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1 **Anthropogenic noise disrupts use of vocal information**
2 **about predation risk**

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24 **Statement of authorship**

25 JMK and ANR conceived and designed the study; JMK collected the data; JMK analysed the
26 data with advice from ANR; JMK wrote the first draft of the manuscript and ANR contributed
27 significantly to revisions.

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34 **Anthropogenic (man-made) noise is rapidly becoming an universal environmental**
35 **feature. While the impacts of such additional noise on avian sexual signals are well**
36 **documented, our understanding of its effect in other terrestrial taxa, on other**
37 **vocalisations, and on receivers is more limited. Little is known, for example, about the**
38 **influence of anthropogenic noise on responses to vocalisations relating to predation risk,**
39 **despite the potential fitness consequences. We use playback experiments to investigate**
40 **the impact of traffic noise on the responses of foraging dwarf mongooses (*Helogale***
41 ***parvula*) to surveillance calls produced by sentinels, individuals scanning for danger**
42 **from a raised position whose presence usually results in reduced vigilance by foragers.**
43 **Foragers exposed to surveillance calls in traffic-noise compared to ambient-noise**
44 **playback exhibited a lessened response (increased personal vigilance). A second**
45 **playback experiment, using noise playbacks without surveillance calls, suggests that the**
46 **increased vigilance could arise in part from the direct influence of additional noise (the**
47 **‘increased threat hypothesis’) as there was an increase in response to traffic-noise**
48 **playback alone. Acoustic masking could also play a role. Foragers maintained the**
49 **ability to distinguish between sentinels of different dominant class, increasing personal**
50 **vigilance when presented with subordinate surveillance calls compared to calls of a**
51 **dominant groupmate in both noise treatments, suggesting complete masking was not**
52 **occurring. However, a signal transmission experiment showed that surveillance calls**
53 **were likely inaudible during periods of peak traffic, but audible during approaching**
54 **traffic noise, thus reducing perceived call rate; in dwarf mongooses, lower surveillance-**
55 **call rates are associated with higher risk situations, necessitating greater vigilance.**
56 **While recent work has demonstrated detrimental effects of anthropogenic noise on**
57 **defensive responses to actual predatory attacks, which are relatively rare, our results**
58 **provide evidence of a potentially more widespread influence since animals should**
59 **constantly assess background risk to optimise the foraging–vigilance trade-off.**

60

61 Anthropogenic noise decreases response to sentinel surveillance calls through partial masking
62 and the direct influence of anthropogenic noise on perceived risk.

63

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65

66

67 **INTRODUCTION**

68 Anthropogenic (man-made) noise is a pervasive pollutant, expanding with the spread of noise-
69 generating human activities such as urbanisation, the development of transportation networks,
70 and the exploitation of energy resources (Francis and Barber 2013; Read et al. 2014). Although
71 background noise is an inherent feature of the environment, the properties of noise generated
72 by humans are such that its impression on the acoustic environment is unprecedented
73 (Hildebrand 2009). Studies have considered a range of effects, from those on communities and
74 ecosystems to those on the physiology of individuals, but the majority of work has examined
75 behavioural impacts (Habib et al. 2007; Gross et al. 2010; Francis et al. 2012; Bennett and
76 Zurcher 2013; Naguib 2013; Wale et al. 2013; Simpson et al. 2016). Much attention has been
77 paid to vocal communication, and in particular how the acoustic properties of sexual signals
78 (e.g. songs of birds and whales) have changed as a consequence of anthropogenic noise, both
79 through behavioural plasticity and across evolutionary time (Brumm and Slabbekoorn 2005;
80 Patricelli and Blickley 2006; Slabbekoorn and Ripmeester 2008; Barber et al. 2010; Shannon
81 et al. 2015). However, receivers as well as signallers are integral to communication systems,
82 and animals produce a wide variety of vocalisations for many other reasons besides mate
83 attraction and territorial defence.

84

85 Anthropogenic noise has the potential to disrupt the detection and discrimination of
86 vocalisations, and affect responses of receivers, through three main mechanisms which are not
87 mutually exclusive (Kight and Swaddle 2011). Noise could inhibit vocal communication via
88 acoustic masking, which affects the perception of signals with frequencies overlapping
89 background noise; in the case of anthropogenic noise, predominantly low frequencies (Klump
90 1996; Lohr et al. 2002; Brumm and Slabbekoorn 2005). Masking can be complete, whereby
91 the signal is inaudible, or partial, whereby the signal remains detectable but the information
92 content is altered (Brumm and Slabbekoorn 2005; Barber et al. 2010). Anthropogenic noise
93 can also act as a stressor, as has been demonstrated in many taxa (Wright et al. 2007; Rolland
94 et al. 2012; Naguib 2013; Recio 2016), which may result in detrimental behavioural changes,
95 such as inappropriate responses to vocal cues. Finally, anthropogenic noise may be distracting,
96 redistributing the finite attention capabilities of animals (Dukas 2004) and reducing attention
97 available for important tasks, such as detection and response to anti-predator cues (Chan et al.
98 2010; Chan and Blumstein 2011).

