
187 babysitting (Clutton-Brock & Manser, 2016) from the same set of individuals and time  
188 period used to analyse the onset of sentinel behaviour.

189

### 190 *Acoustic recordings*

191 We recorded a total of 189 sentinel events in eight groups (5-69 recordings per group;  
192 mean=21) containing 7119 calls from 48 different individuals between 112 and 380 days  
193 old. Recordings were conducted during naturally occurring sentinel bouts using a  
194 Sennheiser directional microphone (ME66/K6) connected to a Marantz PMD-670 solid-  
195 state recorder (Marantz Japan Inc.; sampling frequency 44.2 kHz, 16 bits accuracy). A  
196 windshield (Rainhardt, W200) was attached to the microphone to ensure high quality  
197 recordings under variable wind conditions. The microphone was attached to a 1.5m  
198 telescopic pole in order not to disturb the calling meerkats by keeping a distance of 1m  
199 between the meerkat and the recording person, while at the same time the recording  
200 distance was <0.5m and thus allowing for high signal-to-background ratio.

201

#### 202 *Extraction of acoustic parameters*

203 Each vocalisation in the recordings was manually assigned to one of the six described  
204 sentinel call types (Fig.1) or alarm calls using a combination of visual inspection of the  
205 spectrogram and acoustic classification of calls in Adobe Audition (2015.0 Release)  
206 (Manser, 1999; Rauber & Manser, 2017). Previous work on meerkat call combinations  
207 demonstrated that silence intervals between calls are significantly shorter than within  
208 call combinations, such as the double or triple note calls (Collier, Townsend, & Manser,  
209 2017), allowing us to categorize each call by visual and audio inspection as one of the six  
210 described sentinel call types. To extract acoustic parameters of one of the two most  
211 commonly produced sentinel call types, the double note call, we used Avisoft SASLab Pro  
212 (version 5.2.12). Upon loading the sound file into the program, we first removed noise  
213 levels below 250Hz applying a high-pass domain finite impulse response (FIR) filter.  
214 Afterwards we created spectrograms (FFT length=512, overlap=87%) and visually  
215 checked the tracking of the fundamental frequency (F0), which for sentinel double note  
216 calls is the same as the peak frequency, and the duration of first note of the call. Calls that

217 were not of high enough signal to noise quality and thus were not tracked correctly by the  
218 program were removed from the analysis. The minimum number of high quality calls we  
219 collected from the same individual was 16 (range 16-106, mean = 58.6), recorded from at  
220 least three independent sentinel events (min=3, max=7, mean=4.6), resulting in a sample  
221 size of 72 recordings containing 937 double note calls from 18 individuals. Fundamental  
222 frequency (which was equal to peak frequency in the measured calls), peak amplitude and  
223 entropy were measured at 10 regular segments throughout the first note of each double  
224 note call. Similar to work on transmission characteristics in primate vocalisations (Maciej,  
225 Fischer, & Hammerschmidt, 2011) only measurements 2-9 were used to calculate the  
226 means as the very beginning and end of calls were often most imprecise and affected by  
227 background noise. Duration was measured for the complete first note of each double note  
228 call.

229

### 230 *Statistical analysis*

231 All statistical analyses were done using R Version 3.3.0 (R Core Team, 2018). To analyse  
232 the effect of group size on the age at first sentinel bout, we applied a linear mixed model  
233 (LMM) with age (in days) as a response and sex and group size as fixed effect. Group  
234 identity was included as a random factor. As the proportion of time that individuals spend  
235 on sentinel guard is higher in smaller groups compared to larger groups (Clutton-Brock,  
236 O'Riain, et al., 1999), the acquisition of experience gained by acting as a sentinel may likely  
237 differ depending on group size rather than absolute age, whereby individuals from  
238 smaller groups are expected to gain experience faster than individuals in larger groups.  
239 Hence, for further analysis of the ontogeny of sentinel vocalisations, we used "GuardSum"  
240 as a proxy for experience, which has been calculated as the total duration of all sentinel  
241 events of a given individual until the day of the recording. To test whether the presence  
242 of a given call type in the recordings was affected by experience, we used a generalized

243 linear mixed model (GLMM) with the presence of a call type as binomial response variable  
244 and group size and GuardSum as fixed effects. Sentinel ID nested in group ID and date  
245 were used as random factors. To determine whether the fixed effects had any significant  
246 effect on the response variable, we used likelihood ratio tests (LRT) to compare whether  
247 the model with the fixed effect included differed significantly from the same model with  
248 the fixed effect excluded (Crawley, 2012). To analyse the development of call rates (total  
249 number of calls for each call type divided by the duration of the sentinel bout) with  
250 increasing experience, while at the same time reducing the number of multiple testing,  
251 we grouped the six sentinel calls into categories, which have been previously  
252 demonstrated to represent functionally distinct call categories: single and double note  
253 calls together as sentinel calming calls and didrrr and wheek calls as warning calls  
254 (Rauber & Manser, 2017). The last two call types, the triple- and multiple note calls were  
255 grouped together as 'middle calls'. This was done to reduce the number of multiple  
256 testing. We then used all recordings where the call rate of each of these categories was  
257 above zero and log transformed them to use as response variable in a GLMM. Again, we  
258 used GuardSum (our proxy for experience), group size and the potential interaction  
259 between them as fixed effects as well as sentinel ID nested in group ID and date as random  
260 factors. To investigate how the acoustic parameters produced in the first note of double  
261 note calls changed with increasing age, we conducted a LMM with the mean fundamental  
262 frequency, mean peak amplitude, duration and mean entropy as response variables, age  
263 as fixed effect and Sentinel ID as well as a unique recording ID as random factors.  
264 Following the methods used in (Salmi et al., 2014) we also compared the variation  
265 between the first note of the double note calls of different individuals to the variation  
266 measured within individuals to assess whether calls show the potential for individual  
267 coding (PIC). To do this we measured the acoustic variability of each acoustic parameter  
268 (derived for each first note of a double note call) by calculating the inter-individual  
269 variation means ( $MEAN_{inter}$  = average mean of the measured parameter over the calls of

