



**University of
Zurich**^{UZH}

**Zurich Open Repository and
Archive**

University of Zurich
Main Library
Strickhofstrasse 39
CH-8057 Zurich
www.zora.uzh.ch

Year: 2019

Drought decreases cooperative sentinel behavior and affects vocal coordination in meerkats

Rauber, Ramona ; Clutton-Brock, Tim H ; Manser, Marta B

Abstract: Cooperative breeding often evolved in harsh and arid habitats characterized by high levels of environmental uncertainty. Most forms of cooperative behavior have energetic costs and previous studies have shown that the contributions of individuals to alloparental provisioning are conditional on their food intake. However, the effect of naturally occurring, extreme environmental conditions on the persistence of costly forms of cooperative behaviors and their coordination by communication remain unknown. Here, we show that in meerkats (*Suricata suricatta*) the probability to act as sentinel, a cooperative vigilance behavior, was the same for typically occurring dry and wet conditions, but significantly reduced during a drought condition with almost no rain, especially in young individuals, members of small groups and groups with pups. The duration an individual stayed on sentinel guard, however, was most reduced during dry conditions. Besides reductions in sentinel behavior, the vocal coordination of foraging meerkats differed when comparing drought and wet conditions. Individuals responded more strongly to playbacks of sentinel “all-clear” calls and close calls, resulting in less vigilance and more foraging behavior during the drought condition. We conclude that while meerkats are adapted to commonly occurring dry periods with low rainfall, the extreme drought period with almost no rain, led to a decrease of the frequency of costly forms of cooperative behaviors in favor of behaviors that maximize direct fitness benefits and also affected the vocal coordination among group members.

DOI: <https://doi.org/10.1093/beheco/arz112>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-183031>

Journal Article

Accepted Version

Originally published at:

Rauber, Ramona; Clutton-Brock, Tim H; Manser, Marta B (2019). Drought decreases cooperative sentinel behavior and affects vocal coordination in meerkats. *Behavioral Ecology*, 30(6):1558-1566.

DOI: <https://doi.org/10.1093/beheco/arz112>

1 **Drought decreases cooperative sentinel behaviour and affects**
2 **vocal coordination in meerkats**

3

4

5 R. Rauber^{1,2*}, T. H. Clutton-Brock^{2,3,4} & M. B. Manser^{1,2,4}

6

7 ¹Animal Behaviour, Department of Evolutionary Biology and Environmental Studies,

8 University of Zurich, Winterthurerstrasse 190, 8057, Zurich, Switzerland

9 ²Kalahari Meerkat Project, Kuruman River Reserve, Northern Cape, South Africa

10 ³Large Animal Research Group, Department of Zoology, University of Cambridge,

11 Downing Street, Cambridge CB2 3EJ, UK.

12 ⁴Mammal Research Institute, University of Pretoria, Pretoria 0002, South Africa.

13

14 Running title: Effect of drought on cooperative sentinel behaviour

15

16

17

18

19

20 * Corresponding author: Ramona Rauber

21 Animal Behaviour, Department of Evolutionary Biology and Environmental Studies,

22 University of Zurich, Winterthurerstrasse 190, 8057, Zurich, Switzerland

23 ramona.rauber@ieu.uzh.ch

24

25 ABSTRACT

26

27 Cooperative breeding often evolved in harsh and arid habitats characterised by high levels of
28 environmental uncertainty. Most forms of cooperative behaviour have energetic costs and
29 previous studies have shown that the contributions of individuals to alloparental provisioning
30 are conditional on the food intake of individuals. However, the effect of naturally occurring,
31 extreme environmental conditions on the persistence of costly forms of cooperative
32 behaviours and their coordination by communication remain unknown. Here, we show that in
33 meerkats (*Suricata suricatta*) the probability to act as sentinel, a cooperative vigilance
34 behaviour, was the same for typically occurring dry and wet conditions, but significantly
35 reduced during a drought condition with almost no rain, especially in young individuals,
36 members of small groups and groups with pups. The duration an individual stayed on sentinel
37 guard, however, was most reduced during dry conditions. Besides reductions in sentinel
38 behaviour, the vocal coordination of foraging meerkats differed when comparing drought and
39 wet conditions. Individuals responded more strongly to playbacks of sentinel ‘all-clear’ calls
40 and close calls, resulting in less vigilance and more foraging behaviour during the drought
41 condition. We conclude that while meerkats are adapted to commonly occurring dry periods
42 with low rainfall, the extreme drought period with almost no rain, led to a decrease of the
43 frequency of costly forms of cooperative behaviours in favour of behaviours that maximize
44 direct fitness benefits and also affect the vocal coordination among group members.

45

46 Key words: drought, cooperative breeders, sentinel behaviour, sentinel calls, acoustic
47 communication

48

49 INTRODUCTION

50

51 Both in birds (Jetz and Rubenstein, 2011) and mammals (Lukas and Clutton-Brock, 2017),
52 cooperative breeding systems, where individuals forego their own independent reproduction

53 while helping others in the group to rear their young, are commonly associated with
54 environments where resources are scarce. In many of these environments, rainfall and
55 temperature vary widely within and between years (Jetz and Rubenstein, 2011; Lukas and
56 Clutton-Brock, 2017), generating unpredictable fluctuations in resource availability that are
57 commonly associated with variation in breeding success and survival (Clutton-Brock et al.,
58 1999a; Dai, 2011). A recent study on cooperatively breeding birds showed a decrease in
59 cooperative provisioning of young by adult group members during days with unusually high
60 temperatures (Wiley and Ridley, 2016) and previous studies of meerkats (*Suricata suricatta*)
61 have provided experimental evidence that cooperative behaviours are conditional on foraging
62 success and are reduced when daily weight gain of animals is low (Clutton-Brock et al., 2001;
63 Clutton-Brock et al., 1999b). Together, these results suggest that cooperative breeders need to
64 adjust their investment in cooperative behaviours in relation to variation in weather conditions
65 as well as in food availability, especially in response to extreme events, such as droughts,
66 defined as prolonged periods with rainfall significantly below the level received in commonly
67 occurring dry years (Botai et al., 2016). Currently, the effect of naturally occurring, extreme
68 environmental conditions, including reduced food availability, on the persistence of
69 cooperative behaviours has not been explored.

70 It has been suggested that cooperative breeders may have evolved a more complex
71 communicative system than less social species in order to coordinate group living and
72 cooperative activities (Freeberg et al., 2012; Leighton, 2017; Manser et al., 2014). It is well
73 known that social factors, such as sex, life history stages, or dominance status, influence the
74 behavioural responses to vocal signals (Fischer et al., 2004; Mitani and Brandt, 1994;
75 Snowdon and Elowson, 1999) but the extent to which extreme environmental conditions
76 affect vocal coordination remains unclear. For example, warning or alert calls that are not
77 associated with an immediate threat but rather with a general increase in perceived predation
78 risk or uncertainty might be more likely to be ignored during adverse environmental
79 conditions when individuals need to maximize foraging in order to survive. Thus, drought

80 conditions might affect the behavioural responses of individuals to specific vocal signals and
81 the coordination of cooperative behaviour.

