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Sentinel Dominance Status Influences Forager Use of Social Information

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Animals in social groups can acquire information about the need for anti-predator behavior by personally sampling the environment or from information provided by others. Use of such social information is expected to be adjusted according to its reliability, but experimental tests are rare and tend to focus just on alarm calls. We use detailed behavioral observations, acoustic analyses and playback experiments to investigate how differences in sentinel dominance status affect the behavioral decisions of foraging dwarf mongooses (*Helogale parvula*). Dominant individuals acted as sentinels considerably more often than subordinate group members, and used higher sentinel posts for guarding, making them potentially higher quality sentinels in terms of experience and optimal positioning for predator detection. Surveillance calls produced during sentinel bouts contained vocal information about dominance status. Playback experiments showed that foragers used surveillance calls to detect sentinel presence and identity, and adjusted their vigilance behavior accordingly. When a dominant sentinel was on duty, compared to a subordinate groupmate, foragers increased reliance on social information, gathered less information through personal vigilance and focused more on foraging. Our study contributes novel evidence that a major benefit of individual and class-specific vocalizations is the potential to assess differences in caller information quality.

Keywords: social information; reliability; anti-predator vigilance; vocal communication; sentinel behavior

30 **1. Introduction**

31 To make informed decisions, animals use ‘personal’ information from their own experiences and
32 ‘social’ information gathered from other individuals (Giraldeau et al. 2002; Danchin et al. 2004).
33 Although social information can be obtained quickly and relatively cheaply (Giraldeau et al.
34 2002), there is discernible variation in quality (Blumstein et al. 2004a). Where using poor quality
35 information is costly to the receiver, individuals should adjust their reliance on social information
36 according to its potential quality (Barrera et al. 2011). By compiling information gathered during
37 prior interactions, receivers can maximize use of high quality sources whilst ignoring other
38 individuals (van Bergen et al. 2004, Dall et al. 2005).

39

40 Variation in quality has been best-studied in a predatory context with respect to alarm calls,
41 vocalizations given to warn of approaching danger (Hollén and Radford 2009). Individuals in
42 mixed-species groups discriminate between the alarm calls of heterospecifics, responding more
43 strongly to species with whom they share most threats, or which are more accurate in their
44 classification of predators (reviewed in Magrath et al. 2015). Receivers might also be expected
45 to discriminate between conspecific alarm callers, given that the threat of predation differs
46 depending on intrinsic biological factors such as age, sex and body condition (e.g. Werner et
47 al. 1983; Lima 1988; Lea and Blumstein 2011), ‘personality’ (Dall et al. 2004), and experience
48 with predators (Dill 1974; Stankowich and Blumstein 2005). While individuals in some species
49 disregard acoustic differences in alarm calls and respond similarly to all callers (Schibler and
50 Manser 2007), several studies have found that receivers discriminate between reliable and
51 unreliable callers (Cheney & Seyfarth 1988; Hare & Atkins 2001; Blumstein et al. 2004a),
52 often on the basis of age class (e.g. adult/juvenile; Gouzoules et al. 1996; Hanson and Coss
53 2001; Blumstein and Daniel 2004).

54

55 Sentinel behavior, in which an individual adopts a raised position, scanning for predators and
56 warning others of danger, has been documented in a range of social bird and mammal species
57 (reviewed in Bednekoff 2015). Benefits accrued to groupmates from sentinel behavior (early
58 warning of predators, decreased forager vigilance and increased biomass intake; Manser 1999;
59 Hollén et al. 2008; Ridley et al. 2010) are likely to vary depending on the quality of the sentinel.
60 Individuals may differ in their ability to detect and correctly identify a threatening stimulus for
61 a variety of reasons, including variation in ecological conditions, motivation, visual acuity,
62 sentinel position and experience. Groupmates would be expected to adjust their own vigilance

63 behavior depending on sentinel quality, reducing vigilance effort when foraging in the presence
64 of better sentinels. To our knowledge, however, only one study has examined this possibility:
65 Radford et al. (2009) found that pied babbler (*Turdoides bicolor*) foragers reduced vigilance
66 more when sentinels were positioned higher.

67

68 In several species, individuals produce low-amplitude surveillance calls when acting as a
69 sentinel (Manser 1999; Hollén et al. 2008; Kern and Radford 2013). Surveillance calls are
70 known to provide key information about sentinel presence, satiation level and height (Manser
71 1999; Hollén et al. 2008; Radford et al. 2009, 2011; Bell et al. 2010), and an estimate of current
72 risk levels (Bell et al. 2009; Kern and Radford 2013), thus allowing receivers to optimize their
73 foraging (Manser 1999; Hollén et al. 2008; Bell et al. 2010). Surveillance calls can also provide
74 information about sentinel identity (Manser 1999), including age, sex and dominance status.
75 Foragers could potentially use this vocal information in combination with prior knowledge
76 about individual reliability, to adjust their vigilance and foraging behavior accordingly, but this
77 possibility remains unexplored.

78

79 Here we investigate information available in dwarf mongoose (*Helogale parvula*) surveillance
80 calls, and its use by foraging group members. Dwarf mongooses are cooperatively breeding
81 carnivores living in groups of up to 30 individuals (Rasa 1977). The dominant pair monopolizes
82 reproduction, with related and unrelated subordinates of both sexes helping to rear offspring
83 (Rood 1980). Dwarf mongooses search for the majority of their prey by digging, and so are
84 unable to forage and be fully vigilant simultaneously (Rasa 1989). They are at risk from a wide
85 range of avian and terrestrial predators (Rasa 1986), and sentinels are often posted (Sharpe et
86 al. 2010; Kern and Radford 2013). Dwarf mongoose sentinels produce low-amplitude
87 surveillance calls in approximately half of sentinel bouts, predominantly calling when guarding
88 in denser habitats and when group members are more spread out (Rasa 1986; Kern and Radford
89 2013). Subordinate sentinels are more likely to vocalize than dominants, though the likelihood
90 of a dominant sentinel vocalizing increases in larger groups (Kern & Radford 2013).