270 all individuals) and the standard deviation ( $SD_{inter}$  = sd of the measured parameter over  
271 the calls of all individuals). Then we calculated the coefficients of variation between  
272 individuals ( $CV_{inter} = 100 * SD_{inter} / MEAN_{inter}$ ) and within individuals ( $CV_{intra}$  = mean of  
273 individual CV values; with  $CV = 100 * SD / MEAN$  for each individual). PIC was calculated as  
274  $CV_{inter} / CV_{intra}$ , whereby values above 1 indicate higher variation between individuals than  
275 within individuals and thus the potential for this variable to encode individual  
276 information (Salmi et al., 2014). To test for any changes in individual distinctiveness  
277 across ontogeny, we used discriminant function analysis (DFA; (Klecka & Iversen, 1980))  
278 on the measured acoustic variables of ten individuals, when they were younger than 250  
279 days, and ten individuals at the age between 250 and 380 days of age to get the percentage  
280 of correct assignment of calls to individuals, using the leave-one-out cross validation  
281 method (Hair, Anderson, Tatham, & Black, 1995; McGarigal, Cushman, & Stafford, 2013;  
282 Mundry & Sommer, 2007). Since we had 13 individuals between 250 and 380 days with  
283 enough high quality calls, of which five were the same as in the younger category (younger  
284 than 250 days) and eight were different individuals, we randomly selected ten of these 13  
285 using the sample function in R. For both age categories we used 16 calls per individual  
286 resulting in 160 calls each. Whenever we had more than 16 calls from an individual, we  
287 randomly selected 16 calls using the sample function in R. To calculate the chance level  
288 correct assignment, we used a randomisation approach, whereby correct assignment by  
289 chance was averaged from DFAs conducted on 1'000 randomised permutations of the  
290 dataset (separately for younger and older individuals) (McGarigal et al., 2013; Solow,  
291 1990).

292

293 *Ethical note*

294 All the recordings and observations used in this study were conducted with the  
295 permission of the ethical committee of Pretoria University and the Northern Cape  
296 Conservation Service, South Africa (Permit Number: ECO31-13).

297

## 298 RESULTS

### 299 *Starting age to act as sentinel*

300 Mean age when meerkats first began to act as sentinel for one minute or longer was  
301  $202.12 \pm 65.4$  days (mean  $\pm$  std. dev.). Young meerkats in larger groups conducted their  
302 first sentinel bout at a later age than meerkats in smaller groups (LRT:  $\chi^2_1 = 161.53$ ,  $P$   
303  $< 0.001$ ; LMM:  $\beta = 0.12$ ,  $se = 0.009$ ,  $P < 0.001$ ; Fig. 2). Males did not differ significantly from  
304 females in the age at first sentinel bout (LRT:  $\chi^2_1 = 0.511$ ,  $P = 0.475$ ; LMM:  $\beta = -0.07$ ,  $se =$   
305  $0.10$ ,  $P = 0.475$ ). Comparing the starting age to act as sentinels with the starting age of  
306 other cooperative behaviours for the same set of individuals showed that age when  
307 meerkats first demonstrated pup feeding at  $191.43 \pm 73.84$  days and the first babysitting  
308 at  $211.77 \pm 76.44$  days were similar.

309

### 310 *Likelihood to produce different sentinel call types and call rates*

311 All six described sentinel call types were present in recordings of the youngest individuals  
312 (112-127 days old; see Fig. A1. for spectrograms of the six sentinel call types produced by  
313 subadults). Accordingly, the likelihood to find any of the six sentinel call types in a given  
314 recording was not affected by the sentinel experience, i.e. the total amount of time  
315 (GuardSum in minutes) an individual had been recorded as sentinel (Table 1; Fig. 3).  
316 However, the call rates of sentinel calming calls (single and double note calls) and sentinel  
317 warning calls (didrrr and wheek calls) emitted during sentinel behaviour changed with  
318 experience of the calling individuals (Table 2). Calming calls significantly increased with

319 increasing experience as sentinel, i.e. GuardSum, whereby individuals in larger groups  
320 had shallower slopes than individuals in smaller groups (Table 2.). In contrast, the call  
321 rate of warning calls decreased with increasing experience of the caller. Again, this effect  
322 was smaller in larger groups, i.e. individuals in smaller groups decreased the call rate of  
323 sentinel warning calls faster than individuals in larger groups.

324

### 325 *Acoustic parameters and individuality*

326 Visual inspection of the plotted mean fundamental frequency ( $f_0$ ), mean peak amplitude  
327 (ampl), duration and mean entropy of the first note of the double note calls showed high  
328 variation in the amount (total difference between first and last recording) and degree of  
329 change (slopes) for different individuals over age (Fig. 4). Accordingly, we found  
330 consistent individual differences in the mean of all measured parameters (different  
331 intercepts; LRT,  $f_0$ :  $\chi^2_1=46.47$ ,  $P < 0.001$ ; ampl:  $\chi^2_1=14.71$ ,  $P < 0.001$ ; duration:  $\chi^2_1=63.09$ ,  
332  $P < 0.001$ ; entropy:  $\chi^2_1=8.90$ ,  $P = 0.003$ ), but no general effect of age (Table 3; Fig. 4). Due  
333 to the current data structure we were unable to test whether individuals also differed  
334 from each other across age (different slopes). The potential for individual coding (PIC) of  
335 all measured variables was above 1 (duration: PIC=1.65; mean fundamental frequency:  
336 PIC=1.46; mean peak amplitude: PIC=1.46; mean entropy: PIC=1.22), thus all variables  
337 had the potential to be individually distinct. DFA analysis resulted in 65% correct  
338 assignment of ten individuals younger than 250 days, which was significantly higher than  
339 expected by chance (C.I.=0.57-0.72, mean  $\pm$  sd chance correct assignment = 10%  $\pm$  5%,  $P$   
340  $< 0.001$ ). Call analysis of 10 individuals between 250 and 400 days showed a correct  
341 assignment of 57.7% (C.I. = 0.57-0.77, mean  $\pm$  sd chance correct assignment = 10%  $\pm$  5%,  
342  $P < 0.001$ ), which suggests consistent individual distinctiveness when individuals first act  
343 as sentinels up to six months later.

344



345 DISCUSSION

346           This study addressed the ontogeny of sentinel behaviour in meerkats, in  
347 particular the age at which they first start to act as sentinels, the likelihood to produce the  
348 six distinct sentinel call types and their respective call rates, as well as the acoustic  
349 properties and the development of individual signatures in sentinel calls. We  
350 demonstrate that the onset of acting as a sentinel guard was highly dependent on group  
351 size. Individuals from smaller groups exhibited sentinel behaviour at an earlier age than  
352 individuals from larger groups. This study also provides new evidence that, although all  
353 six described sentinel call types were already present in the repertoire upon first  
354 emergence of the behaviour, subadult meerkats increased the call rate of calming calls  
355 (single and double note calls) and decreased the call rate of warning calls (didrrr and  
356 wheek calls) with increasing experience as sentinel guard. For both categories of sentinel  
357 calls individuals from smaller groups demonstrated faster changes in call rates compared  
358 to individuals from larger groups given the same amount (total duration) of sentinel  
359 experience. Analysis of double note calls indicated that mean fundamental frequency,  
360 mean amplitude, duration and entropy differed consistently between individuals, but we  
361 found no general effect of age. Lastly, our results provide evidence that the individual  
362 signature of meerkats was already developed in their calls when they first started to go  
363 on sentinel guard and changed little later on in age.