82 In this study, we investigated potential differences in cooperative sentinel behaviour
83 and its vocal coordination in meerkats between a year of drought, three years of dry
84 conditions and three years of wet conditions (Table 1). Meerkats forage in small groups from
85 3 to 50 individuals composed of different age classes (pups < 3 months, juveniles 4-6 months,
86 subadults 7-12 months, yearlings 13-24 months and adults > 24 months) (Clutton-Brock et al.,
87 1999a; Clutton-Brock et al., 2006). Each group consists of a dominant, reproductive pair and
88 subordinates, which help to rear the dominant pair's offspring by providing them with food
89 and protection (Clutton-Brock et al., 1998). Meerkats have an elaborate sentinel system where
90 one individual is on raised guard at an elevated location, scanning the surroundings for the
91 presence of predators and alerting the group in case of danger (Clutton-Brock et al., 1999b).
92 Besides alarm calls elicited in response to an approaching predator (Manser, 2001; Manser et
93 al., 2001), sentinels also produce functionally specific sentinel calls, which inform the rest of
94 the group about the guard's temporary perceived predation risk and lead to the adjustment of
95 vigilance behaviours by foraging group members (Manser, 1999; Rauber and Manser, 2017).
96 Sentinel calls include calming calls, which have an 'all clear' function and lead to an increase
97 in foraging and a decrease in vigilance behaviour in receivers, and warning calls, which
98 decrease foraging and increase vigilance behaviour for the rest of the group (Rauber and
99 Manser, 2017).

100 Contributions to sentinel behaviour reduce foraging opportunities. The costs of
101 foregoing foraging are likely to increase under adverse environmental conditions, leading to
102 stronger trade-offs between cooperative behaviours and individual survival. Average rainfall
103 in our study area in the Southern Kalahari since 2009 has been 98 mm between December and
104 January but due to the severe El Nino event in 2015/16 rainfall was less than 1 mm during the
105 same time period and the weight and breeding success of resident animals was reduced
106 ((Wiley and Ridley, 2016); unpublished data long-term database). To test whether and how
107 drought conditions affected cooperative behaviours, we measured the contributions of

108 individuals to sentinel behaviour during a year of drought, three dry years of low rain
109 conditions and three wet years of high rain conditions (Table 1). In particular, we investigated
110 the effects of drought on the probability to act as a sentinel and the duration of guarding
111 periods. We predicted that while meerkats should be adapted to dry years, drought conditions
112 increase the costs of cooperative behaviours. As a consequence, we expected to find that
113 animals reduce both the probability that individuals would go on sentinel guard and the
114 duration of sentinel bouts in order to increase foraging time and thus individual survival. We
115 expected this effect to be most pronounced in younger individuals and members of small
116 groups, whose foraging success is relatively low (Clutton-Brock et al., 1999b; English et al.,
117 2014). Furthermore, we expected drought to decrease the skew in guarding contribution
118 within groups as single individuals might not be able to maintain higher sentinel frequencies
119 compared to the rest of the group. In regards to vocal coordination, we investigated the
120 consequences of drought on the responses of individuals to sentinel warning and calming
121 calls, using a series of playback experiments. We predicted that under drought conditions
122 foraging meerkats respond stronger to sentinel calming calls ('all-clear' function) and reduce
123 their response to sentinel warning calls (pre-stages of alarm calls) to increase foraging
124 efficiency in comparison to non-drought conditions (Rauber and Manser, 2017).

125

126 METHODS

127

128 *Study site and species*

129 Data were collected at the Kalahari Meerkat Project (KMP) located at the Kuruman River
130 Reserve in the southern Kalahari Desert, Northern Cape, South Africa (for more information
131 about habitat at the study site see (Clutton-Brock et al., 1999; Russell et al., 2002). The
132 climate at the study site is characterised by two distinct seasons: a cold-dry season from May
133 to September (mean monthly rainfall 5.5ml) and a hot-wet season from October to April

134 (mean monthly rainfall 45.7ml) (Clutton-Brock et al., 1999; Russell et al., 2002). As part of
135 the KMP's long-term data collection, all group members were uniquely dye marked to allow
136 individual recognition, and one or two individuals of each group were fitted with radio-collars
137 to facilitate localisation of the group (Jordan et al., 2007). All groups were habituated to close
138 human observations and to the playback equipment, allowing us to perform recordings and
139 playbacks within a distance of 0.5 m to the test subjects.

140

141 *Analysis of long-term data*

142 Individual sentinel events and their durations were collected between December and January
143 from 2009 to 2016 by volunteers of the Kalahari Meerkat Project as part of the daily long-
144 term data collection. We assigned each period of these seven years to one of three
145 environmental conditions – wet, dry and drought- based on the amount of rainfall measured
146 directly at the study site during the middle of the wet season, which includes the months
147 December and January. To account for any carry-over effects from previous rainfalls, we also
148 added the amount of rainfall during the three months before the analysed periods, i.e.
149 September to November. This resulted in the following categorisation: 2009/2010, 2010/2011
150 and 2011/2012 represented wet years, 2012/2013, 2013/2014 and 2014/2015 were dry years,
151 and 2015/2016 was a drought year with almost no rain between December and January (Table
152 1). A sentinel event always consisted of an individual climbing on an elevated position of at
153 least 10cm above ground and actively scanning the environment (Clutton-Brock et al.,
154 1999b). To investigate whether the different environmental conditions affected the probability
155 of individuals to go on guard we included every individual (total n=750; n=266 adults, n=504
156 yearlings, n=370 subadults, n=193 juveniles, due to the multi-year data structure some
157 individuals appear in several age categories) from every group (n=26) in the analysis and
158 checked whether each of these individuals acted as sentinel or not for each observation day
159 (n=28*773 observations). This resulted in a daily yes/no response variable for every group

160 member present on the day of data collection. Following this, we compared observed daily
161 sentinel durations by calculating the total time individuals were on sentinel guard during the
162 3.2±0.02 hours of observations per day (including morning and evening sessions) resulting in
163 a total of 3969 sentinel events of 480 different individuals (n=179 adults, 312 yearlings, 180
164 subadults, 21 juveniles, due to the multi year data structure some individuals appear in several
165 age categories). All individuals' age, sex, dominance status, group size, and whether and how
166 many pups were in the group were documented. We investigated the effect of any interaction
167 between environmental condition and age, sex, dominance status, group size, presence of
168 pups and number of pups on the observed time (min) individuals spent on sentinel duty per
169 day.

170

171 *Sound recordings*

172 Sound recordings for the playbacks of the different sentinel call types were collected in May
173 2014 prior to the start of the first playback experiments. Calls from naturally occurring
174 sentinel events were recorded using a Sennheiser directional microphone (ME66/K6)
175 connected to a Marantz PMD-670 solid-state recorder (Marantz Japan Inc.; sampling
176 frequency 44.2 kHz, 16 bits accuracy). A Rainhardt microphone windshield (W200) was
177 permanently attached to the microphone to ensure high quality recordings in the meerkats'
178 natural environment. The microphone was fixed to a telescopic pole in order to maintain a
179 recording distance of less than 0.5 meters and a high signal-to-background ratio.