99

100 Acoustic communication is a vital component of anti-predator behaviour for numerous species
101 (Bradbury and Vehrencamp 2011). For example, many animals depend on both conspecific
102 and heterospecific alarm calls for rapid, often threat-specific responses to immediate predation
103 risk (Hollén and Radford 2009; Magrath et al. 2015). Studies have demonstrated that
104 anthropogenic noise can impact alarm-call production, with signallers increasing call
105 amplitude to minimise masking effects (Lowry et al. 2013; Rogerson 2014). Recent evidence
106 suggests that noise also has the potential to impact the behaviour of receivers in various ways
107 (Rabin et al. 2006; Lowry et al. 2013; Rogerson 2014; Mahjoub and Swaddle 2015). Receivers
108 may be at greater risk of predation if anthropogenic noise masks alarm calls or causes a reduced
109 or slowed response to them as a consequence of stress or distraction (Lowry et al. 2013;
110 McIntyre et al. 2014; Read et al. 2014; Mahjoub et al. 2015; Grade and Sieving 2016);
111 decreased response thresholds to predatory threats could alternatively lead to inappropriate
112 startle responses and disrupted energy budgets (Karp and Root 2009, Meillière et al. 2015;
113 Shannon et al. 2016). Important information about background predation risk is also provided
114 by vocalisations other than alarm calls, including ‘close’ calls (Radford and Ridley 2007), all-
115 clear signals (Townsend et al. 2011), and surveillance calls (Manser 1999; Hollén et al. 2008).
116 If individuals are unable correctly to detect or evaluate such cues relating to background risk
117 assessment, they may be more vulnerable to attack or, if they remain in a constant state of high
118 alert, may suffer detrimental performance effects, such as a decrease in foraging efficiency
119 (Purser and Radford 2011). However, whether responses to these vocalisations are affected by
120 anthropogenic noise has not previously received experimental consideration.

121

122 Our aim was to investigate how anthropogenic noise affects responses to surveillance calls
123 produced by sentinels, using the cooperatively breeding dwarf mongoose (*Helogale parvula*)
124 as a model system. Sentinel behaviour, where an individual adopts a raised position, scanning
125 for predators and warning others of danger, has been documented in a range of social species
126 (reviewed in Bednekoff 2015). Sentinels publicise threats using specific alarm calls, providing
127 receivers with crucial information about immediate danger (Bednekoff 2015). In several
128 species, sentinels also produce low-amplitude surveillance calls, providing essential
129 information about sentinel presence, identity, satiation level and height (Manser 1999; Hollén
130 et al. 2008; Bell et al. 2009, 2010; Radford et al. 2009, 2011; Kern et al. 2016), and an estimate
131 of current risk levels (Bell et al. 2009; Kern and Radford 2013). Surveillance calls provide
132 tangible benefits to groupmates, helping to mitigate indirect predation effects by enabling
133 receivers to optimize the foraging–vigilance trade-off (Manser 1999; Hollén et al. 2008; Bell

134 et al. 2010; Kern et al. 2016). If receiver detection of surveillance calls is disrupted by masking
135 or distraction, or their responses lessened as a result of other noise-related effects, then
136 receivers may have to increase reliance on personal information, negating at least some of the
137 benefits of sentinel presence.

138

139 Dwarf mongooses are small cooperatively breeding carnivores living in groups of up to 30
140 individuals (Rasa 1977). A dominant pair reproduces, with help provided in rearing offspring
141 by related and unrelated subordinates (Rood 1980). While groups are foraging, sentinels are
142 often posted, and produce loud threat-specific alarm calls which trigger an escape response by
143 receivers (Beynon and Rasa 1989; Kern and Radford 2014). Sentinels also produce low-
144 amplitude surveillance calls, which are used by foragers to detect sentinel presence and identity
145 (Rasa 1986; Sharpe et al. 2010; Kern et al. 2016). Sentinels vocalise more often when visual
146 cues are less readily available – in dense habitats and when foragers are further away – and
147 reduce call rate in high-risk situations, such as following an alarm call (Kern and Radford
148 2013). Foragers reduce personal vigilance in the presence of a sentinel in general, but are
149 significantly less vigilant when a dominant rather than a subordinate groupmate acts as a
150 sentinel (Kern et al. 2016).

151

152 In this study, we begin by using a playback experiment to investigate whether anthropogenic
153 noise (specifically traffic noise) results in a lessened response (increased personal vigilance) to
154 surveillance calls. We also use this experiment to test whether the previously observed
155 difference in response to dominant and subordinate sentinels is maintained in additional noise.
156 Since the surveillance calls of dominants are lower in pitch than those of subordinates (Kern et
157 al. 2016), we predict that low-frequency traffic noise may disrupt receiver responses to
158 dominant calls more than those to subordinate calls. Having found that dwarf mongooses
159 exhibit heightened personal vigilance in response to surveillance calls when experiencing
160 traffic noise compared to ambient noise, we use further experiments to consider possible
161 underlying reasons. First, we use another playback experiment to test whether traffic noise
162 itself results in a general increase in vigilance, as would be predicted by the ‘increased threat’
163 hypothesis (Owens et al. 2012). Second, we use an acoustic-transmission experiment to
164 consider whether surveillance calls might be masked by traffic noise, thus causing the increase
165 in vigilance.