364           The mean onset of sentinel behaviour of around 202 days of age was similar to  
365 the onset of the other cooperative behaviours including pup feeding (191 days) and  
366 babysitting (212 days). This might suggest that young individuals, which may be less  
367 efficient foragers and are still investing energy into growth did not have the necessary  
368 condition to contribute to the different cooperative behaviours. Supplementary feeding  
369 experiments of adult meerkats demonstrated that sentinel behaviour, as well as pup  
370 feeding, is highly condition dependent (Clutton-Brock et al., 2001; Clutton-Brock, O'Riain,

371 et al., 1999; Wright, Berg, de Kort, et al., 2001). However, it is also possible that acting as  
372 a sentinel requires individuals to have the necessary experience to correctly assess the  
373 surroundings regarding potential threats. In line with this, meerkats younger than six  
374 months have been demonstrated to produce fewer correct predator specific alarm calls  
375 compared to adults, suggesting that individuals gradually learn to associate specific  
376 external stimuli with the correct calls (Hollén & Manser, 2007). Our result that group size  
377 highly affected when young meerkats start to act as sentinels suggests that the  
378 development of sentinel behaviour is not related to absolute age or maturity, but highly  
379 dependent on the social environment. This is supported by previous work demonstrating  
380 that individual contribution to sentinel behaviour decreases with increasing group size  
381 (Clutton-Brock, O'Riain, et al., 1999). The risk of being predated is higher in smaller  
382 groups, and potentially therein even higher for young individuals (Clutton-Brock, Gaynor,  
383 et al., 1999). Therefore, young individuals benefit from acting as sentinel as this is  
384 supposed to be the safest position in the group (i.e. sentinels usually reach shelter first)  
385 (Bednekoff, 2001; Clutton-Brock, O'Riain, et al., 1999; Wright, Berg, de Kort, et al., 2001).  
386 Future research could investigate if in smaller groups young individuals that start acting  
387 as a guard might even be lighter in weight, but because of the higher predation pressure  
388 invest more into antipredator behaviours than same-aged and potentially heavier  
389 individuals from larger groups. We would like to encourage more work on the onset of  
390 sentinel behaviour and other cooperative behaviours in other species in order to enable  
391 cross-species comparisons of ontogenetic development of these behaviours.

392         The fact that all the six different sentinel call types were already produced when  
393 individuals first start to act as sentinels could be due to several reasons. First, sentinel call  
394 types might be innate and thus appear in their repertoire as soon as the context (sentinel  
395 behaviour) is shown by young meerkats. Second, sentinel call types are not exclusively  
396 used in the context of sentinel behaviour, but also in social and other vigilance contexts  
397 including allo-grooming and sunning behaviour in the morning and baby-sitting at the

398 burrow (Collier et al., 2017; Manser, 1998). Pups themselves already produce the single  
399 note calls within the first weeks of their life either as single calls or as units within longer  
400 call series (Manser, 1998). Consequently, by the time young meerkats start to go on guard,  
401 they have already learned how to produce the different call types in other contexts. Third,  
402 it is likely that young individuals pick up the different sentinel call types from an early age  
403 on, as they are exposed to these calls from the first days of foraging with the group when  
404 they are about four weeks old. Previous work on the ontogeny of the behavioural  
405 response to alarm calls showed mixed results: while some behavioural responses seemed  
406 to undergo the biggest ontogenetic changes before young become independent foragers  
407 (within three months), other characteristics, such as reaction time and response duration  
408 only developed later (Hollén & Manser, 2006). Further research, such as acoustic  
409 recordings of younger individuals, i.e. pups and juveniles, during different contexts, is  
410 needed to fully understand when and how young meerkats include acoustically similar or  
411 the same call types used in sentinel context in their vocal repertoire. Moreover, while we  
412 have accounted for potential differences among groups by adding group ID as a random  
413 effect, additional factors, including social learning from group members or habitat  
414 characteristics may further influence the ontogenetic development of sentinel behaviour,  
415 such as the likelihood to produce specific call types or the order of use of call types.

416         While previous work on the ontogeny of meerkat alarm calls demonstrates that  
417 young meerkats (<12months) show a high correct classification along the level of urgency  
418 (correct assignment of low and high urgency contexts) (Hollén & Manser, 2007), we found  
419 an increase in the call rate of sentinel calming calls (low perceived risk) and a decrease in  
420 the call rate of sentinel warning calls (higher perceived risk) with increasing experience  
421 of the caller. We did not find any change in call rates of sentinel middle calls, which may  
422 indicate that these changes are more subtle than changes of either sentinel calming calls  
423 or sentinel warning calls, thus requiring a larger sample size to be able to detect any  
424 potential change with increasing experience. In both cases where we see a change in call

425 rates, sentinel calming and warning calls, there was a significant interaction with group  
426 size, with smaller groups showing a faster increase or decrease in call rate compared to  
427 larger groups. The increase in calming calls, is likely due to meerkats becoming more  
428 confident in their assessment of urgency levels with more experience. The higher call rate  
429 of warning calls when individuals are younger, could be an overestimation of the  
430 perceived predation risk, similar to infant vervet monkeys (*Cercopithecus aethiops*),  
431 which frequently produce alarm calls to non-threatening stimuli and only restrict their  
432 alarm calls to actual predator species over time (Seyfarth & Cheney, 1986). In such  
433 situations, when young show a stronger reaction to non-threatening stimuli, the question  
434 is whether this represents an adaptive adjustment to age-dependent differences in  
435 predation risk, or whether young are just overreacting and still need to improve  
436 discrimination between threatening and non-threatening situations. As young meerkats  
437 did not show an increased fear response to predators that present a greater threat for  
438 young compared to adults (Hollén, Clutton-Brock, et al., 2008), this may indicate that in  
439 the context of sentinel behaviour higher call rates of warning calls may not necessarily be  
440 adaptive, but rather increasing experience improves the discrimination abilities between  
441 different levels of danger. This is supported by the results that young from smaller groups,  
442 which still experience higher relative predation pressures than young from larger groups,  
443 but are faster in accumulating experience as sentinels, show a faster decrease in warning  
444 calls and a faster increase in calming calls.