180

181 *Playback experiments*

182 In order to compare behavioural responses to sentinel vocalisations during a non-drought and
183 a drought condition we repeated the same series of playbacks we had done for previous work
184 (Rauber and Manser, 2017) in the non-drought period from June to August 2014 in the
185 drought period of 2015/2016 from January to the 8th of March 2016. The rainfall
186 measurements for these two periods differed substantially in regards to the amount of rain in

187 the 3 months period before and the 3 months period of the playback experiments, with the
188 non-drought period having received 112ml and the drought period 15.2ml over the total of 6
189 months. When testing the probability to act as sentinel, this was significantly higher during
190 the non-drought period compared to the drought period (GLMM; $\beta \pm se = 1.32 \pm 0.39$, $z =$
191 3.41 , $p < 0.001$), indicating that, besides any other potential seasonal differences,
192 environmental conditions were less constraining for meerkats during the non-drought period.
193 We conducted playback experiments in a total of 12 groups with group size of three to 24
194 individuals. Following the same protocol as previous work on the behavioural response to
195 sentinel vocalisations (Rauber and Manser, 2017), we selected single calls with a high signal-
196 to-noise ratio using Cool Edit Pro (Syntrillium Software Corporation) to compose playback
197 files consisting of sentinel calls and close calls (control) from the same individual. Close calls
198 are soft, close range contact calls that are frequently emitted during foraging and used for
199 group coordination (Fichtel and Manser, 2010; Gall and Manser, 2017).

200 Sentinel calls of recordings from at least six different and independent recording events from
201 the same individual ($n=8$) were used for each playback file. The calls from at least three
202 different individuals were played back to each group, using a Marantz PMD-670 solid-state
203 recorder, connected to a portable speaker (iHome IHM79SC). The amplitude was assessed
204 according to how the calls occur under similar natural weather and wind conditions. The call
205 rate of the specific sentinel calls and close calls was kept the same as observed in natural
206 recordings (close calls: 8.25 ± 2.28 calls/min; single note calls: 3.79 ± 0.43 calls/min; double
207 note calls: 3.19 ± 0.37 calls/min) with background noise between each call (Rauber and
208 Manser, 2017). For the sentinel warning calls context we always played a total of four calls,
209 two “di-drrr” and two “wheek” calls in alternating order and with at least one minute of
210 background noise in between, which also lies in the range of natural recordings (di-drrr: $0.34 \pm$
211 0.12 calls/min; wheek calls: 0.39 ± 0.09 calls/min (Rauber and Manser, 2017)). Playback
212 experiments were only conducted when no predator had been seen for at least 15 minutes and
213 only if the majority of the group was foraging undisturbed for at least five minutes. If any of
214 the conditions, including the absence of predators, were violated after the playback had been

215 started, the playback was paused and resumed only after the majority of the group was back to
216 normal foraging behaviour for a minimum of five minutes or the sentinel finished its guarding
217 session. We played back a series of six five-minutes sound files to an adult foraging meerkat,
218 resulting in playbacks of a length of 30 minutes each. The full playback consisted of five
219 minutes of the two different sentinel call types (i.e. calming and warning calls), five minutes
220 of close calls (cc) in the beginning, between the two types of sentinel calls and afterwards and
221 also five minutes of background noise (bkg) either at the very beginning or the end (e.g. cc-
222 calming-cc-warning-cc-bkg). During the playbacks each behaviour of the test subjects was
223 recorded as a focal follow using the program Cybertracker (Cybertracker Conservation 2013
224 version 3.376) on a handheld tablet (Acer IconiaOne 7 B1-750). Four adult individuals (>12
225 months, the dominant pair and one subordinate of each sex) of eight groups were tested to
226 playbacks, resulting in a sample size of 32 playbacks for each year. To keep the playback
227 procedure the same as in 2014, when we were also interested in the potential difference
228 between calls from the same versus from another group, half of the playbacks were from
229 individuals from the same group and the other half from individuals from another group.

230

231 *Analysis of behavioural focals*

232 Behavioural responses to sentinel calls are of short duration and are only obvious within the
233 first 30 seconds after the playback of a call (Rauber and Manser, 2017). Therefore, to analyse
234 the response of the test subjects we calculated the proportion of time the meerkats spent
235 foraging and being vigilant during the first 30 seconds after four randomly (sample function
236 of the R base package) chosen calls of each of the different playback contexts (close calls,
237 calming sentinel calls, warning sentinel calls). As each playback file consisted of three
238 identical copies of five-minute tracks of close calls the proportions of time spent for each
239 behaviour was averaged for the analysis (here after called average cc). For the background
240 noise context we chose four random time points and analysed the behaviour in the following
241 30 seconds. As foraging behaviour we grouped foraging (digging in a hole for prey),

242 scabbling (head down while scratching at multiple small holes or surface), processing
243 (processing food items in sand, or chewing off tail of scorpions, etc.) and eating. Regarding
244 the alert-related behaviours, we focused on two types of vigilance behaviour: quadrupedal
245 (head up while scanning the sky and the surroundings on all four legs) and bipedal (scanning
246 of sky and surroundings standing on the hind legs with upright body position).

247

248 *Statistical analysis*

249 All analyses in this study were done using R version 3.2.0 (R Development Core Team 2016).
250 To determine the relationship between sentinel behaviour and the different parameters we
251 conducted linear mixed effects models (LMM) and generalized linear mixed effects models
252 (GLMM), depending on whether the data met the assumptions of normality and homogeneity
253 of variance (Bates D., 2014). To determine the fit of linear mixed models we examined the
254 model diagnostic plots and response variables were transformed where assumptions of the
255 models were not met (Crawley, 2012) . Post-hoc multiple comparison tests with manually set
256 contrasts were done whenever the predictor variable consisted of more than two categories to
257 compare the different categories not specified by the intercept (Hothorn T., 2008).

258 To analyse the effect of environmental conditions on an individual's observed daily
259 probability to go on guard, we fitted a generalized linear mixed effects model with guarding
260 (0/1) as response variable, thus, using binomial distribution. Because there was no significant
261 difference of guarding between wet and dry years while they were both significantly different
262 from the drought year we pooled those together as 'non-drought years' to facilitate model
263 convergence. Age class, sex, dominance status, group size, presence of pups and number of
264 pups were each tested as interaction with drought as fixed effects and Individual ID nested in
265 Group ID and Observation Date were added as random effects.