166

167 **MATERIALS AND METHODS**

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

169 This study took place on Sorabi Rock Lodge Reserve, a 4 km² private game reserve in Limpopo
170 Province, South Africa (24°11'S, 30°46'E), part of southern Africa's Savanna Biome (see Kern
171 and Radford 2013 for full details). Data were collected from eight groups of wild dwarf
172 mongooses (mean group size = 8.3; range = 3–17), habituated to close observation (<5 m) on
173 foot (Kern and Radford 2013). All animals are individually identifiable either from markings
174 of blonde hair dye (Wella UK Ltd, Surrey, UK), applied with an elongated paintbrush, or from
175 natural features such as scars or facial irregularities. The population has been monitored since
176 2011, thus the age of most individuals is known; individuals can be sexed through observations
177 of ano-genital grooming.

178

179 **(b) Acoustic recordings**

180 All recordings were made at a sampling rate of 44.1 kHz with a 16-bit resolution onto a
181 SanDisk SD card (SanDisk, Milipitas, California, USA), using a Marantz PMD660
182 professional solid-state recorder (Marantz America, Mahwah, NJ, USA) and a handheld highly
183 directional Sennheiser ME66 shotgun microphone (Sennheiser UK, High Wycombe,
184 Buckinghamshire, UK) with a Rycote Softie windshield (Rycote Microphone Windshields,
185 Stroud, Gloucestershire, UK). Surveillance calls from individuals on sentinel duty were
186 recorded opportunistically from a distance of 0.5–10 m during behavioural observations.
187 Ambient noise was recorded at similar times of day from approximately the centre of the
188 territory of the focal group. Traffic noise was recorded at a distance of 10 m from the main tar
189 road adjacent to the south-east boundary of the reserve, perpendicular to the road. Vehicles
190 were divided into four types (car, 4x4, minibus and truck) and their frequency of occurrence
191 recorded during 10 1-h traffic counts (Rogerson 2014). The maximum amplitude of
192 surveillance calls, ambient noise and traffic noise (passing vehicles) was measured using a
193 HandyMAN TEK1345 Mini Sound Level Meter (Metrel UK Ltd., Normanton, West
194 Yorkshire, UK).

195

196 **(c) Playback experiments**

197 To investigate receiver responses to surveillance calls by sentinels of different dominance class
198 in different noise conditions, a playback experiment was conducted from 11th July to 26th
199 August 2014. Each focal forager (dominant female) in eight groups was exposed to playback
200 of four treatments: surveillance calls of (i) their group's dominant male during ambient noise,
201 (ii) their group's dominant male during traffic noise, (iii) a subordinate adult male group
202 member during ambient noise, and (iv) the same subordinate adult male group member during
203 traffic noise. The four treatments took place across two days, with two treatments per day,
204 separated by a minimum of 1 h and played when the entire group was foraging in the same
205 habitat type under calm conditions. Playback order was counterbalanced between groups.
206 Playbacks took place when there had been no natural sentinel present for at least 5 min and no
207 natural alarm call for at least 10 min. Following any major disturbances, such as an inter-group
208 encounter or mobbing event, a minimum of 15 min elapsed before the next playback.

209

210 Surveillance-call tracks consisted of randomly chosen calls from each male that were extracted
211 from the original recordings and pasted into 3 min of ambient noise, using Raven Pro 1.5 (as
212 in Kern et al. 2016). All tracks were constructed with calls at 12 s intervals creating a uniform
213 call rate of 5 calls per minute (previous research has found this to be the mean call rate during
214 bouts taking place over 10 min since an alarm call; Kern and Radford 2013). Tracks did not
215 include any other mongoose vocalizations. Surveillance-call tracks were broadcast from an
216 mp3 player (Apple Inc., Cupertino, California, USA) connected to a single SME-AFS portable
217 field speaker (Saul Mineroff Electronics Inc., New York, USA) positioned at a height of 1 m
218 to mimic a sentinel. Playback amplitude was standardised according to the amplitude of
219 naturally occurring surveillance calls (peak amplitude = 55 dB sound pressure level A (SPLA)
220 at 1 m).

221

222 Noise-treatment tracks consisted of 220 s of ambient or traffic noise. Each traffic-noise track
223 comprised 13 vehicle passes, constructed using a combination of all four vehicle types in
224 proportion to their frequency of road use. The same ambient-noise and traffic-noise tracks were
225 used for each of the two relevant treatments to a given group, but eight different ambient-noise
226 and traffic-noise tracks were used in the experiment as a whole to ensure that each group
227 received unique tracks. Both ambient-noise and traffic-noise tracks started 20 s before the 3
228 min sentinel bout, to minimise any disruption to vigilance resulting from initial startle effects
229 of loud noise. Noise-treatment tracks were broadcast from a second mp3 player (iBRIGHTSPOT,
230 Manchester, UK) connected to a second SME-AFS portable field speaker placed on the ground,

231 2–5 m from the focal forager and approximately 1 m to the side of the speaker playing
232 surveillance calls. Playback amplitude was standardised according to the amplitude of naturally
233 occurring noise levels (ambient noise: peak amplitude = 40 dB SPLA at 1 m; traffic noise: peak
234 amplitude = 65 dB SPLA at 10 m).