445         In line with the absence of changes in acoustic parameters of the double note calls,  
446 one of the two most frequently emitted, individually distinct sentinel calls (Manser,  
447 1999), our results indicate that individual distinctiveness is already as high as in adults  
448 when individuals started to act as sentinels. This is in contrast to studies showing an  
449 increase in individuality with increasing age in domestic goat kids (*Capra hircus*; (Briefer  
450 & McElligott, 2011), goitred gazelles (*Gazella subgutturosa*; (Lapshina et al., 2012) and  
451 chicks of non-passerine birds (Insley, Phillips, & Charrier, 2003; Jones, Falls, & Gaston,

452 1987; Klenova, Volodin, & Volodina, 2009; Lefevre, Montgomerie, & Gaston, 1998).  
453 However, meerkats only started to act as sentinels when they were 200 days old, and it is  
454 therefore possible that they do undergo acoustic development and changes in individual  
455 distinctiveness at a younger age. This seems likely when considering that the double note  
456 calls are also produced in several other contexts which are shown before the onset of  
457 sentinel behaviour (Collier et al., 2017). Alternatively, it has been argued that  
458 discrimination among signallers may play an important role in particular in systems  
459 where callers have variable thresholds to call, such as for example in young or  
460 inexperienced individuals (Blumstein & Daniel, 2004) or where calls refer to the  
461 perceived risk of the caller (Blumstein & Armitage, 1997), potentially leading to an early  
462 development of individual distinctiveness for these calls. This supports recent work  
463 demonstrating that sentinel double note calls refer to the caller's perceived risk (Rauber  
464 & Manser, 2017), whereby individuals likely differ in their assessment of the level of risk.  
465 Moreover, foraging meerkats (adults and subadults) discriminate between the calming  
466 calls of different sentinel individuals and adjust the extent to which they rely on social  
467 information provided by these individuals (Rauber & Manser, 2018).

468 To conclude, we show that subadult meerkats started acting as sentinels when  
469 they were around 200 days old (simultaneous with other cooperative behaviours) and  
470 other than slight adjustments in call rates demonstrated little change in vocal call patterns  
471 with increasing age and experience. As the majority of sentinel calls are also produced in  
472 other contexts, it is possible that vocal ontogeny takes place at a younger age.  
473 Alternatively, but not mutually exclusive, our results may suggest strong selective  
474 pressures on antipredator behaviours such as the sentinel system, resulting in a fully  
475 functional behavioural and vocal response upon first emergence of sentinel behaviour. A  
476 third possibility is that the similar vocal calling behaviour of subadults and young adults  
477 may indicate that, in contrast to the alarm call system, which are directly related to the  
478 presence of a predator and show ontogenetic development (Hollén, Clutton-Brock, et al.,

479 2008; Hollén & Manser, 2006, 2007), individuals of different ages experience similar  
480 levels of risk when producing sentinel calls, i.e. in the absence of a predator, therefore  
481 showing the same behavioural and vocal responses. Further research on individual  
482 vocalisations of pups (up to three months) and juveniles (three to six months) is needed  
483 to understand the extent of ontogenetic development on the different call types and the  
484 roles of social environment and age specific selection pressure.

485

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503

#### 504 COMPETING INTERESTS

505 We declare we have no competing interests.

506

507 REFEEERENCES

508 Bednekoff, P. A. (2001). Coordination of safe, selfish sentinels based on mutual benefits.

509 *Annales Zoologici Fennici*, 38(1), 5-14.

510 Bednekoff, P. A. (2015). Sentinel Behavior: A Review and Prospectus. In M. Naguib, H. J.

511 Brockmann, J. C. Mitani, L. W. Simmons, L. Barrett, S. Healy, & P. J. B. Slater (Eds.),

512 *Advances in the Study of Behavior, Vol 47* (Vol. 47, pp. 115-145). San Diego: Elsevier

513 Academic Press Inc.

514 Berg, K. S., Beissinger, S. R., & Bradbury, J. W. (2013). Factors shaping the ontogeny of

515 vocal signals in a wild parrot. *Journal of Experimental Biology*, 216(2), 338-345.

516 doi:10.1242/jeb.073502

517 Blumstein, D. T., & Armitage, K. B. (1997). Alarm calling in yellow-bellied marmots .1. The

518 meaning of situationally variable alarm calls. *Animal Behaviour*, 53, 143-171.

519 Blumstein, D. T., & Daniel, J. C. (2004). Yellow-bellied marmots discriminate between the

520 alarm calls of individuals and are more responsive to calls from juveniles. *Animal*

521 *Behaviour*, 68, 1257-1265.

522 Blumstein, D. T., Verneyre, L., & Daniel, J. C. (2004). Reliability and the adaptive utility of

523 discrimination among alarm callers. *Proceedings of the Royal Society B-Biological*

524 *Sciences*, 271(1550), 1851-1857. doi:10.1098/rspb.2004.2808

525 Briefer, E., & McElligott, A. G. (2011). Mutual mother-offspring vocal recognition in an

526 ungulate hider species (*Capra hircus*). *Animal cognition*, 14(4), 585-598.

527 Caro, T. M. (2005). Antipredator Defense in Birds and Mammals. *Antipredator Defense in*

528 *Birds and Mammals*.

529 Cleveland, J., & Snowdon, C. T. (1982). The Complex Vocal Repertoire of the Adult Cotton-

530 top Tamarin (*Saguinus oedipus oedipus*) 1. *Zeitschrift für Tierpsychologie*, 58(3),

531 231-270.

532 Clutton-Brock, T. H., Brotherton, P. N. M., O'Riain, M. J., Griffin, A. S., Gaynor, D., Kansky, R.,  
533 . . . McIlrath, G. M. (2001). Contributions to cooperative rearing in meerkats.  
534 *Animal Behaviour*, 61, 705-710. doi:10.1006/anbe.2000.1631

535 Clutton-Brock, T. H., Gaynor, D., Kansky, R., MacColl, A. D. C., McIlrath, G., Chadwick, P., . . .  
536 Skinner, J. D. (1998). Costs of cooperative behaviour in suricates (*Suricata*  
537 *suricatta*). *Proceedings of the Royal Society B-Biological Sciences*, 265(1392), 185-  
538 190.

539 Clutton-Brock, T. H., Gaynor, D., McIlrath, G. M., Maccoll, A. D. C., Kansky, R., Chadwick, P.,  
540 . . . Brotherton, P. N. M. (1999). Predation, group size and mortality in a  
541 cooperative mongoose, *Suricata suricatta*. *Journal of Animal Ecology*, 68(4), 672-  
542 683. doi:10.1046/j.1365-2656.1999.00317.x

543 Clutton-Brock, T. H., & Manser, M. B. (2016). Meerkats: cooperative breeding in the  
544 Kalahari. *Cooperative breeding in vertebrates: Studies of ecology, evolution, and*  
545 *behavior*, 294-317.