91

92 Using a combination of natural observations, acoustic analysis of sound recordings and field
93 playback experiments, we answer four main questions. First, do foraging dwarf mongooses use
94 vocal cues to detect the presence of a sentinel and adjust their behavior accordingly, as has
95 been shown in other species (Manser 1999; Hollén et al. 2008)? Second, do dominant and
96 subordinate individuals differ in their contributions to sentinel behavior and choice of sentinel

97 post height? Third, do vocal cues provide information about sentinel dominance status? Fourth,
98 do foragers adjust their vigilance behavior according to vocal information about sentinel
99 dominance status?

100

101 **2. Material and methods**

102 **(a) Study site and population**

103 This study took place on Sorabi Rock Lodge Reserve, a 4 km² private game reserve in Limpopo
104 Province, South Africa (24°11'S, 30°46'E), part of southern Africa's Savanna Biome (see Kern
105 and Radford 2013 for full details). Data were collected from eight groups of wild dwarf
106 mongooses (mean group size = 8.3; range = 3–17), habituated to close observation (<5 m) on
107 foot (Kern and Radford 2013). All animals are individually identifiable either from markings
108 of blonde hair dye (Wella UK Ltd, Surrey, UK) applied with an elongated paintbrush or from
109 natural features such as scars or facial irregularities. The population has been monitored since
110 2011, thus the age of most individuals is known; individuals can be sexed through observations
111 of ano-genital grooming.

112

113 **(b) Observational data collection**

114 To investigate contributions to sentinel duty by individuals of different dominance status,
115 observations were conducted between January 2014 and March 2015. Once groups had left the
116 overnight refuge to begin foraging, scan samples were carried out every 30 min to record
117 whether a sentinel was present and, if so, the sentinel's identity (and thus sex and dominance
118 status), sentinel post height (to the nearest 10 cm), and group size. Individuals younger than
119 one year seldom contribute to sentinel behavior (JM Kern unpublished data), therefore group
120 size included only individuals of 12 months and older. Adult group members were classified
121 as either 'dominant' (male and female pair) or 'subordinate' (the remaining individuals). The
122 dominant pair could be identified through observations of aggression, feeding displacement,
123 scent marking and greeting behavior (Rasa 1977). Sentinels were defined as individuals whose
124 feet were at least 10 cm above ground and who were actively scanning the surroundings while
125 groupmates were engaged in other activities, primarily but not exclusively foraging (Sharpe et
126 al. 2010; Kern and Radford 2013, 2014).

127

128 **(c) Acoustic recordings and analysis**

129 To investigate acoustic variation in the surveillance calls of dominant and subordinate
130 sentinels, vocal recordings were collected in tandem with observations of sentinel behavior
131 from December 2012 to September 2013. Vocalizations from known individuals were recorded
132 from a distance of 0.5–10 m at a sampling rate of 44.1 kHz with a 16-bit resolution onto a
133 SanDisk SD card (SanDisk, Milipitas, California, USA), using a Marantz PMD660
134 professional solid-state recorder (Marantz America, Mahwah, NJ, USA) and a handheld highly
135 directional Sennheiser ME66 shotgun microphone (Sennheiser UK, High Wycombe,
136 Buckinghamshire, UK) with a Rycote Softie windshield (Rycote Microphone Windshields,
137 Stroud, Gloucestershire, UK). Whole bouts were recorded (mean \pm SE bout duration = 157.3
138 \pm 34.8 s, range = 0.3–18.9 min, N = 101).

139
140 From recordings, spectrograms were created in Raven Pro 1.5 using a 1024 point fast Fourier
141 transformation (Hamming window, 69.9% overlap, 1.45 ms time resolution, 43 Hz frequency
142 resolution). From spectrograms of three randomly selected surveillance calls per individual (N
143 = 44; 16 dominant, 28 subordinate), the following parameters were measured: (1) peak
144 frequency of the fundamental (kHz), defined as the frequency at which maximum power occurs
145 within the lowest formant; (2) bandwidth (kHz), defined as the difference between the upper
146 and lower frequency limits of the call; (3) duration of the first element (s); (4) total call
147 duration; and (5) the number of elements per call (Fig. 1). Raven's manual selection tool was
148 used to select the time and frequency range of the element to be analyzed (by JK); means were
149 calculated for each parameter for each individual. Selected calls came from recordings with
150 good signal-to-noise ratio (at least 20 dB above ambient noise). Where possible (N = 18; 8
151 dominant, 10 subordinate), each call came from a separate sentinel bout. Where fewer than
152 three bouts were available for an individual, calls came from two bouts (N = 10; 3 dominant, 7
153 subordinate) or one bout (N = 16; 5 dominant, 11 subordinate).