235

236 Behavioural observations were conducted in tandem with playback experiments. The total
237 number and duration of vigilance scans by the dominant female in the group were recorded
238 during the 3 min of surveillance-call playback. Trials were abandoned ($N = 5$) if an alarm call
239 occurred during the 3 min, if a natural sentinel went on duty or if the forager ceased foraging
240 to interact socially with another group member (e.g. grooming, feeding displacement); these
241 trials were repeated after at least 1 h.

242

243 To investigate whether traffic noise *per se* results in a general increase in vigilance, a second
244 playback experiment was conducted from 23rd August to 5th September 2014. The same
245 protocol was used as above, with the exception that no mongoose vocalisations were broadcast.
246 Instead, an ambient-noise track was broadcast from the speaker positioned at a height of 1 m.
247 As in the first experiment, a second track was simultaneously broadcast from the speaker
248 positioned on the ground, playing back either ambient noise or traffic noise. All tracks were
249 the same as those used in the first experiment. The same focal forager in each of the eight
250 groups was exposed to the two treatments: (i) ambient noise and ambient noise, and (ii) ambient
251 noise and traffic noise. Both treatments took place in a single session, separated by a minimum
252 of 1 h, and playback order was counterbalanced between groups. Behavioural observations
253 were again conducted in tandem with playbacks, recording the total number and duration of
254 vigilance scans during the 3 min playback period.

255

256 **(d) Transmission experiment**

257 To investigate the impact of traffic noise on the signal-to-noise ratio (SNR) of surveillance
258 calls, a transmission experiment was conducted in September 2014. All experimental trials
259 were performed at the same time of day, in calm weather conditions. Playbacks took place at a
260 site approximately in the centre of each group's territory, where groups had previously been
261 observed foraging. At each site, playbacks were conducted of surveillance calls from: (i) the
262 group's dominant male during ambient noise; (ii) the group's dominant male during traffic

263 noise; (iii) a subordinate adult male group member during ambient noise; and (iv) the same
264 subordinate adult male group member during traffic noise. Surveillance calls were the same as
265 those used in the first playback experiment. All playbacks per site were carried out during a
266 single visit to ensure conditions were as similar as possible.

267

268 Surveillance-call tracks were 20 s in duration with an inter-call interval of 2 s, to allow for
269 continuous calls throughout the increasing and decreasing amplitude associated with the
270 approach and passing of vehicles. Noise-treatment tracks consisted of 40 s of ambient or traffic
271 noise. Each traffic-noise track comprised two vehicle passes. Surveillance calls were broadcast
272 from an mp3 player connected to a single SME-AFS portable field speaker positioned at a
273 height of 1 m to mimic a sentinel. Noise-treatment tracks were broadcast from a second mp3
274 player connected to a second SME-AFS portable field speaker placed on the ground 1 m to the
275 side of the first speaker. Playback amplitude was standardised according to the amplitude of
276 naturally occurring sounds (as above). Stimuli were re-recorded at a sampling rate of 44.1 kHz
277 with a 16-bit resolution using a Marantz PMD660 professional solid-state recorder and a
278 handheld highly directional Sennheiser ME66 shotgun microphone positioned at 10 cm above
279 ground level (representing the height of a foraging mongoose), 5 m in front of the two speakers.
280 A distance of 5 m was chosen to match the protocol of the playback experiments described
281 above.

282

283 Spectrograms of re-recorded stimuli were created in Raven Pro 1.5 using a 1024 point fast
284 Fourier transformation (Hann window, 75% overlap, 1.45 ms time resolution, 43 Hz frequency
285 resolution; Fig. 1). Recordings were measured for average signal power (dB). Raven's manual
286 selection tool was used to select the time and frequency range of the surveillance calls to be
287 analyzed. SNR were calculated from recordings as the average power of background noise
288 (ambient or traffic) subtracted from the average power at the time of the vocalisation (as in
289 LaZerte et al. 2015). Background-noise amplitudes were measured from a section of the
290 recording which was of equal length to the stimulus. Where possible, these sections were
291 immediately adjacent to that containing the stimulus, but if these sections were overlapped by
292 other sounds, background-noise measurements were made from the closest possible section of
293 the same recording. Two surveillance calls from each recording were measured: the first at 2 s
294 into background noise during the approach of traffic; the second at 10 s coinciding with peak
295 traffic noise. In peak traffic noise, the surveillance call of interest was not always visible on the
296 spectrogram, in which case a time stamp was used to select the area where the call was known

297 to be. To compare the surveillance calls of dominant and subordinate sentinels, peak frequency
298 of the fundamental (kHz), defined as the frequency at which maximum power occurs within
299 the lowest formant, was also measured from spectrograms of the first surveillance call per
300 individual in ambient noise ($N = 16$; 8 dominant, 8 subordinate). Raven's manual selection tool
301 was used to select the time and frequency range of the element to be analyzed.