546 Clutton-Brock, T. H., O'Riain, M. J., Brotherton, P. N. M., Gaynor, D., Kansky, R., Griffin, A. S.,  
547 & Manser, M. (1999). Selfish sentinels in cooperative mammals. *Science*,  
548 284(5420), 1640-1644.

549 Collier, K., Townsend, S. W., & Manser, M. B. (2017). Call concatenation in wild meerkats.  
550 *Animal Behaviour*, 134, 257-269.

551 Crawley, M. J. (2012). *The R Book*. Jon Wiley & Sons Ltd., Chichester.

552 Doolan, S. P., & Macdonald, D. W. (1996). Diet and foraging behaviour of group-living  
553 meerkats, *Suricata suricatta*, in the southern Kalahari. *Journal of Zoology*, 239,  
554 697-716.

555 Hair, J. F., Anderson, R. E., Tatham, R. L., & Black, W. C. (1995). *Multivariate data analysis*  
556 New York. NY: Macmillan.



557 Hare, J. F., & Atkins, B. A. (2001). The squirrel that cried wolf: reliability detection by  
558 juvenile Richardson's ground squirrels (*Spermophilus richardsonii*). *Behavioral*  
559 *Ecology and Sociobiology*, 51(1), 108-112. doi:10.1007/s002650100414

560 Hollén, L. I., Bell, M. B. V., & Radford, A. N. (2008). Cooperative sentinel calling? Foragers  
561 gain increased biomass intake. *Current Biology*, 18(8), 576-579.  
562 doi:10.1016/j.cub.2008.02.078

563 Hollén, L. I., Bell, M. B. V., Russell, A., Niven, F., Ridley, A. R., & Radford, A. N. (2011). Calling  
564 by Concluding Sentinels: Coordinating Cooperation or Revealing Risk? *Plos One*,  
565 6(10).

566 Hollén, L. I., Clutton-Brock, T., & Manser, M. B. (2008). Ontogenetic changes in alarm-call  
567 production and usage in meerkats (*Suricata suricatta*): adaptations or  
568 constraints? *Behavioral Ecology and Sociobiology*, 62(5), 821-829.  
569 doi:10.1007/s00265-007-0508-x

570 Hollén, L. I., & Manser, M. B. (2007). Motivation before meaning: motivational information  
571 encoded in meerkat alarm calls develops earlier than referential information. *The*  
572 *American Naturalist*, 169(6), 758-767.

573 Hollén, L. I., & Radford, A. N. (2009). The development of alarm call behaviour in mammals  
574 and birds. *Animal Behaviour*, 78(4), 791-800.

575 Hollén, L. I., & Manser, M. B. (2006). Ontogeny of alarm call responses in meerkats,  
576 *Suricata suricatta*: the roles of age, sex and nearby conspecifics. *Animal Behaviour*,  
577 72(6), 1345-1353.

578 Hollén, L. I., & Manser, M. B. (2007). Motivation before meaning: motivational information  
579 encoded in meerkat alarm calls develops earlier than referential information. *The*  
580 *American Naturalist*, 169(6), 758-767.

581 Horrocks, J., & Hunte, W. (1986). Sentinel behaviour in vervet monkeys: who sees whom  
582 first? *Animal Behaviour*, 34(5), 1566-1568.

583 Insley, S., Phillips, A. V., & Charrier, I. (2003). A review of social recognition in pinnipeds.  
584 *Aquatic Mammals*, 29(2), 181-201.

585 Jansen, D. A., Cant, M. A., & Manser, M. B. (2012). Segmental concatenation of individual  
586 signatures and context cues in banded mongoose (*Mungos mungo*) close calls.  
587 *BMC Biology*, 10(1), 97.

588 Jones, I. L., Falls, J. B., & Gaston, A. J. (1987). Vocal recognition between parents and young  
589 of ancient murrelets, *Synthliboramphus antiquus* (Aves: Alcidae). *Animal*  
590 *Behaviour*, 35(5), 1405-1415.

591 Jouventin, P., & Aubin, T. (2002). Acoustic systems are adapted to breeding ecologies:  
592 individual recognition in nesting penguins. *Animal Behaviour*, 64(5), 747-757.

593 Kern, J. M., & Radford, A. N. (2013). Call of duty? Variation in use of the watchman's song  
594 by sentinel dwarf mongooses, *Helogale parvula*. *Animal Behaviour*, 85(5), 967-  
595 975.

596 Klecka, W. R., & Iversen, G. R. (1980). *Discriminant analysis* (Vol. 19): Sage.

597 Klenova, A. V., Volodin, I. A., & Volodina, E. V. (2009). The variation in reliability of  
598 individual vocal signature throughout ontogenesis in the red-crowned crane *Grus*  
599 *japonensis*. *Acta ethologica*, 12(1), 29-36.

600 Krause, J., & Ruxton, G. D. (2002). Living in groups. *Living in groups*, i.

601 Kruuk, H. (1964). Predators and anti-predator behaviour of the black-headed gull (*Larus*  
602 *ridibundus* L.). *Behaviour. supplement*, III-129.

603 Lapshina, E. N., Volodin, I. A., Volodina, E. V., Frey, R., Efremova, K. O., & Soldatova, N. V.  
604 (2012). The ontogeny of acoustic individuality in the nasal calls of captive goitred  
605 gazelles, *Gazella subgutturosa*. *Behavioural processes*, 90(3), 323-330.

606 Lefevre, K., Gaston, A. J., & Montgomerie, R. (2001). Repertoire, structure, and individual  
607 distinctiveness of Thick-billed Murre calls. *The Condor*, 103(1), 134-142.

608 Lefevre, K., Montgomerie, R., & Gaston, A. J. (1998). Parent-offspring recognition in thick-  
609 billed murres (Aves: Alcidae). *Animal Behaviour*, 55(4), 925-938.

610 Maciej, P., Fischer, J., & Hammerschmidt, K. (2011). Transmission characteristics of  
611 primate vocalizations: implications for acoustic analyses. *PloS one*, 6(8), e23015.

612 Manser, M. B. (1998). *The evolution of auditory communication in suricates, Suricata*  
613 *suricatta* (Doctoral dissertation). Cambridge, UK: University of Cambridge.