266 To investigate the effect of environmental conditions on sentinel duration we fitted a LMM
267 with individual sentinel guarding time per observation day as response variable and again age
268 class, sex, dominance status, group size and presence of pups were each tested separately as

269 interaction with drought as fixed effects. Individual ID nested in Group ID were added as
270 random effects. To determine whether sentinel duties were more evenly distributed within the
271 group during the drought compared to wet and dry years we calculated the proportion of
272 different sentinel individuals as the number of all individuals acting as sentinel per
273 observation day divided by the total group size (not including pups which don't contribute to
274 sentinel behaviour (Hollen et al., 2008)). We then used the log-transformed proportion of
275 sentinels as response variable in a LMM with environmental conditions, group size and the
276 interaction between drought and group size as fixed effects and Group ID as random factor.
277 Since there was again no difference between dry and wet years while both being significantly
278 different from drought, we pooled these two conditions together as non-drought period to
279 improve model convergence. Lastly, to analyse the effect of environmental conditions on the
280 response to sentinel calls (playback experiments) and the two different control conditions
281 (close calls and background noise), we conducted generalized mixed models with the
282 proportion of the behaviour of interest (number of seconds out of the total 30 seconds after a
283 call) as response variable using the cbind function and family binomial (Crawley, 2012).
284 Individual ID was nested in Group ID as random factors. The three behaviours of interest
285 were foraging, quadrupedal vigilance and bipedal vigilance. Whenever the explanatory
286 variable consisted of more than two categories multiple comparison test with manually set
287 contrasts (glht function of multcomp package) were used to compare the different categories
288 not specified by the intercept, or to compare specific contrasts (Hothorn T., 2008). The p
289 values were generated using adjusted p values using Bonferroni correction (Hothorn T.,
290 2008).

291

292 *Ethical note*

293 All the experiments and recordings conducted within the course of this study fall under the
294 permission of the ethical committee of Pretoria University and the Northern Cape

295 Conservation Service, South Africa (Permit number: EC031-13) and were carried out
296 adhering to the approved guidelines in this permit.

297

298 RESULTS

299

300 *Effect of environmental conditions on probability that individuals act as sentinel*

301 While there was no difference in the probability that individuals acted as sentinels during wet
302 and dry years ($\beta = 0.13 \pm 0.23$, $z = 0.55$, $p = 0.583$), meerkats went on sentinel guard
303 significantly less during the drought condition compared to the dry ($\beta = -1.01 \pm 0.32$, $z = -3.18$,
304 $p = 0.001$) and wet conditions ($\beta = -0.89 \pm 0.33$, $z = -2.67$, $p = 0.007$). Therefore, wet and dry
305 conditions were pooled together as ‘non-drought’ conditions and then compared to the
306 drought condition. During the drought condition, we found that, juveniles and subadults
307 reduced the frequency of them acting as sentinel significantly more than adults (Table 2;
308 Figure 1a). The same decrease was observed with yearlings, however, less strong. This
309 reduction in sentinel frequency was stronger in smaller groups and in groups where pups were
310 present (Table 2; Figure 1a,b). There was no interaction between environmental conditions
311 and either dominance status or sex on the likelihood to show sentinel behaviour.

312

313 *Effect of environmental conditions on sentinel duration*

314 The dry condition had a negative effect on the duration to stay on sentinel guard compared to
315 wet conditions ($\beta = -0.11 \pm 0.03$, $t = -3.5$, $p < 0.001$; Figure 2). The drought condition was not
316 significantly different from dry ($\beta = 0.04 \pm 0.05$, $t = 0.84$, $p = 0.403$; Figure 2) or wet ($\beta = -$
317 0.06 ± 0.05 , $t = -1.03$, $p = 0.304$; Figure 2) conditions. None of the tested variables including
318 age class, sex, dominance status, group size and presence of pups showed a significant
319 interaction with the three environmental conditions (wet, dry and drought).

320

321 *Effect of environmental conditions on distribution of sentinel duties among group*
322 *members*

323 The proportion of individuals contributing to sentinel behaviour within a group was
324 significantly lower during the drought compared to the dry ($\beta = -0.06 \pm 0.02$, $t = -3.04$, $p =$
325 0.003) and the wet ($\beta = -0.05 \pm 0.02$, $t = -2.16$, $p = 0.031$) conditions. Dry and wet conditions
326 did not differ ($\beta = 0.01 \pm 0.01$, $t = 1.16$, $p = 0.247$), thus were pooled together to non-drought
327 conditions. There was an interaction between environmental conditions and group size such
328 that, for small groups during drought conditions, the proportion of individuals contributing to
329 sentinel behaviour was the same or slightly higher than during non-drought conditions, while
330 the opposite was true for larger groups. They showed significantly lower proportions of
331 sentinels during the drought (Table 3; Figure 3). Follow up analyses excluding very small
332 groups of less than six individuals, as well as very large groups of more than 22 individuals,
333 confirmed the robustness of this result.

334

335 *Effects of environmental conditions on response to sentinel calls*

336 Foraging meerkats responded differently to the four tested playback conditions during the
337 drought in comparison to the non-drought period. The playback of sentinel calming calls
338 elicited less bipedal vigilance in the drought compared to the non-drought period (Table 4;
339 Figure 4c). Close calls (average cc), on the other hand, led to more foraging behaviour during
340 the drought (Table 4; Figure 4a), while background noise tended ($p < 0.1$) to elicit less foraging
341 behaviour (Table 4, Figure 4a) and more quadrupedal vigilance behaviour (Table 4; Figure
342 4b) during the drought period. We did not, however, find any evidence, that warning sentinel
343 calls were more likely to be ignored during the drought period (Table 4; Figure 4c).

344

345 DISCUSSION

346

347 Our results show the frequency of cooperative behaviours in meerkats to be
348 significantly reduced during naturally occurring, extreme environmental conditions with

349 limited food availability, supporting previous work on food dependency of cooperative
350 behaviours. While the probability of cooperative sentinel behaviour was the same during
351 commonly occurring dry and wet years, in the extreme drought year with almost no rain, a
352 shift in the investment from cooperative behaviours to foraging behaviour with immediate
353 individual benefits was observed, and vocal group coordination was also affected. During the
354 drought year, individual meerkats reduced the frequency with which they contributed to
355 sentinel behaviour. These reductions were largest in young individuals of less than two years,
356 members of smaller groups, and in groups with pups. Compared to smaller groups, in larger
357 groups the contribution to sentinel behaviour was less evenly distributed among group
358 members during the drought compared to the non-drought (dry and wet years taken together)
359 periods. Meerkats also responded more strongly to calming sentinel calls and contact calls,
360 showing more foraging and less vigilance behaviour in the drought year than in a year with
361 wet conditions. Background noise, however, led to less foraging and more vigilance
362 behaviour in the drought year.

363 In accordance with our predictions, we found that within groups, especially young
364 individuals, i.e. juveniles and subadults, were less likely to act as sentinel during the drought.
365 Yearlings (1-2 years old) also showed less sentinel behaviour during the drought compared to
366 adults, however, the effect was less strong than in the younger age class. Furthermore, we
367 found that group size and composition significantly affected the probability to act as sentinel
368 when comparing the drought year with the dry and wet years. Members of small groups and
369 groups with pups reduced the sentinel frequency during the drought more than members of
370 larger groups and groups without dependent offspring. The effect of group size is likely
371 explained by the higher individual contribution to sentinel behaviour in smaller groups
372 (Clutton-Brock et al., 1999b). The found effect of presence of pups suggests that having
373 dependent offspring (pups) comes with additional costs of helping behaviours such as
374 allolactation, pup feeding and protection of pups (Clutton-Brock and Manser, 2016). As the
375 survival of young is critically dependent on provisioning from adults, it is not surprising that
376 these behaviours are prioritized over sentinel behaviour as a response to limited resources.