154

155 **(d) Playback experiments**

156 To assess the influence of both a vocalizing sentinel and vocal cues to sentinel dominance
157 status on forager vigilance, two playback experiments were conducted in August – September
158 2013 and April – May 2014. In the first experiment, seven groups were presented with two
159 treatments: surveillance calls of the group's dominant male and ambient noise (as per Hollén
160 et al. 2008). Composition of the eighth group at the time precluded their inclusion in the first
161 experiment. In the second experiment, eight groups received two treatments: surveillance calls

162 of the group's dominant male and surveillance calls of a subordinate adult male from the same
163 group from whom surveillance calls had been recorded. All playback tracks were 3 min in
164 duration and included recording of ambient noise from the center of the territory of the focal
165 group made at similar times of day. Playback tracks of sentinel presence also included
166 surveillance calls, recorded opportunistically from the relevant male in the focal group and
167 inserted at 12 s intervals to create a uniform call rate of 5 calls per minute (cpm); previous
168 research has found this to be the mean call rate during sentinel bouts taking place more than 10
169 min since an alarm call (Kern and Radford 2013). Tracks did not include any other
170 vocalizations, from conspecifics or heterospecifics.

171

172 During both experiments, each group was presented with one pair of playback trials in a
173 counterbalanced order. Calls were broadcast from an mp3 player connected to single SME-
174 AFS portable field speaker (Saul Mineroff Electronics Inc., New York, USA) positioned at a
175 height of 1 m. Playback amplitude was standardized to the natural amplitude of ambient noise
176 (peak amplitude: 40 dB sound pressure level A at 1 m) and of dwarf mongoose surveillance
177 calls (peak amplitude: 55 dB SPLA at 1 m) using a HandyMAN TEK1345 sound meter
178 weighting A (Metrel UK Ltd., Normanton, West Yorkshire, UK). The two trials to the same
179 focal individual in a given experiment were separated by a minimum of 1 h and played when
180 the entire group was foraging in the same habitat type. Playbacks took place when there was
181 no natural sentinel on duty, when there had been no sentinel present for at least 5 min, and no
182 natural alarm call for at least 10 min. Following any major disturbances, such as an inter-group
183 encounter or snake mobbing, a minimum of 15 min was left before the next playback took
184 place.

185

186 Observers conducted behavioral observations in tandem with playback experiments. The same
187 female forager was selected in both trials to the same group in a given experiment. Using a
188 stopwatch and tally counter, observers measured the number of vigilance scans performed and
189 the cumulative time spent vigilant. Trials were abandoned ($N = 3$) if a natural alarm call
190 occurred during the 3 min, if a natural sentinel went on duty, or if the forager ceased foraging
191 to interact socially with another group member (e.g. grooming, feeding displacement) and were
192 later repeated after at least 1 h.

193

194 **(e) Statistical analysis**

195 All analyses were performed using R version 2.15.1 (R Development Core Team 2012). All
196 tests were two-tailed and were considered significant at $P < 0.05$. Parametric tests were
197 conducted where data fitted the relevant assumptions of normality and homogeneity of
198 variance. Logarithmic transformations were conducted to achieve normality of errors in some
199 cases (Crawley 2005); non-parametric tests were otherwise used. The specific nature of
200 independent and dependent variables as well as the statistical technique used to address each
201 of our four questions are outlined below.

202

203 (i) Do foragers use vocal cues to detect the presence of a sentinel and adjust their behavior
204 accordingly?

205 Data on the number and duration of vigilance scans collected during the first playback
206 experiment (surveillance calls vs. ambient noise) were analyzed using Wilcoxon signed-rank
207 tests.

208

209 (ii) Do dominant and subordinate individuals differ in their contributions to sentinel
210 behavior and choice of sentinel post height?

211 Observers conducted 2,970 scans on 420 sample days in eight groups (mean \pm SE scans per
212 group = 371 ± 23), with a natural sentinel present in 1,678 (56.5%) scans. To investigate
213 variation in contributions to sentinel duty and the height adopted by dominant and subordinate
214 individuals, linear mixed models (LMMs) and generalized linear mixed models (GLMMs)
215 were used to analyse behavioral data from scan samples. Mixed models allow the incorporation
216 of both fixed and random terms, the latter allowing repeated measures from the same group or
217 individual to be taken into consideration. Model simplification was conducted using stepwise
218 backward elimination (Crawley, 2005) with terms sequentially removed until the minimal
219 model contained only terms whose elimination significantly reduced the explanatory power of
220 the model. Removed terms were returned to the minimal model individually to confirm that
221 they were not significant. χ^2 and P -values were obtained by comparing the minimal model with
222 models in which the term of interest had been removed (for significant terms) or added (for
223 non-significant terms). For fixed terms, presented effect sizes \pm SE were obtained from the
224 minimal model, as were estimated variance components for random terms.

225

226 For assessment of sentinel contributions, two GLMMs with binomial error structure were
227 conducted using the glmer function in package 'lme4' (Bates et al. 2012). In both models, the

228 proportion of sentinel bouts performed by each individual was included as the response
229 variable. The first model bound the number of scan samples in which a given individual was
230 acting as a sentinel with the number of scans conducted that day when that individual was not
231 a sentinel, testing the likelihood of an individual being a sentinel over a given period. The
232 second model bound the number of scan samples in which a given individual was acting as a
233 sentinel with the number of scans during which a different individual was acting as a sentinel,
234 testing the likelihood of a sentinel being a dominant individual. In both models, group size,
235 dominance status and sex were fitted as fixed effects, with both individual identity nested in
236 group identity and observation day included as random terms. All two-way interactions of
237 biological interest were included in the maximal model. To investigate the influence of age as
238 well as status, two additional GLMMs were conducted using a subset of the data containing
239 just the dominant pair and the oldest subordinate male and female from each group. Eight
240 individuals in five groups changed dominance status (from subordinate to dominant) over the
241 course of the study period, providing a natural experiment, and so two further GLMMs
242 considered scans involving these reduced datasets.