614 Manser, M. B. (1999). Response of foraging group members to sentinel calls in suricates,  
615 *Suricata suricatta*. *Proceedings of the Royal Society B-Biological Sciences*,  
616 266(1423), 1013-1019. doi:10.1098/rspb.1999.0737

617 Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator  
618 type and the level of response urgency. *Proceedings of the Royal Society B-*  
619 *Biological Sciences*, 268(1483), 2315-2324. doi:10.1098/rspb.2001.1773

620 Manser, M. B., Bell, M. B., & Fletcher, L. B. (2001). The information that receivers extract  
621 from alarm calls in suricates. *Proceedings of the Royal Society B-Biological Sciences*,  
622 268(1484), 2485-2491. doi:10.1098/rspb.2001.1772

623 Manser, M. B., Seyfarth, R. M., & Cheney, D. L. (2002). Suricate alarm calls signal predator  
624 class and urgency. *Trends in Cognitive Sciences*, 6(2), 55-57. doi:10.1016/s1364-  
625 6613(00)01840-4

626 McGarigal, K., Cushman, S. A., & Stafford, S. (2013). *Multivariate statistics for wildlife and*  
627 *ecology research*: Springer Science & Business Media.

628 McGowan, K. J., & Woolfenden, G. E. (1989). A sentinel system in the Florida scrub jay.  
629 *Animal Behaviour*, 37, 1000-1006.

630 Miller, C. T., & Thomas, A. W. (2012). Individual recognition during bouts of antiphonal  
631 calling in common marmosets. *Journal of Comparative Physiology A*, 198(5), 337-  
632 346.

633 Mundry, R., & Sommer, C. (2007). Discriminant function analysis with nonindependent  
634 data: consequences and an alternative. *Animal Behaviour*, 74(4), 965-976.

635 R Core Team. (2018). R: A language and environment for statistical computing. R  
636 Foundation for Statistical Computing, Vienna, Austria. 2012. URL [http://www.R-](http://www.R-project.org)  
637 [project.org](http://www.R-project.org).

638 Radford, A. N., & Ridley, A. R. (2008). Close calling regulates spacing between foraging  
639 competitors in the group-living pied babbler. *Animal Behaviour*, 75(2), 519-527.

640 Ramakrishnan, U., & Coss, R. G. (2000). Age differences in the responses to adult and  
641 juvenile alarm calls by bonnet macaques (*Macaca radiata*). *Ethology*, 106(2), 131-  
642 144. doi:10.1046/j.1439-0310.2000.00501.x

643 Rasa, O. A. E. (1986). Coordinated vigilance in dwarf mongoose family groups - the  
644 watchmans song hypothesis and the costs of guarding. *Ethology*, 71(4), 340-344.

645 Rasa, O. A. E. (1989). The costs and effectiveness of vigilance behaviour in the dwarf  
646 mongoose: implications for fitness and optimal group size. *Ethology Ecology &*  
647 *Evolution*, 1(3), 265-282.

648 Rauber, R., Clutton-Brock, T. H., & Manser, M. B. (2019). Drought decreases cooperative  
649 sentinel behavior and affects vocal coordination in meerkats. *Behavioral Ecology*,  
650 30(6), 1558-1566.

651 Rauber, R., Kranstauber, B., & Manser, M. B. (2020). Call order within vocal sequences of  
652 meerkats contains temporary contextual and individual information. *BMC*  
653 *Biology*, 18(1), 119. doi:10.1186/s12915-020-00847-8

654 Rauber, R., & Manser, M. B. (2017). Discrete call types referring to predation risk enhance  
655 the efficiency of the meerkat sentinel system. *Scientific reports*, 7, 44436.

656 Rauber, R., & Manser, M. B. (2018). Experience of the signaller explains the use of social  
657 versus personal information in the context of sentinel behaviour in meerkats.  
658 *Scientific Reports*, 8(1), 11506.

659 Ridley, A. R., & Raihani, N. J. (2006). Facultative response to a kleptoparasite by the  
660 cooperatively breeding pied babbler. *Behavioral Ecology*, 18(2), 324-330.

661 Salmi, R., Hammerschmidt, K., & Doran-Sheehy, D. M. (2014). Individual distinctiveness in  
662 call types of wild western female gorillas. *PloS one*, 9(7), e101940.

663 Schneiderova, I., Schnitzerova, P., Uhlíková, J., Brandl, P., Zouhar, J., & Matějů, J. (2015).  
664 Differences in alarm calls of juvenile and adult European ground squirrels  
665 (*Spermophilus citellus*): Findings on permanently marked animals from a semi-  
666 natural enclosure. *Zoo biology*, 34(6), 503-512.

667 Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal*  
668 *Behaviour*, 34(6), 1640-1658.

669 Sharpe, L. L., Hill, A., & Cherry, M. I. (2013). Individual recognition in a wild cooperative  
670 mammal using contact calls. *Animal Behaviour*, 86(5), 893-900.

671 Sherman, P. W. (1977). Nepotism and the evolution of alarm calls. *Science*, 197(4310),  
672 1246-1253.

673 Snowdon, C. T., & Cleveland, J. (1980). Individual recognition of contact calls by pygmy  
674 marmosets. *Animal Behaviour*, 28(3), 717-727.

675 Solow, A. R. (1990). A randomization test for misclassification probability in discriminant  
676 analysis. *Ecology*, 2379-2382.

677 Theis, K. R., Greene, K. M., Benson-Amram, S. R., & Holekamp, K. E. (2007). Sources of  
678 variation in the long-distance vocalizations of spotted hyenas. *Behaviour*, 144(5),  
679 557-584.

680 Volodin, I. A., Lapshina, E. N., Volodina, E. V., Frey, R., & Soldatova, N. V. (2011). Nasal and  
681 oral calls in juvenile goitred gazelles (*Gazella subgutturosa*) and their potential to  
682 encode sex and identity. *Ethology*, 117(4), 294-308.

683 Wright, J., Berg, E., De Kort, S. R., Khazin, V., & Maklakov, A. A. (2001). Cooperative sentinel  
684 behaviour in the Arabian babbler. *Animal Behaviour*, 62, 973-979.  
685 doi:10.1006/anbe.2001.1838

686 Wright, J., Berg, E., de Kort, S. R., Khazin, V., & Maklakov, A. A. (2001). Safe selfish sentinels  
687 in a cooperative bird. *Journal of Animal Ecology*, 70(6), 1070-1079.  
688 doi:10.1046/j.0021-8790.2001.00565.x

689 Zahavi, A. (1990). Arabian babblers: the quest for social status in a cooperative breeder.  
690 *Cooperative breeding in birds*, 103-130.

691 Zoratto, F., Santucci, D., & Alleva, E. (2009). Theories commonly adopted to explain the  
692 antipredatory benefits of the group life: the case of starling (*Sturnus vulgaris*). *Atti*  
693 *della Accademia Nazionale dei Lincei Classe di Scienze Fisiche Matematiche e*  
694 *Naturali Rendiconti Lincei Scienze Fisiche e Naturali*, 20(2), 163-176.