377 Duration of sentinel behaviour per guarding event was longest during wet years. A
378 likely explanation is that during these conditions vegetation is usually much taller and denser
379 compared to dry years and the drought year and meerkats need to stay on sentinel guard
380 longer in order to scan the area for the presence of predators, in particular terrestrial
381 predators. In addition, there is more food available in the wet season leading to individuals
382 being faster satiated and thus able to afford to be on sentinel guard for longer periods of time.
383 Against our predictions, we did not find a difference in sentinel duration between the dry
384 years and the drought year. The reduction in sentinel duration in dry years may be due to the
385 fact that compared to the drought year meerkats still keep up the same frequency of sentinel
386 behaviour during dry years as during wet years when food is plentiful. Therefore, when
387 conditions get harder there seems to be a trade-off between frequency of cooperative
388 behaviours and duration. During dry years it seems that mainly duration was reduced while
389 during the drought year it was mainly the frequency that decreased with which individuals
390 maintain cooperative behaviours. Further research is needed to explore this relationship in
391 other cooperative behaviours, in particular using more drought years.

392 In terms of how sentinel behaviour is distributed among group members, we provide
393 evidence that larger groups showed a bigger decrease in the number of different individuals
394 going on sentinel guard per day in the drought, while the proportion of individuals acting as
395 sentinel of smaller groups stayed the same as in non-drought years. Together with the effect
396 of group size on the probability to act as sentinel, this suggests that in smaller groups, the
397 same number of animals go on shorter sentinel bouts, while in larger groups fewer animals act
398 as sentinels in the drought, but those can afford to keep the total time the group has a sentinel
399 similar to non-drought years. Thus, larger groups were able to maintain cooperative
400 behaviours, while cooperative behaviours in smaller groups were significantly reduced in the
401 drought year. This is in line with previous work that shows the benefits of living in larger
402 groups due to lower individual contribution to cooperative behaviours (Clutton-Brock et al.,
403 1999b).

404 Not only investment into sentinel behaviour changed depending on environmental
405 conditions, but also the vocal coordination of foraging meerkats. Test subjects responded
406 more strongly to playbacks of sentinel calming calls, which act as ‘all-clear’ signal, resulting
407 in less vigilance and more foraging behaviour in the drought period in comparison to the non-
408 drought period. A likely explanation is that during demanding conditions individuals rely
409 more on ‘all-clear’ signals in order to maximize foraging. We did not, however, find any
410 evidence that meerkats were more likely to ignore sentinel warning calls in the drought period
411 compared to the non-drought period. This is in line with work on alarm calls, where the costs
412 of not responding to calls related to predators have been suggested to be too high to ignore
413 (Schibler and Manser, 2007). The fact that meerkats were more vigilant during the drought
414 when they heard background noise may indicate, that as a consequence of the decrease in
415 cooperative vigilance behaviour, individuals experience higher levels of uncertainty in
416 perceived predation risk and thus invest more time into personal vigilance behaviours.
417 Additionally, hearing no calls from other group members might increase the perceived risk of
418 losing the group (Gall and Manser, 2017), due to meerkats being more spread out when food
419 is spatially and temporally more scattered (Rymer et al., 2016). This is supported by findings
420 that during drought conditions foraging meerkat groups split more often compared to dry
421 conditions (Gall, 2017) and can also explain our result that meerkats were less vigilant when
422 they heard contact calls during the drought, indicating close proximity to other group
423 members (Gall and Manser, 2017). However, other differences in seasonal related factors, e.g.
424 spatial cohesion or foraging time, between the two playback periods, besides the amount of
425 rain and sentinel frequency, can not be excluded to have impacted the behavioural response of
426 foraging meerkats to sentinel calls. Further playbacks are needed to confirm the importance of
427 specific environmental factors on a species’ communication system.

428 In conclusion, our results suggest that naturally occurring, extreme environmental
429 conditions, such as droughts, decrease the contribution to cooperative behaviours, as shown
430 on the sentinel behaviour in meerkats. Furthermore, these reductions in frequency and to a
431 lesser extent duration of cooperative vigilance behaviour were associated with changes in the

432 vocal coordination of foraging meerkats. Although meerkats, and cooperative breeders in
433 general, are adapted to arid, unpredictable environments (for example (Cockburn and Russell,
434 2011; Schneider and Kappeler, 2014), extreme environmental conditions that reduce food
435 availability affect the investment of individuals in cooperative activities and the vocal
436 coordination of cooperative behaviours. Therefore, we argue that there is likely an ecological
437 threshold beyond which some aspects of cooperation including cooperative vigilance
438 behaviour and provisioning of young (Wiley and Ridley, 2016) seem to collapse. Our study
439 offers new insights about how extreme environmental conditions influence the occurrence of
440 cooperative behaviours and the consequences for group coordination in cooperative breeders.

441

442 AUTHORS' CONTRIBUTIONS

443 RR and MBM were involved in planning the study. RR conducted the experiments
444 and statistical analyses. RR, MBM and THCB equally contributed to the writing of
445 the manuscript. THCB and MM organised the long-term data collection at the KMP
446 on cooperative behaviour, weights and life history data.

447

448 COMPETING INTERESTS

449 We declare we have no competing interests.

450

451 FUNDING

452 RR, MBM and research expenses were funded by the University of Zurich, THCB was
453 funded by the University of Cambridge. The long-term field site KMP was financed by
454 University of Cambridge and Zurich, and the MAVA foundation. This paper has relied on
455 records of individual identities and/or life histories maintained by the KMP, which has been
456 supported financially by the European Research Council (Grant No 294494 to T.H. Clutton-
457 Brock since 1/7/2012) and the University of Zurich, as well as logistically by the Mammal
458 Research Institute of the University of Pretoria.

459

460 ACKNOWLEDGEMENTS

461 We thank the Kalahari Research Trust and the Northern Cape Conservation Authority for
462 research permission (FAUNA 1020/2016). We also thank Dave Gaynor for organising the
463 field site as well as the managers and volunteers of the Kalahari Meerkat Project (KMP) for
464 organising and helping to collect the data about sentinel behaviour and life history of the
465 meerkats. Furthermore, we thank Matthew Petelle, Gabriella Gall and Sabrina Engesser and
466 two anonymous reviewers for comments on the manuscript.

467

468 Data accessibility: Analyses reported in this article can be reproduced using the data provided
469 by (Rauber et al., 2019).