243

244 For assessment of sentinel post height, two LMMs were used following logarithmic
245 transformation of the data. Sentinel dominance status and sex were fitted as fixed effects, with
246 individual identity nested in group identity included as a random term for both the complete
247 data set ($N = 1430$ bouts, 75 individuals, eight groups), and a reduced data set containing only
248 the seven individuals who changed status and for which height data were available before and
249 after the switch.

250

251 (iii) Do vocal cues provide information about sentinel dominance status?

252 Differences between dominance classes in peak frequency of the fundamental, bandwidth and
253 duration of the first element were analyzed using independent-samples t -tests, and number of
254 elements using Wilcoxon signed-rank tests. All tests were performed on the mean values for
255 each individual. Total call duration was not analyzed as this was strongly correlated with the
256 number of elements (Spearman rank correlation: $R_s = 0.93$, $N = 130$, $P < 0.0001$). As multiple
257 comparisons were made, the sequential Bonferroni method was used to correct those
258 parameters reaching significance (Rice 1989).

259

260 (iv) Do foragers adjust their vigilance behavior according to vocal information about
261 sentinel dominance status?

262 To investigate whether foragers alter vigilance behavior depending on the dominance status of
263 a sentinel, data from the second playback experiment (dominant surveillance calls vs.
264 subordinate surveillance calls) were analyzed using a paired *t*-test (number of vigilance scans)
265 and a Wilcoxon signed-rank test (duration of vigilance scans).

266

267 **3. Results**

268 (i) Do foragers use vocal cues to detect the presence of a sentinel and adjust their behavior
269 accordingly?

270 Foraging dwarf mongooses conducted significantly fewer vigilance scans (Wilcoxon signed-
271 rank test: $Z = 27$, $N = 7$, $P = 0.034$; Fig. 2a) and spent significantly less time vigilant ($Z = 26$,
272 $N = 7$, $P = 0.047$; Fig. 2b) when subjected to playback of surveillance calls compared to
273 playback of ambient noise.

274

275 (ii) Do dominant and subordinate individuals differ in their contributions to sentinel
276 behavior and choice of sentinel post height?

277 The likelihood of an individual conducting a sentinel bout at the time of a scan sample was
278 significantly affected by the interaction between dominance status and group size (GLMM: χ^2
279 $= 7.99$, $df = 1$, $P = 0.0047$, random terms: group < 0.0001 , individual in group $= 0.236$,
280 occurrence $= 0.092$, intercept $= -2.574 \pm -0.268$). Dominants were more likely to act as a
281 sentinel than subordinates, but that difference was most apparent in large groups (Fig. 3a).
282 Individual sex did not significantly influence sentinel contribution ($\chi^2 = 0.55$, $df = 1$, $P =$
283 0.460).

284

285 The likelihood of a given individual conducting a particular sentinel bout was significantly
286 affected by dominance status: dominant individuals were more likely to act as a sentinel than
287 subordinate individuals (GLMM: $\chi^2 = 21.20$, $df = 1$, $P < 0.005$, random terms: group < 0.0001 ,
288 individual in group $= 0.242$, observation day < 0.0001 , intercept $= -0.312 \pm 0.212$; Fig. 3b).
289 Individuals were also significantly more likely to act as sentinel in smaller groups ($\chi^2 = 25.22$,
290 $df = 1$, $P < 0.005$), but individual sex did not significantly influence sentinel contribution ($\chi^2 =$
291 0.47 , $df = 1$, $P = 0.494$).

292

293 When analyzing the subset of the data containing only the dominant pair and the oldest
294 subordinate male and female from each group, dominant individuals were still more likely to
295 act as a sentinel than subordinate groupmates. Dominant individuals were significantly more
296 likely to conduct a sentinel bout at the time of a scan sample than the oldest subordinates
297 (GLMM: $\chi^2 = 6.65$, $df = 1$, $P = 0.011$, random terms: group = 0.07, individual in group = 0.39,
298 observation day = 0.15, intercept = -2.11 ± 0.105). None of group size ($\chi^2 = 0.015$, $df = 1$, $P =$
299 0.903), sex ($\chi^2 = 0.16$, $df = 1$, $P = 0.689$) or the interaction between group size and status ($\chi^2 =$
300 2.17 , $df = 1$, $P = 0.338$) significantly influenced sentinel contribution. Dominant individuals
301 were also significantly more likely to conduct a particular sentinel bout than the oldest
302 subordinate group members ($\chi^2 = 6.80$, $df = 1$, $P = 0.009$, random terms: group <0.0001 ,
303 individual in group = 0.16, occurrence = 0.000, intercept = -0.437 ± 0.24). All individuals were
304 significantly more likely to conduct a sentinel bout in smaller groups ($\chi^2 = 16.42$, $df = 1$, P
305 <0.0001), but there was no significant interaction between group size and status ($\chi^2 = 0.93$, df
306 $= 1$, $P = 0.337$), and individual sex did not significantly influence sentinel contribution ($\chi^2 =$
307 0.09 , $df = 1$, $P = 0.767$).

308

309 When analyzing the subset of the data containing only the eight individuals whose status
310 changed, qualitatively the same results were obtained as with the overall dataset: dominant
311 individuals were more likely to be acting as a sentinel than subordinate groupmates, but that
312 effect was more pronounced in larger groups. There was a significant interaction between
313 group size and dominance status when considering the likelihood of an individual conducting
314 a sentinel bout at the time of a scan sample (GLMM: $\chi^2 = 12.82$, $df = 1$, $P = 0.0003$, random
315 terms: group <0.0001 , individual in group = 0.049, intercept = -2.536 ± 0.350), but no
316 significant effect of sex ($\chi^2 = 1.54$, $df = 1$, $P = 0.214$). There was also a significant interaction
317 between group size and dominance status when considering the likelihood of an individual
318 being on duty in a given sentinel bout ($\chi^2 = 9.10$, $df = 1$, $P = 0.003$, random terms: group =
319 0.123 , individual in group = 0.028, intercept = -0.866 ± 0.497), but no significant effect of sex
320 ($\chi^2 = 1.91$, $df = 1$, $P = 0.167$).