302

303 (e) Statistical analysis

304 All analyses were performed using R version 3.2.4 (R Development Core Team 2012). All tests
305 were two-tailed and were considered significant at $P < 0.05$. Parametric tests were conducted
306 where data fitted the relevant assumptions of normality and homogeneity of variance.
307 Logarithmic transformations were conducted to achieve normality of errors in some cases
308 (details below), otherwise non-parametric tests were used.

309

310 For analysis of data from the first playback experiment and transmission experiment, linear
311 mixed models (LMMs) were used to take account of repeated measures from the same group
312 and/or individual using the lme function in package 'nlme'. All likely explanatory terms were
313 included in the maximal model. Model simplification was then conducted using stepwise
314 backward elimination (Crawley 2005) with terms sequentially removed until the minimal
315 model contained only terms whose elimination significantly reduced the explanatory power of
316 the model. Removed terms were returned to the minimal model individually to confirm that
317 they were not significant. Presented χ^2 and P -values were obtained by comparing the minimal
318 model with models in which the term of interest had been removed (for significant terms) or
319 added (for non-significant terms). Presented effect sizes (\pm SE) were obtained from the minimal
320 model. For categorical terms, differences in average effects are shown relative to one level of
321 the factor, set to zero. Where significant interactions were found, post-hoc Tukey's tests were
322 run, using the 'testInteractions' function in the 'phia' package (De Rosario-Martinez 2013).
323 Tukey's tests correct for multiple testing and thus there is no need for additional use of
324 Bonferroni corrections (Ruxton and Beauchamp 2008). Residuals for all models were visually
325 examined to ensure homogeneity of variance, normality of error and linearity.

326

327 To investigate focal forager response to surveillance-call playback in different noise
328 conditions, two LMMs were used following transformation of the data (number of vigilance

329 scans was square-root transformed, duration of vigilance scans was log 10+1 transformed). For
330 both models, the fixed effects of noise treatment (traffic or ambient), dominance status
331 (dominant or subordinate), treatment order and the interaction between noise treatment and
332 dominance status were fitted, and focal individual was included as a random term. To
333 investigate differences in SNR of surveillance calls in noise (from the transmission
334 experiment), a further LMM was conducted following log 10+100 transformation as the data
335 contained negative values; SNR was calculated by subtracting the average power of
336 background noise (ambient or traffic) from the average power at the time of vocalisation. The
337 fixed effects of noise treatment (traffic or ambient), call position (approaching traffic or peak
338 traffic), dominance status (dominant or subordinate), treatment order and the interactions
339 between noise treatment and call position, and between noise treatment and dominance status
340 were fitted, and caller identity nested in group was included as a random term.

341

342 Data from the second playback experiment, which broadcast simultaneous noise treatments but
343 no mongoose vocalisations, contained responses from only two treatments and no additional
344 fixed effects so did not require mixed modelling. The data did not achieve normality with any
345 transformation, therefore Wilcoxon signed-rank tests were used to account for paired data. For
346 analysis of acoustic differences between surveillance calls of individuals of different
347 dominance class, peak frequencies of the fundamental were analyzed using a Wilcoxon signed-
348 rank test.

349

350 **RESULTS**

351 During playback of surveillance calls, forager vigilance was significantly influenced by noise
352 treatment. Individuals interrupted foraging to scan for predators significantly more often (Table
353 1a; Fig. 2a) and spent significantly more time vigilant (Table 1b; Fig. 2b) during playback of
354 traffic noise compared to ambient noise. Dominance status of the surveillance caller did not
355 significantly affect the number of scans performed (Table 1a), but did significantly affect the
356 cumulative time spent vigilant; foragers spent less time vigilant when played back surveillance
357 calls of dominants compared to those of subordinates (Table 1b; Fig. 2b). However, there was
358 no significant interaction between noise treatment and dominance status of the surveillance
359 caller; qualitatively the same difference in response to dominant and subordinate surveillance
360 calls was found during traffic-noise playback as during ambient-noise playback (Table 1).

361

362 During the second playback experiment, forager vigilance was found to be affected by noise
363 treatment alone. Foragers looked up significantly more often during playback of traffic noise
364 than playback of ambient noise (Wilcoxon signed-rank test: $Z = 35$, $N = 8$, $P = 0.021$; Fig. 3),
365 although noise treatment did not significantly influence the total duration of vigilance scans (Z
366 $= 15$, $N = 8$, $P = 0.742$).

367

368 Noise treatment had a clear effect on the signal transmission of surveillance calls. The SNR of
369 surveillance calls was significantly affected by the interaction between noise treatment and call
370 position (Table 2; Fig. 4). In ambient noise, the SNR did not significantly differ between call
371 positions; SNR was high in both cases. In anthropogenic noise, however, the SNR of
372 surveillance calls coinciding with peak traffic noise was significantly lower than the SNR of
373 calls during approaching traffic. Dominance status did not significantly influence SNR for
374 surveillance calls (Table 2), even though as previously shown with natural recordings (Kern et
375 al. 2016), re-recorded surveillance calls of dominants (mean \pm SE: 1044 ± 38 Hz) were
376 significantly lower in peak frequency of the fundamental than those of subordinates ($1195 \pm$
377 38 Hz; Wilcoxon signed-rank test: $W = 10$, $N = 16$, $P = 0.023$).