470

471 REFERENCES

- 472 Bates D. MM, Bolker B. and Walker S., 2014. lme4: Linear mixed-effects models
473 using Eigen and S4. R package version 1.1-7.
- 474 Botai CM, Botai JO, Dlamini LC, Zwane NS, Phaduli E, 2016. Characteristics of
475 Droughts in South Africa: A Case Study of Free State and North West
476 Provinces. *Water* 8. doi: 10.3390/w8100439.
- 477 Clutton-Brock T, Manser M, 2016. Meerkats: cooperative breeding in the
478 Kalahari. *Cooperative breeding in vertebrates: Studies of ecology,
479 evolution, and behavior*:294-317.
- 480 Clutton-Brock TH, Brotherton PNM, O'Riain MJ, Griffin AS, Gaynor D, Kansky R,
481 Sharpe L, McIlrath GM, 2001. Contributions to cooperative rearing in
482 meerkats. *Animal Behaviour* 61:705-710. doi: 10.1006/anbe.2000.1631.
- 483 Clutton-Brock TH, Gaynor D, Kansky R, MacColl ADC, McIlrath G, Chadwick P,
484 Brotherton PNM, O'Riain JM, Manser M, Skinner JD, 1998. Costs of
485 cooperative behaviour in suricates (*Suricata suricatta*). *Proceedings of the
486 Royal Society B-Biological Sciences* 265:185-190.
- 487 Clutton-Brock TH, Gaynor D, McIlrath GM, Maccoll ADC, Kansky R, Chadwick P,
488 Manser M, Skinner JD, Brotherton PNM, 1999a. Predation, group size and
489 mortality in a cooperative mongoose, *Suricata suricatta*. *Journal of Animal
490 Ecology* 68:672-683. doi: 10.1046/j.1365-2656.1999.00317.x.
- 491 Clutton-Brock TH, Hodge SJ, Spong G, Russell AF, Jordan NR, Bennett NC, Sharpe
492 LL, Manser MB, 2006. Intrasexual competition and sexual selection in
493 cooperative mammals. *Nature* 444:1065-1068. doi:
494 10.1038/nature05386.

495 Clutton-Brock TH, O'Riain MJ, Brotherton PNM, Gaynor D, Kansky R, Griffin AS,
496 Manser M, 1999b. Selfish sentinels in cooperative mammals. *Science*
497 284:1640-1644. doi: 10.1126/science.284.5420.1640.

498 Clutton - Brock T, Maccoll A, Chadwick P, Gaynor D, Kansky R, Skinner J, 1999.
499 Reproduction and survival of suricates (*Suricata suricatta*) in the
500 southern Kalahari. *African Journal of Ecology* 37:69-80.

501 Cockburn A, Russell AF, 2011. Cooperative Breeding: A Question of Climate?
502 *Current Biology* 21:R195-R197. doi: 10.1016/j.cub.2011.01.044.

503 Crawley MJ, 2012. *The R book*: John Wiley & Sons.

504 Dai AG, 2011. Drought under global warming: a review. *Wiley Interdisciplinary*
505 *Reviews-Climate Change* 2:45-65. doi: 10.1002/wcc.81.

506 English S, Bateman AW, Mares R, Ozgul A, Clutton-Brock TH, 2014. Maternal,
507 social and abiotic environmental effects on growth vary across life stages
508 in a cooperative mammal. *Journal of Animal Ecology* 83:332-342. doi:
509 10.1111/1365-2656.12149.

510 Fichtel C, Manser M, 2010. Vocal communication in social groups. *Animal*
511 *behaviour: Evolution and mechanisms*: Springer. p. 29-54.

512 Fischer J, Kitchen DM, Seyfarth RM, Cheney DL, 2004. Baboon loud calls advertise
513 male quality: acoustic features and their relation to rank, age, and
514 exhaustion. *Behavioral Ecology and Sociobiology* 56:140-148. doi:
515 10.1007/s00265-003-0739-4.

516 Freeberg TM, Dunbar RI, Ord TJ, 2012. Social complexity as a proximate and
517 ultimate factor in communicative complexity. *The Royal Society*. p. 1785-
518 1801.

519 Gall GE, Manser MB, 2017. Group cohesion in foraging meerkats: follow the
520 moving 'vocal hot spot'. *Royal Society open science* 4:170004.

521 Gall GEC, 2017. *Group Coordination and Decision-Making during Foraging in*
522 *Meerkats (Suricata suicatta)*. (PhD thesis). University of Zurich, Faculty of
523 Science: University of Zurich.

524 Hollen LI, Clutton-Brock T, Manser MB, 2008. Ontogenetic changes in alarm-call
525 production and usage in meerkats (*Suricata suricatta*): adaptations or
526 constraints? *Behavioral Ecology and Sociobiology* 62:821-829. doi:
527 10.1007/s00265-007-0508-x.

528 Hothorn T. BF, Westfall P., and Heiberger R.M., 2008. multcomp: Simultaneous
529 inference in general parametric models.

530 Jetz W, Rubenstein DR, 2011. Environmental Uncertainty and the Global
531 Biogeography of Cooperative Breeding in Birds. *Current Biology* 21:72-
532 78. doi: 10.1016/j.cub.2010.11.075.

533 Jordan NR, Cherry MI, Manser MB, 2007. Latrine distribution and patterns of use
534 by wild meerkats: implications for territory and mate defence. *Animal*
535 *Behaviour* 73:613-622. doi: 10.1016/j.anbehav.2006.06.010.

536 Leighton GM, 2017. Cooperative breeding influences the number and type of
537 vocalizations in avian lineages. *Proc R Soc B* 284:20171508.

538 Lukas D, Clutton-Brock TH, 2017. Climate and the distribution of cooperative
539 breeding in mammals. *Royal Society Open Science* 4. doi:
540 10.1098/rsos.160897.

541 Manser MB, 1999. Response of foraging group members to sentinel calls in
542 suricates, *Suricata suricatta*. *Proceedings of the Royal Society B-Biological*
543 *Sciences* 266:1013-1019. doi: 10.1098/rspb.1999.0737.

544 Manser MB, 2001. The acoustic structure of suricates' alarm calls varies with
545 predator type and the level of response urgency. *Proceedings of the Royal*
546 *Society B-Biological Sciences* 268:2315-2324. doi:
547 10.1098/rspb.2001.1773.

548 Manser MB, Bell MB, Fletcher LB, 2001. The information that receivers extract
549 from alarm calls in suricates. *Proceedings of the Royal Society B-*
550 *Biological Sciences* 268:2485-2491. doi: 10.1098/rspb.2001.1772.

551 Manser MB, Jansen DA, Graw B, Hollén LI, Bousquet CA, Furrer RD, le Roux A,
552 2014. Vocal complexity in meerkats and other mongoose species.
553 *Advances in the Study of Behavior: Elsevier.* p. 281-310.

554 Mitani JC, Brandt KL, 1994. Social factors influence the acoustic variability in the
555 long-distance calls of male chimpanzees. *Ethology* 96:233-252.

556 Rauber R, Clutton-Brock TH, Manser MB, 2019. Data from: Drought decreases
557 cooperative sentinel behaviour and affects vocal coordination in
558 meerkats. *Dryad Digital Repository.*
559 <https://doi.org/10.5061/dryad.1s73fc5>

560 Rauber R, Manser MB, 2017. Discrete call types referring to predation risk
561 enhance the efficiency of the meerkat sentinel system. *Scientific reports*
562 7:44436.