321

322 The height at which sentinels positioned themselves ranged from 10 cm to 600 cm (mean \pm SE
323 $= 72.8 \pm 1.8$ cm, $N = 1430$ bouts, 75 individuals, eight groups). Dominant sentinels used
324 significantly higher posts than subordinate sentinels (LMM: $\chi^2 = 6.73$, $P = 0.009$, random
325 terms: group = 0.076, individual in group = 0.092, intercept = 1.773 ± 0.03 ; Fig. 3c). Sentinel

326 sex did not significantly influence height choice ($\chi^2 = 1.83, P = 0.17$). When analyzing only
327 those bouts performed by individuals who changed status ($N = 179$ bouts, seven individuals,
328 seven groups), the same result was found: individuals guarded from significantly higher posts
329 when dominant than when they were subordinate ($\chi^2 = 12.02, P < 0.001$, random terms: group
330 < 0.001 , individual in group = 0.16, intercept = 1.75 ± 0.07). Sentinel sex did not significantly
331 influence height choice ($\chi^2 = 0.47, P = 0.489$).

332

333 (iii) Do vocal cues provide information about sentinel dominance status?

334 Surveillance calls of dominants had a significantly lower peak frequency of the fundamental
335 (independent-samples t -test: $t_{40} = 6.97, P < 0.0001$), reduced bandwidth ($t_{41} = 2.83, P = 0.0035$),
336 and longer first element ($t_{37} = 4.91, P < 0.0001$) (Fig. 4; audio files of dominant and surveillance
337 calls can be found in the supplementary material). No significant difference was found in the
338 number of elements per call (dominant: 2.29 ± 0.23 , subordinate: 2.00 ± 0.18 ; Wilcoxon
339 signed-rank test: $T = 241.5, N = 43, P = 0.53$).

340

341 (iv) Do foragers adjust their vigilance behavior according to vocal information about
342 sentinel dominance status?

343 Sentinel status did not significantly influence the number of scans performed by a forager
344 (paired t -test: $t_7 = 1.23, P = 0.259$; Fig. 5a), but foragers spent significantly less time vigilant
345 in response to the playback of surveillance calls from a dominant individual than a subordinate
346 group member ($t_7 = 2.55, P = 0.038$; Fig. 5b).

347

348 **4. Discussion**

349 Our work has demonstrated that dominant dwarf mongooses of both sexes act as sentinels
350 considerably more often than subordinate group members, and that the surveillance calls
351 produced during sentinel bouts contain vocal information about dominance status. Our
352 playback experiments showed that foragers not only use surveillance calls to detect the
353 presence of sentinels (as in other species; Manser et al. 1999; Hollén et al. 2008), but also to
354 determine the dominance status of the sentinel and alter their vigilance accordingly. Foragers
355 reduced their vigilance in the presence of dominant sentinels compared to when subordinate
356 groupmates were acting in that role. We therefore provide novel empirical evidence from a

357 field study that whether and to what extent animals exploit social information depends on the
358 identity of the information provider.

359

360 There are a number of possible reasons why foragers might show a stronger response to the
361 surveillance calls of dominant compared to subordinate sentinels. First, surveillance calls of
362 dominant individuals may be easier to detect as they have lower peak frequency of the
363 fundamental and longer duration, traits generally associated with greater ease of detection
364 (Wiley and Richards 1982). Since dominance is closely related to age in dwarf mongoose
365 groups (Rood 1980), differences in response may stem from age-related differences between
366 dominant and subordinate sentinels. Many species consider alarm calls given by younger
367 individuals to be less reliable (Gouzoules et al. 1996; Hanson and Coss 2001; Blumstein and
368 Daniel 2004), and the same may be true of surveillance calls. However, unlike alarm-call
369 studies which have traditionally compared juveniles and adults, two classes which are known
370 to differ in their vulnerability to predation (Lea and Blumstein 2011), our study compared only
371 adult sentinels.

372

373 Alternatively, differences in response to dominant and subordinate sentinels may relate to
374 differences in height adopted by these classes of individual. By guarding from higher posts
375 than subordinates in general, the probability of dominant sentinels detecting predators is likely
376 to be greater, increasing the reliability of information provided (see also Radford et al. 2009).
377 Speaker height was the same throughout experimental trials, so foragers could not have been
378 responding to differences in height at the time of playback, but they may associate dominant
379 sentinels with higher posts. Another possible reason for the differences in response to sentinels
380 of different dominance status relates to an individual's experience as a sentinel. Dwarf
381 mongoose group composition remains relatively stable, with some group members cohabiting
382 for years at a time (Rood 1983), thereby facilitating the accumulation of class- or individual-
383 specific information about sentinel behavior. Dominant individuals contribute more to sentinel
384 duty when compared both to all subordinates and to only the oldest same-sex subordinate. The
385 results from the natural experiment, comparing the same individuals before and after they
386 switched from being subordinate to dominant, also demonstrated these differences in sentinel
387 behavior; after reaching a position of dominance, individuals were more likely to contribute to
388 sentinel duty (and to guard from higher posts) than when they were subordinate group
389 members. By contributing more to sentinel duty, individuals gain considerably more
390 experience once they become dominant, and may therefore be expected to provide higher

391 quality information, such as a more accurate assessment of background risk level, or what
392 constitutes a threatening stimulus. To explore this fully would require the manipulation of
393 individual reliability, such as has been done with alarm calls (Hare & Atkins 2001; Blumstein
394 et al. 2004a).