378

379 **DISCUSSION**

380 Dwarf mongoose foragers exposed to playback of surveillance calls were more vigilant when
381 also experiencing traffic-noise playback compared to ambient-noise playback, increasing both
382 the total number and the total duration of vigilance scans. By engaging in more vigilance
383 behaviour in noisy conditions, dwarf mongooses compromise time that would otherwise be
384 available for foraging; anthropogenic noise may reduce the advantage that group members
385 usually gain from sentinel presence in terms of decreased personal vigilance and consequential
386 increased biomass intake (Manser 1999; Hollén et al. 2008). Since there is also evidence from
387 other species that foraging efficiency decreases in anthropogenic noise (Siemers and Schaub
388 2011), with individuals making fewer strikes (Burger and Gochfeld 1998) and more food-
389 handling errors (Purser and Radford 2011), additional noise may negatively affect the key
390 trade-off that many animals face between predation and starvation (Lima and Dill 1990).
391 Although increasing vigilance may decrease predation risk and increase survival in the short
392 term, in the longer term it can result in non-lethal fitness consequences, such as reduced
393 resources available for growth and reproduction (Cresswell 2008).

394

395 The observed increase in vigilance in the first playback experiment could arise in part as a
396 direct response to anthropogenic noise itself, since the second playback demonstrated greater
397 vigilance by foragers when exposed to traffic-noise compared to ambient-noise playback. This
398 result is in line with predictions of the ‘increased threat hypothesis’, whereby anthropogenic
399 noise increases the perceived level of threat in an environment (Owens et al. 2012). Noise itself
400 may be seen as threatening, causing inappropriate startle responses (Francis and Barber 2013),
401 or it may cause individuals to respond as if under true predatory threat. For example, if
402 anthropogenic noise potentially deprives individuals of important auditory cues about
403 predatory risk, such as alarm calls or sounds made by approaching predators, they may
404 compensate for the disruption to auditory surveillance by increasing use of the visual medium
405 (Shannon et al. 2016). The ‘increased threat hypothesis’ has garnered support in the last decade,
406 with several studies reporting an increase in vigilance in anthropogenic noise (Rabin et al.
407 2006; Larsen et al. 2014; Lynch et al. 2014; Meillière et al. 2015; Shannon et al. 2016).
408 Increased vigilance in direct response to noise does not provide a full explanation for the results
409 from our first playback experiment, however, as only one aspect of vigilance behaviour (total
410 number of scans) was affected.

411

412 The observed increase in vigilance in the first playback experiment could also be a consequence
413 of partial masking; a lessened response to the surveillance calls themselves. Although foragers
414 increased vigilance behaviour during traffic-noise playback, they maintained the ability to
415 discriminate between surveillance calls of sentinels of different dominance status; foragers
416 exhibited higher levels of vigilance when played back surveillance calls of subordinate
417 sentinels compared to when dominant group members were acting in that role (see also Kern
418 et al. 2016). Thus, surveillance calls could not have been completely masked, a situation which
419 is supported by the results from the transmission experiment. Signal transfer of surveillance
420 calls, regardless of caller dominance status, was negatively affected by traffic-noise playback
421 and SNR suggests that surveillance calls were heavily masked during periods of peak traffic
422 noise. However, although SNR was also reduced during vehicle approach, it was considerably
423 greater than during peak traffic noise and surveillance calls were likely to be audible. This
424 would mean that receivers could still detect sentinel presence and identity during traffic-noise
425 playbacks, but that there may be implications for perceived call rate. That is, if surveillance
426 calls were masked only during peak traffic period of playback, call rate would effectively have
427 been reduced compared to during ambient-noise playback. Sentinels in some species are known
428 to vary surveillance call rate with background risk levels (Bell et al. 2009; Kern and Radford

429 2013), and lower call rates in dwarf mongooses are associated with higher risk situations (Kern
430 and Radford 2013). A reduction in perceived call rate as a consequence of anthropogenic noise
431 could therefore explain the increase in forager vigilance.

432

433 As with most studies to date, we focused on short-term exposure to noise (see also Rabin et al.
434 2006; Chan et al. 2010; Meillère et al. 2015; Shannon et al. 2016). Recent evidence suggests
435 that responses may be modified with repeated exposure to noise. For instance, there may be an
436 increase in tolerance arising either through a shift in hearing threshold or because individuals
437 habituate over time, when they learn that that the noise does not represent an actual threat
438 (Scholik & Yan 2001; Popper et al. 2005; Wale et al. 2013a; Nedelec et al. 2015). Habituation
439 in particular may be less likely in the case of traffic noise, compared to more continuous noise
440 sources, given its unpredictability and fluctuating amplitude. Moreover, where effects are due
441 to masking, habituation is not effective; instead signallers might alter their vocalisations in
442 response to noise, either plastically within their lifetime (Patricelli and Blickley 2006) or across
443 generations (Slabbekoorn and Ripmeester 2008). If increased vigilance and probable
444 associated foraging costs were to continue under exposure to repeated or chronic noise,
445 individuals could be subject to substantial cumulative non-lethal predation effects, but this
446 requires future testing.