563 Russell AF, Clutton-Brock TH, Brotherton PNM, Sharpe LL, McIlrath GM, Dalerum
564 FD, Cameron EZ, Barnard JA, 2002. Factors affecting pup growth and
565 survival in co-operatively breeding meerkats *Suricata suricatta*. *Journal of*
566 *Animal Ecology* 71:700-709. doi: 10.1046/j.1365-2656.2002.00636.x.

567 Rymer TL, Pillay N, Schradin C, 2016. Resilience to drought in mammals: a
568 conceptual framework for estimating vulnerability of a single species.
569 *Quarterly Review of Biology* 91:133-176.

570 Schibler F, Manser MB, 2007. The irrelevance of individual discrimination in
571 meerkat alarm calls. *Animal Behaviour* 74:1259-1268. doi:
572 10.1016/j.anbehav.2007.02.026.

573 Schneider TC, Kappeler PM, 2014. Social systems and life-history characteristics
574 of mongooses. *Biological Reviews* 89:173-198. doi: 10.1111/brv.12050.

575 Snowdon CT, Elowson AM, 1999. Pygmy marmosets modify call structure when
576 paired. *Ethology* 105:893-908. doi: 10.1046/j.1439-0310.1999.00483.x.

577 Wiley EM, Ridley AR, 2016. The effects of temperature on offspring provisioning
578 in a cooperative breeder. *Animal Behaviour* 117:187-195. doi:
579 10.1016/j.anbehav.2016.05.009.

580 TABLES

581

582 **Table 1.** Environmental conditions based on rainfall measured at study site.

Year	Rainfall (ml) December-January (study period)	Rainfall (ml) September-November	Total amount of rain (ml) September - January	Environmental Condition (EC)
2009/2010	178.0	NA	178.0*	Wet
2010/2011	195.2	28.6	223.8	Wet
2011/2012	116.4	1.0	117.4	Wet

2012/2013	16.6	15.4	32.0	Dry
2013/2014	57.4	5.8	63.2	Dry
2014/2015	24.6	16.4	41.0	Dry
2015/2016	0.6	11.6	12.2	Drought

583
584

*minimum estimate due to lack of rain data at study site before December 2009

585 **Table 2.** GLMM model output investigating the interactions between environmental
586 condition (EC) and sex, age class, dominance status, group size, presence and number of pups
587 on observed daily sentinel probability (Number of obs=28773, groups: Code:Group=901;
588 WatchDate= 210; Group=35).

Fixed Effect	Effect±SE	Df	X ²	P
(Intercept)	-2.54±0.26			
Environmental condition (EC)	-1.92±0.52	1	54.20	<0.001
AgeCategoryJuvAndSub	-0.79±0.10			<0.001
AgeCategoryYearling	0.44±0.08			<0.001
SexM	0.48±0.11			<0.001
DomStatusSub	0.11±0.12			0.329
GroupSize	-1.49±0.13			<0.001
PresencePups	0.59±0.05			<0.001
EC:AgeClass		3	22.27	<0.001
EC:JuvAndSub	-1.00±0.39			0.012
EC:Yearling	-0.59±0.27			0.026
EC:Groupsize	1.68±0.53	1		0.002
EC:PresencePups	-0.83±0.27	1	2.71	0.002
Random effects	Var	sd		
Code:Group	1.61	1.27		
WatchDate	1.91	1.38		

589 Significant variables are shown in bold.

590 **Table 3.** Main effects and interaction of environmental condition (EC) and group size on the
 591 proportion of different sentinels within a group (as determined by a linear mixed model;
 592 Number of obs= 883, groups: Watch Date= 175; Group=25).

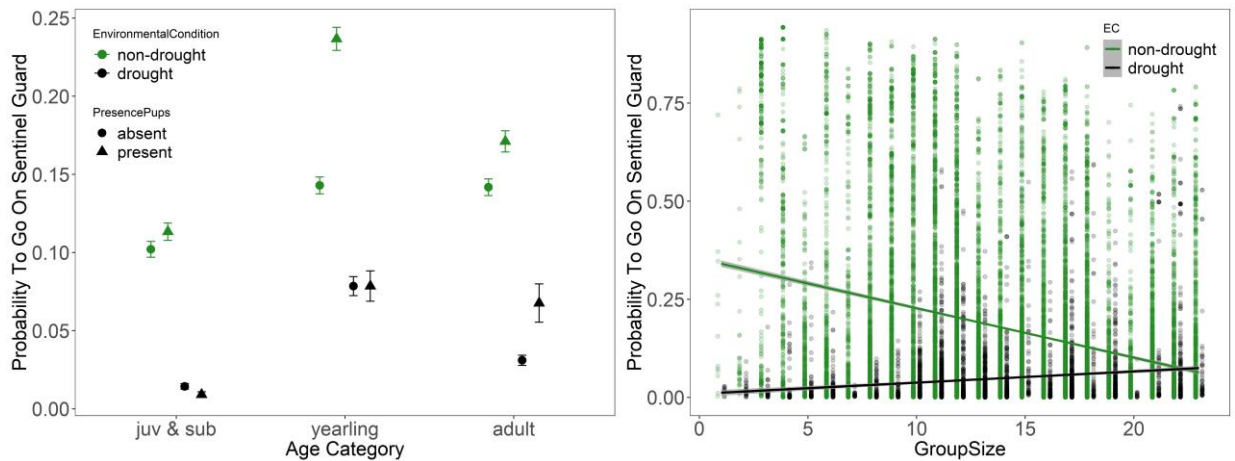
Fixed Effect	Estimate± SE	Df	X ²	P
(Intercept)	-0.99±0.07			
Environmental Condition (EC)	0.20±0.21	1	35.65	0.335
Group size	-0.05±0.01	1	215.25	<0.001
EC:Group size	-0.04±0.01	1	0.99	0.003
Random effects	Var	sd		
Group	0.04	0.21		
WatchDate	0.01	0.09		

593 Significant variables are shown in bold.

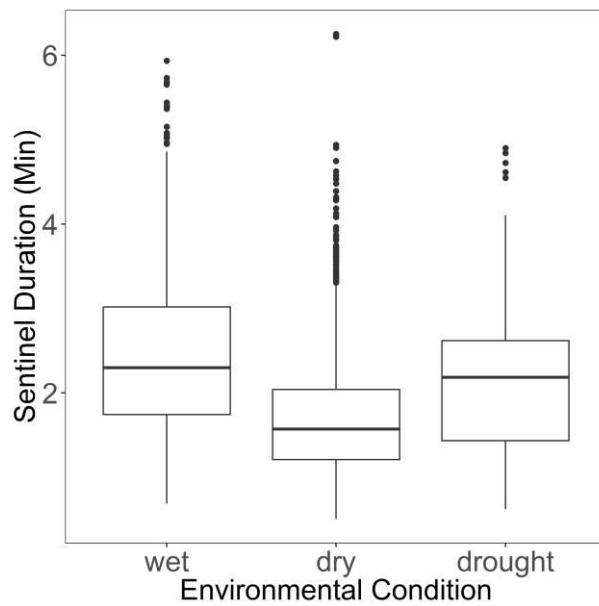
594 **Table 4.** GLMM model output and post-hoc multiple comparison test to compare foraging,
 595 quadrupedal vigilance and bipedal vigilance during the different playback conditions between
 596 drought and non-drought year (Numer of obs=946, number of playbacks=60,
 597 Code:Group=56, Group=12).