395

396 Individuals can obtain risk estimates by visually monitoring the behavior of surrounding
397 groupmates (Pays et al. 2010), but it has become increasingly apparent that foragers also make
398 use of vocal information (Radford and Ridley 2007; Hare et al. 2014). A growing body of
399 evidence over recent years has highlighted the importance of vocal cues in sentinel systems
400 (Manser 1999; Hollén et al. 2008; Bell et al. 2009; 2010; Radford et al. 2009, 2011; Kern and
401 Radford 2013), especially for species foraging in denser habitats, where line of sight is
402 interrupted, or whose feeding strategies prevent simultaneous foraging and scanning. Through
403 use of surveillance calls, dwarf mongoose foragers gain valuable information without the need
404 to interrupt digging behavior and scan the environment for themselves, thereby increasing
405 foraging efficiency and reducing risk of starvation (Manser 1999; Hollén et al. 2008). Class
406 and individual differences in call structure further allow receivers to fine-tune behavioral
407 responses depending on the identity of a social partner, thereby minimizing fitness costs
408 associated with inappropriate responses (Pollard 2010). Such acoustic differences have been
409 found in a multitude of call types (Stoddard et al. 1991; McCowan and Hooper 2002; Rendall
410 2003; Sharp and Hatchwell 2005; Charrier et al. 2009), yet whether receivers attend to potential
411 differences in caller identity has received little attention outside of alarm calling situations.
412 There are several other signaling contexts, however, where caller identity might considerably
413 impact receiver fitness, such as mobbing calls, food calls and vocalization coordinating group
414 travel (Conradt and List 2009; Boeckle et al. 2012; Micheletta et al. 2012).

415

416 The finding that dominants do more sentinel duty raises the question as to why. Whether an
417 individual acts as sentinel is closely related to its nutritional state (Clutton-Brock et al. 1999;
418 Wright et al. 2001; Bell et al. 2010). Dominants, with access to higher quality resources, and
419 being older and more experienced at finding food (Heinsohn 1991), are usually in a better state
420 than subordinates, and therefore may be expected to do more. Dominants may gain additional
421 benefits from sentinel behavior, using elevated posts not only to scan for predators, but also to
422 observe the behavior of group members, although subordinates could also gain additional
423 benefits from sentinel behavior, using it to search for potential roving opportunities.
424 Alternatively, there may be trade-offs between contributions to different cooperative activities,

425 including babysitting, pup provisioning, and territorial defense. Dominants may perform more
426 sentinel behavior but reduce effort to other helping activities. Were contributions moderated by
427 effort to other activities, one might expect dominant females to do less since they suffer
428 considerable energetic costs associated with reproduction (Clutton-Brock et al. 1999). Somewhat
429 surprisingly, however, we found no effect of sex on sentinel behavior.

430

431 A further question raised by our results is why dominants generally guard from higher posts.
432 Variation in post height is likely to influence the probability of a sentinel detecting a predator:
433 higher sentinels may be better placed to detect predators sooner (especially terrestrial
434 predators), able to see further and with a wider field of view (Blumstein et al. 2004b;
435 Fernández-Juricic et al. 2004; Radford et al. 2009). On the other hand, post height is also likely
436 to influence a sentinel's risk of predation, with higher sentinels more vulnerable to detection
437 by aerial predators. Dominant individuals, being more experienced sentinels, may be better
438 able to afford the risk entailed by guarding from higher posts. Alternatively, if dominants also
439 use sentinel duty to monitor the behavior of subordinates, they may adopt higher posts in an
440 effort to watch more of the group, as well as to enhance predator detection.

441

442 Use of vocal information such as surveillance calls, facilitates optimization of the foraging–
443 vigilance trade-off by foragers. Where information quality varies, reliable information should
444 be weighted more heavily (McLinn and Stephens 2006). Our results demonstrate that the
445 dominance status of a sentinel is a key factor taken into consideration by receivers when
446 determining the value of social information. When a dominant sentinel is on duty, foragers rely
447 more heavily on social information, gather less information through personal vigilance and
448 concentrate on foraging. Dominant individuals gain more experience of sentinel duty and guard
449 from higher posts, thus may potentially be able to provide higher quality information about
450 risk. Our study contributes novel evidence that a major benefit of individual and class-specific
451 vocalizations is the potential to assess differences in information between callers, and we
452 suggest that future work should investigate the presence of reliability assessment in different
453 call types.

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Figure legends

Figure 1. Spectrogram of a surveillance call showing variables analyzed: (1) peak frequency of the fundamental, (2) bandwidth, (3) duration of the first element, (4) total call duration and (5) number of elements per call.

Figure 2. Response – (a) total number of vigilance scans and (b) total duration of vigilance scans – of foraging dwarf mongooses to the playback of sentinel surveillance calls and ambient noise. Lines join values for the same individuals in the two treatments ($N = 7$).

Figure 3. The effect of dominance status on (a) likelihood of acting as a sentinel during a given scan sample (dominant: open triangles and dotted line, subordinate: black circles and solid line), (b) likelihood of an individual being the sentinel during a given sentinel bout, and (c) height of guard post. For (a) lines were plotted using back-transformed means predicted from GLMM. For (b) and (c) mean and standard errors calculated from raw data are shown.

Figure 4. Acoustic variables differing significantly between dominance classes: (a) peak frequency of the fundamental, (b) bandwidth, and (c) duration of the first element. Means \pm SE shown ($N = 43$; 16 dominant, 27 subordinate).