447

448 Recent experimental work with anthropogenic noise has demonstrated detrimental effects on
449 anti-predator behaviour in terms of reduced responses to simulated and actual predatory attacks
450 (Chan et al. 2010; Wale et al. 2013b; Voellmy et al. 2014; Simpson et al. 2015, 2016). Here,
451 we show a potential influence on risk perception as well. While predatory attacks are relatively
452 rare, risk fluctuates often and individuals should constantly update their assessment of
453 background risk to optimise the foraging–vigilance trade-off (Bell et al. 2009). With the
454 potential to disrupt risk assessment, the overall effect of anthropogenic noise could be more
455 extensive than previously thought. More studies examining the impact of noise on risk
456 perception are encouraged, alongside those investigating diverse vocalisations.

457

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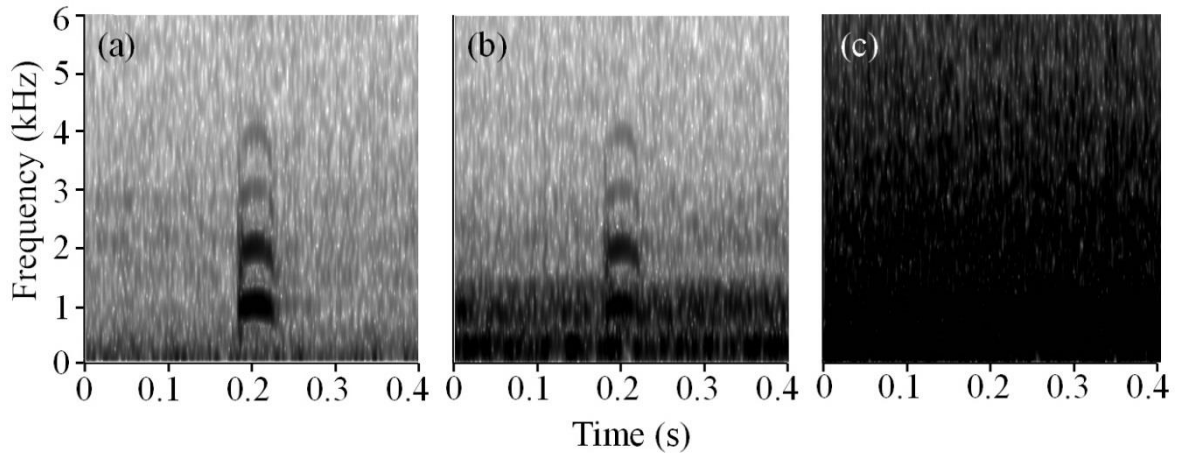
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722 **Figure legends**

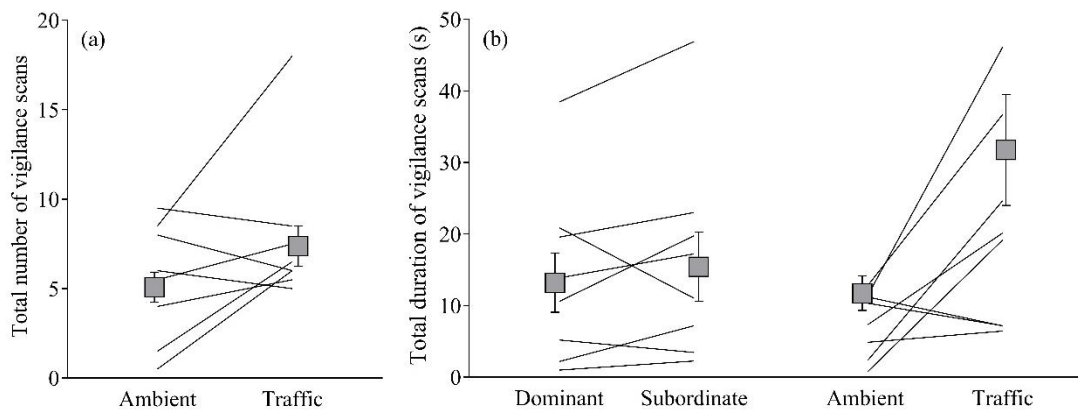
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725 **Figure 1.** Illustrative spectrograms of dwarf mongoose surveillance calls: (a) in ambient noise,
726 (b) in approaching traffic noise, and (c) in peak traffic noise. Spectrograms were created using
727 Raven Pro 1.5 (FFT length 1024, Hann window, 75% overlap, 1.45 ms time resolution, 43 Hz
728 frequency resolution).

729



730

731 **Figure 2.** Response – (a) total number of vigilance scans and (b) total duration of vigilance
732 scans – of foraging dwarf mongooses ($N = 8$) to the playback of sentinel surveillance calls in
733 different noise treatments. For (b), pale grey bars = dominant sentinel; dark grey bars =
734 subordinate sentinel. Means and standard errors calculated from raw data are shown.