695

696 TABLES

697 **Table 1:** Effect of sentinel experience on the probability to produce each of the six sentinel  
698 call types.

Call Type	Call Category	Estimate	Std error	<i>P</i>
Single note (sn)	Calming calls	0.32	0.34	0.336
Double note (dn)	Calming calls	0.38	0.38	0.320
Triple note (tn)	Middle calls	-0.11	0.27	0.701
Multiple note (mn)	Middle calls	0.84	0.44	0.078
Di-drrr call (didr)	Warning calls	-0.49	0.32	0.123
Wheek (wh)	Warning calls	-0.03	0.24	0.908

699 Estimates, standard errors and p-values resulting from the GLMM.

700

701 **Table 2:** Effect of sentinel experience and group size on changes in call rate of the sentinel  
702 calming calls (single and double note calls), middle calls (triple and multiple note calls)  
703 and sentinel warning calls (didrrr and wheek calls).

CallType	Variable	Estimate	Standard error	<i>P</i>
<b>Calming calls</b>	<b>GuardSum</b>	<b>1.01</b>	<b>0.43</b>	<b>0.023</b>
	GroupSize	0.74	0.54	0.193
	<b>GuardSum*GroupSize</b>	<b>-1.01</b>	<b>0.44</b>	<b>0.027</b>
Middle calls	GuardSum	0.23	0.16	0.167
	GroupSize	0.39	0.54	0.472
<b>Warning calls</b>	<b>GuardSum</b>	<b>-1.19</b>	<b>0.44</b>	<b>0.008</b>
	GroupSize	-0.61	0.56	0.263
	<b>GuardSum*GroupSize</b>	<b>1.05</b>	<b>0.43</b>	<b>0.018</b>

704 Estimates, standard errors and p-values resulting from the LMM.

705

706 **Table 3.** Effect of age on mean fundamental frequency, mean peak amplitude, duration  
707 and mean entropy of the first note produced in double note calls.

Acoustic parameter	Est±se	t	<i>P</i>
Mean Fundamental Frequency	0.03±0.25	0.15	0.88
Mean Peak Amplitude	-0.03±0.02	-1.71	0.09
Duration	-0.01±0.01	-0.79	0.43
Mean Entropy	-0.02±0.02	-1.19	0.24

708 Estimates, standard errors and p-values resulting from the LMM.



709 FIGURE LEGENDS

710

711 **Figure 1.** Spectrograms of the six distinct sentinel call types produced by adult meerkats  
712 acting as sentinel: a) single note call, b) double note call, c) triple note call, d) multiple  
713 note call, e) di-drrr call, f) wheek call. Sentinel calming calls: a) and b), middle calls: c) and  
714 d) and sentinel warning calls: e) and f) (reproduced after Manser 1999, Figure 1,  
715 permission granted by MM).

716

717 **Figure 2.** Influence of group size on age when females (grey) and males (black) were first  
718 recorded to act as sentinels for at least one minute. Plotted are predicted values from the  
719 LMM, the shaded areas represent 95% confidence intervals.

720

721 **Figure 3.** Appearance of each of the six sentinel call types in sentinel recordings of  
722 meerkats between the age of six and 15 months in relation to sentinel experience, i.e. the  
723 total amount of time (GuardSum in minutes) an individual has been recorded as sentinel.  
724 Each panel shows one of the six described sentinel call types

725

726 **Figure 4.** Ontogenetic development of mean fundamental frequency, mean peak  
727 amplitude, duration and mean entropy of the first note produced in double note calls with  
728 increasing age of the caller. Colours and connecting lines indicate identity of the 18  
729 individuals with three or more high quality recordings.

730

731 **Figure A1.** Spectrograms of the six distinct sentinel call types produced by subadult  
732 meerkats on sentinel guard. From left to right: single note call, double note call, triple note  
733 call, multiple note call, di-drrr call and wheek call.

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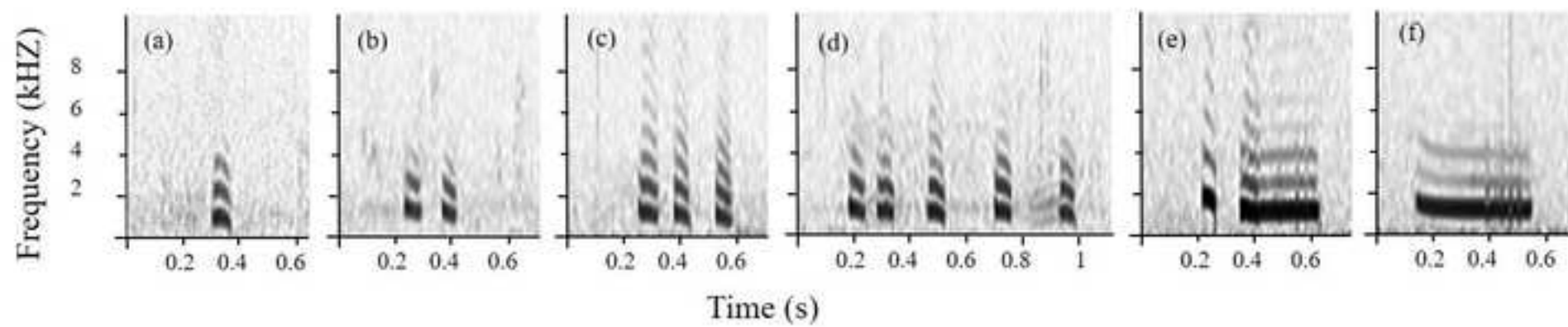
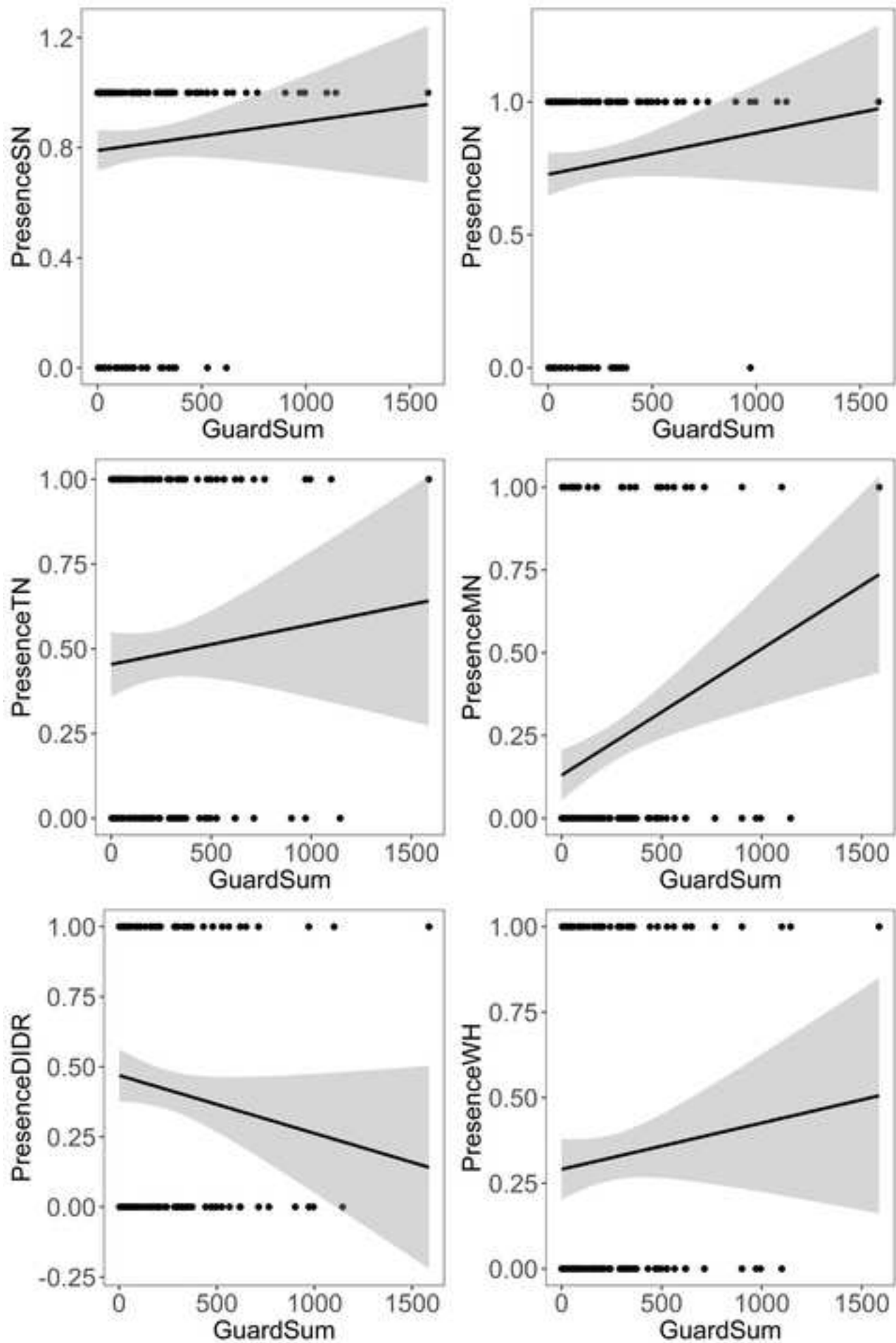