Figure 5. Response – (a) number of vigilance scans and (b) duration of vigilance scans – of foraging dwarf mongooses to the playback of sentinel calls by different classes. Lines join values for the same individuals in the two treatments ($N = 8$).

Figure 1

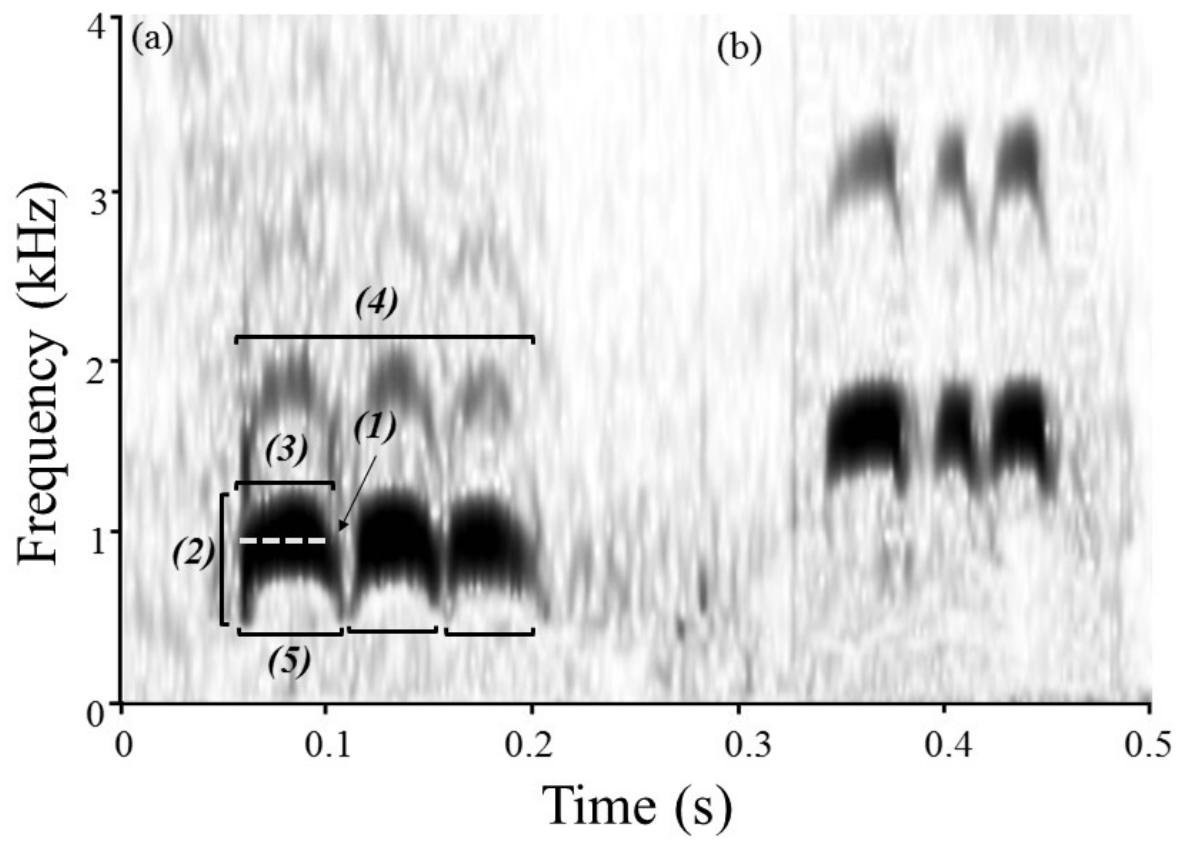


Figure 2

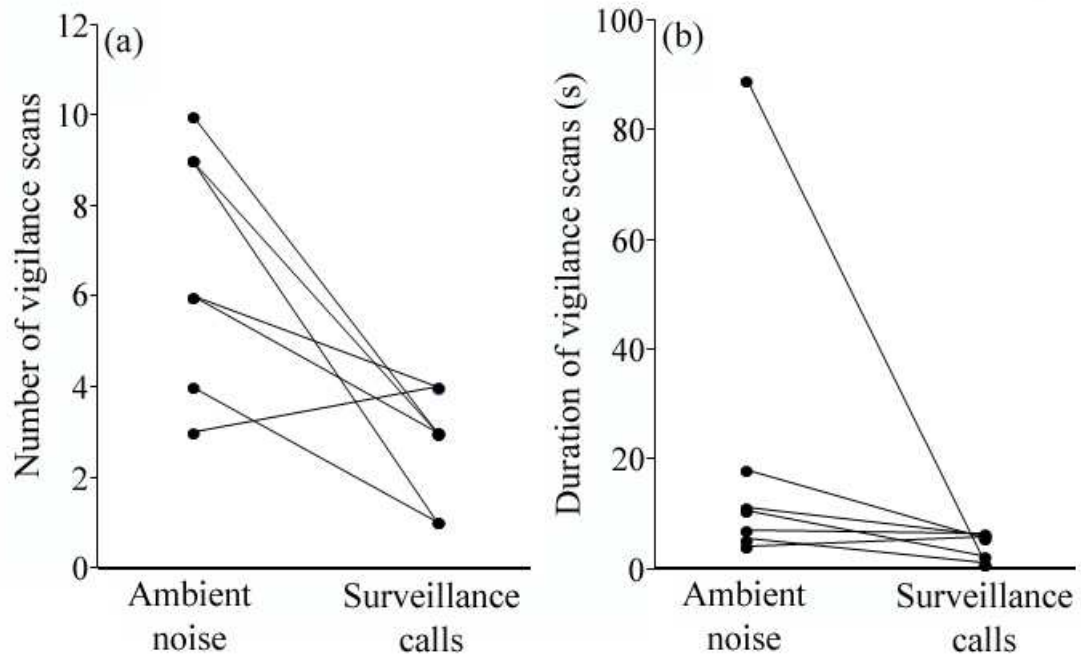


Figure 3

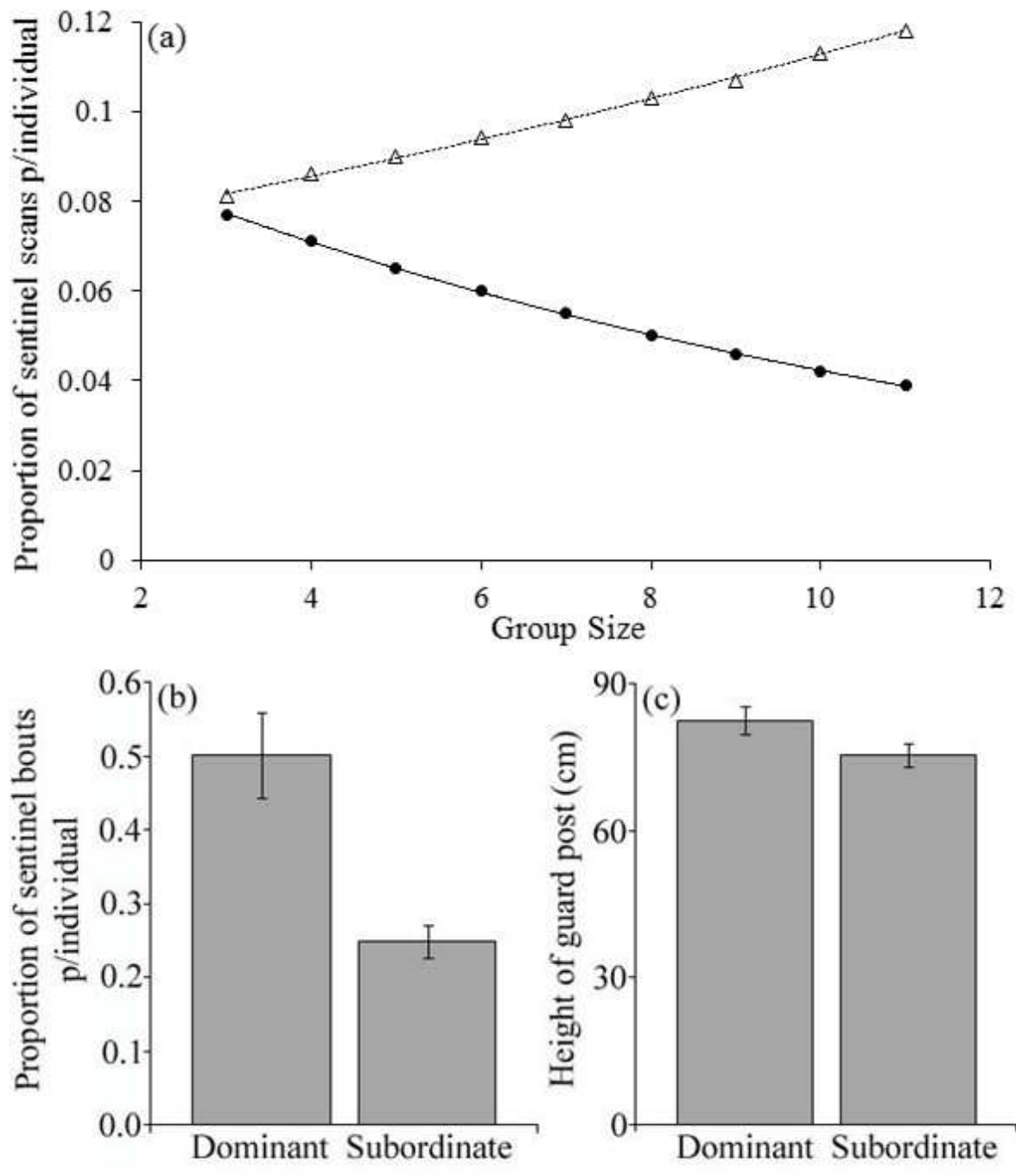


Figure 4

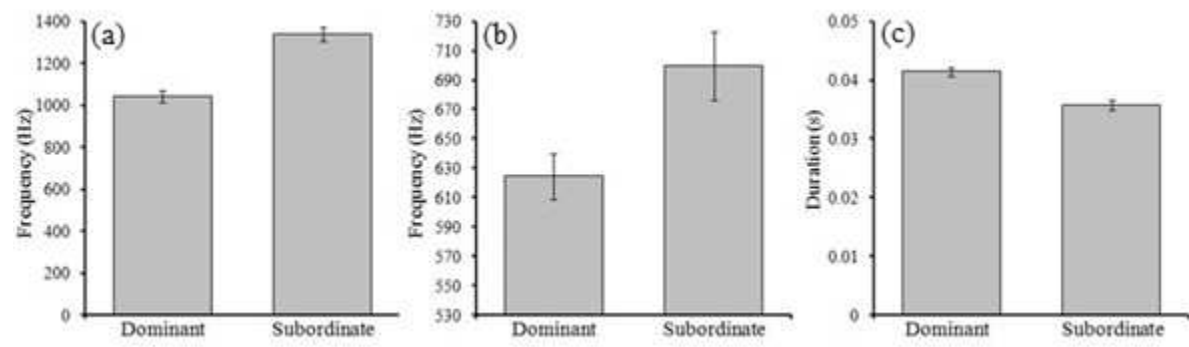


Figure 5