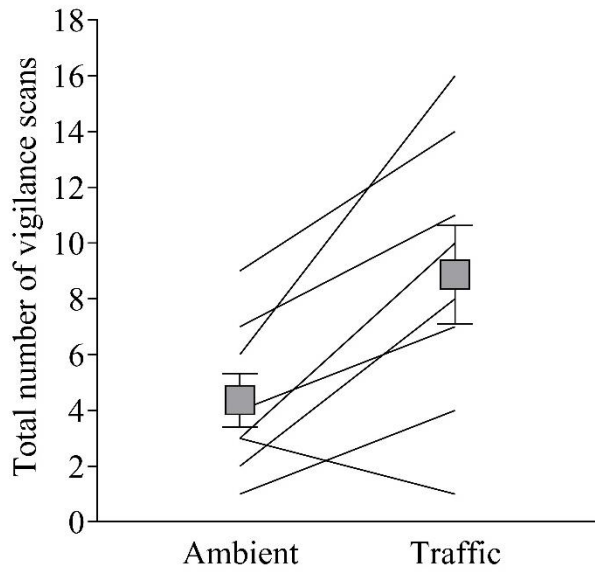
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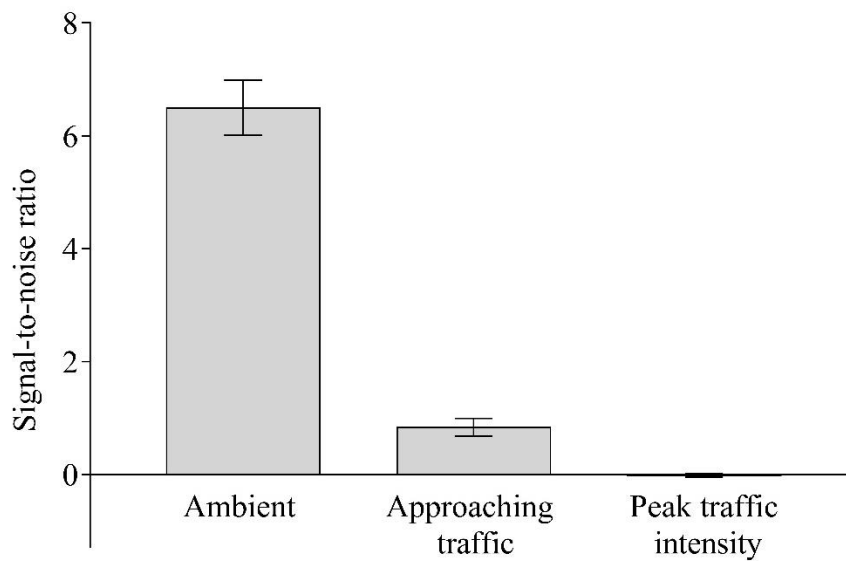
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741 **Figure 3.** Total number of vigilance scans by foraging dwarf mongooses ($N = 8$) in response
 742 to the playback of different noise treatments without mongoose vocalisations. Means and
 743 standard errors calculated from raw data are shown.

744



745

746 **Figure 4.** The effect of noise treatment on the signal-to-noise ratio of surveillance calls ($N =$
 747 32). Pale grey bars = call position during ‘approaching traffic’; dark grey bars = call position
 748 during ‘peak traffic’. Means and standard errors calculated from raw data are shown.

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751

752 **Tables**

753

Table 1. Model outputs from two LMMs investigating forager vigilance in response to playback of surveillance calls in different noise treatments: (a) total number of scans (square root transformed), and (b) total duration of scans (log 10+1 transformed) ($N = 16$). Significant fixed terms shown in bold; variance \pm SE reported for random terms.

	Fixed effect	Effect \pm SE	χ^2	<i>P</i>
(a) Total number of scans				
Minimal model	(Intercept)	2.14 \pm 0.26		
	Noise		4.17	0.041
	Ambient	0.00 \pm 0.00		
	Traffic	0.54 \pm 0.26		
Dropped terms	Noise:Dominance status		2.10	0.350
	Dominance status		0.61	0.435
	Treatment order		0.16	0.693
Random terms	Individual ID nested in group	0.36 \pm 0.71		
(a) Total duration of scans				
Minimal model	(Intercept)	0.80 \pm 0.14		
	Noise		6.87	0.009
	Ambient	0.00 \pm 0.00		
	Traffic	0.36 \pm 0.13		
	Dominance status		5.81	0.016
	Dominant	0.00 \pm 0.00		
	Subordinate	0.32 \pm 0.13		
Dropped terms	Noise:Dominance status		1.52	0.220
	Treatment order		0.32	0.569
Random terms	Individual ID nested in group	0.14 \pm 0.36		

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757

Table 2. Model output from LMMs investigating transmission of surveillance calls ($N = 32$ calls, 16 individuals) in different noise treatments. Significant fixed terms shown in bold; variance \pm SE reported for random terms.

	Fixed effect	Effect \pm SE	χ^2	<i>P</i>
Minimal model	(Intercept)	2.09 \pm 0.00		
	Noise:Position	0.01 \pm 0.00	4.70	0.030
	Noise			
	Ambient	0.00 \pm 0.00		
	Traffic	-0.10 \pm 0.00		
	Position			
	Peak traffic	0.00 \pm 0.00		
	Approaching traffic	0.00 \pm 0.00		
Dropped terms	Dominance status		0.63	0.427
	Noise:Dominance status		0.69	0.709
Random terms	Caller ID	0.00 \pm 0.01		

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759