Behaviour	Condition	Estimate± SE	z-value	P
Foraging	(Intercept)	2.88±0.30		
	Close calls	0.84±0.41	2.04	0.04
	Background	-0.70± 0.41	-1.73	0.08
	Calming	0.49±0.43	1.12	0.26
	Warning	0.04±0.39	0.09	0.93
Quadrupedal	(Intercept)	-4.13±0.28		
Vigilance	Close calls	-0.22±0.33	-1.42	0.15
	Background	0.71±0.32	2.45	0.01
	Calming	-0.08±0.35	-0.29	0.77
	Warning	-0.11±0.31	-0.65	0.52
Bipedal	(Intercept)	-3.11±0.27		
Vigilance	Close calls	-0.62±0.37	-0.67	0.09
	Background	-0.42±0.37	-1.12	0.26
	Calming	-1.02±0.38	2.67	0.007
	Warning	-0.17±0.36	0.48	0.63

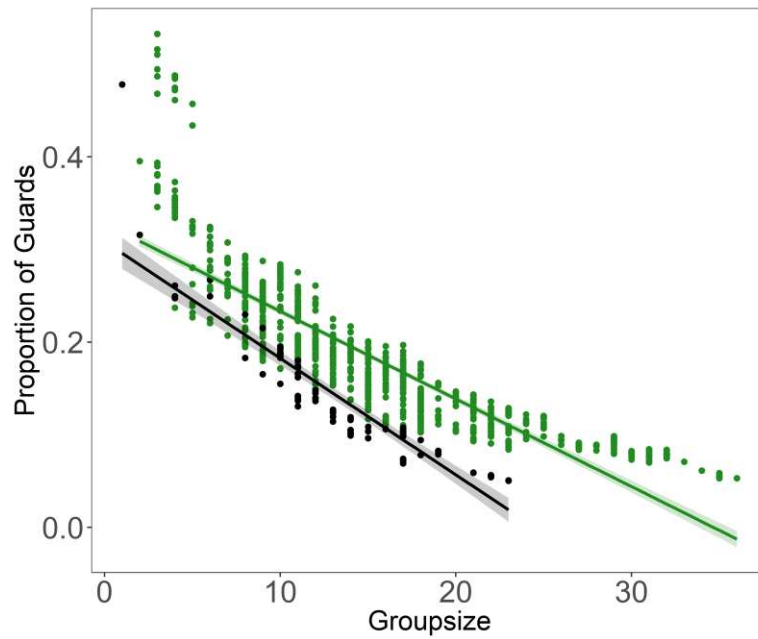
598 Significant variables are shown in bold.



600
 601 **Figure 1.** Model estimates of the daily probability to go on sentinel guard during drought
 602 (black) and non-drought (green; wet and dry conditions pooled together as they were
 603 statistically not different) for a) the different age classes and whether there were pups present
 604 in the group or not and b) different group sizes. Shown are estimates for subordinates only,
 605 which did not differ from dominant individuals.
 606



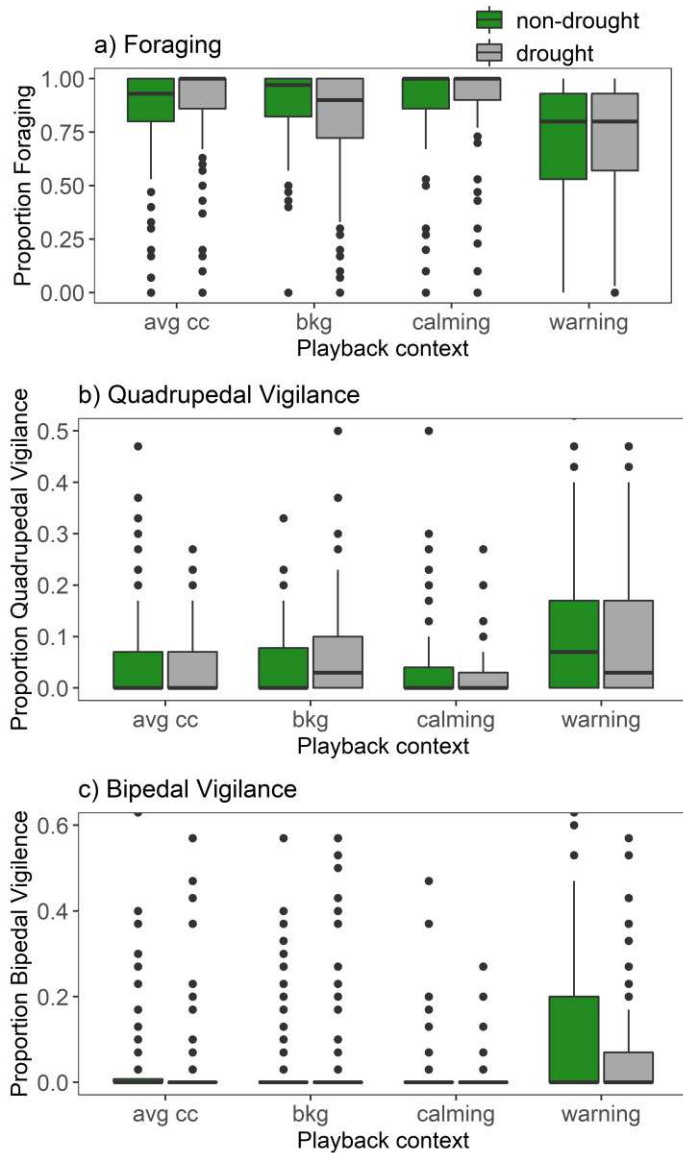
607
 608 **Figure 2.** Boxplots of average predicted duration of a single sentinel event (in min)
 609 during each of the three environmental conditions (wet, dry, drought). The bold
 610 horizontal line represents the median while the box shows the interquartile range
 611 between the 25% and 75% percent quartiles. Whisker show data range of 1.5 times
 612 the interquartile range from the 25% and the 75% quartiles.
 613



614

615 **Figure 3.** Relationship between predicted daily proportions of individuals in a group
616 that acted as sentinels during drought and non-drought periods (wet and dry conditions
617 pooled together as they were statistically not different).

618



619

620 **Figure 4.** Comparison of (a) foraging, (b) quadrupedal vigilance and (c) bipedal vigilance
 621 behaviour given in response to the four different playback conditions (close calls (= average
 622 cc), background noise (bkg), calming sentinel calls, warning sentinel calls) between drought
 623 and non-drought period.