Figure 3

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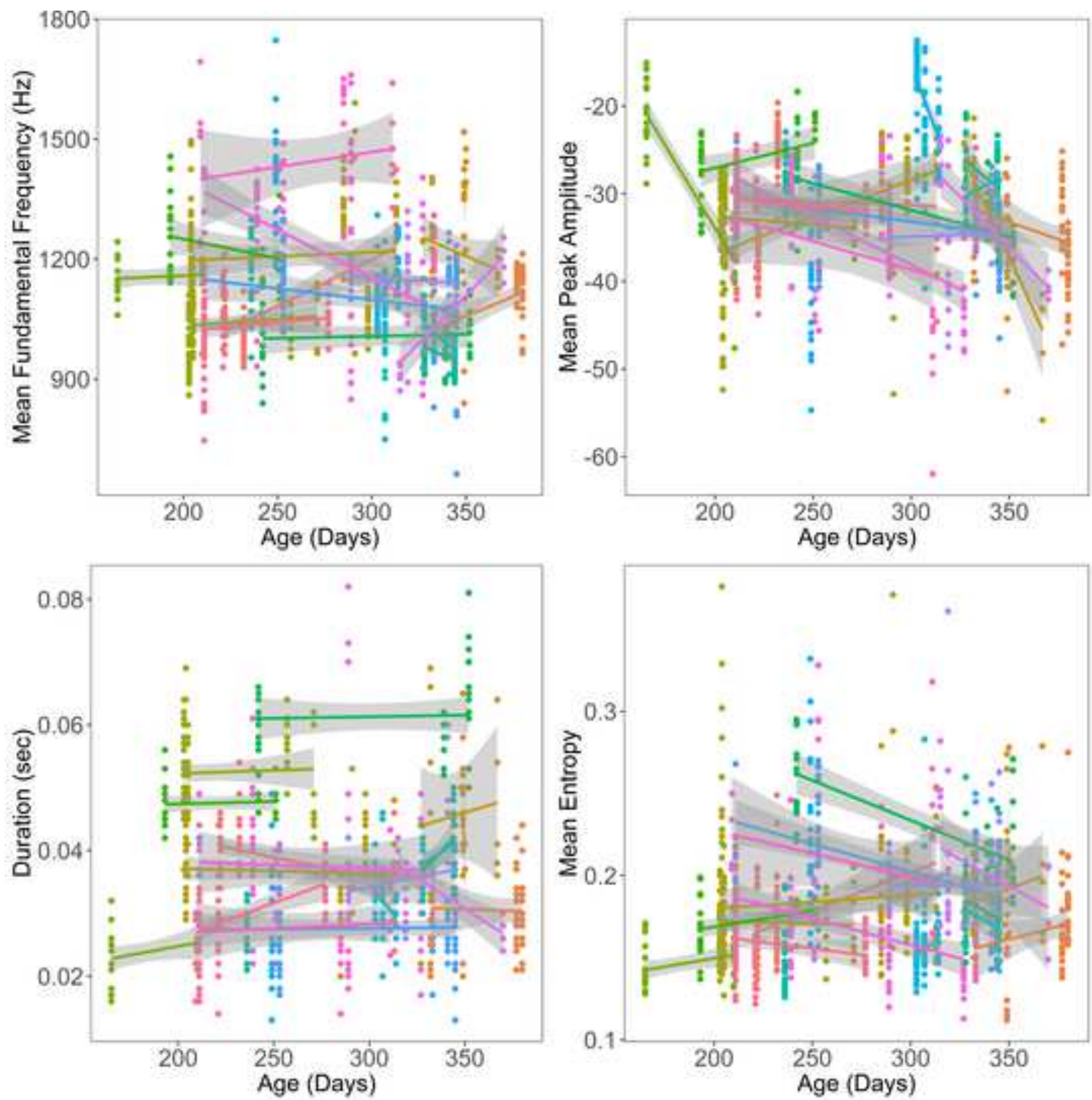


Figure A.1.

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