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Anthropogenic noise disrupts use of vocal information about predation risk

Julie M. Kern[1] *Julie.Kern@bristol.ac.uk*
Andrew N Radford[1] *Andy.Radford@bristol.ac.uk*

[1]School of Biological Sciences, Life Sciences Building, 24 Tyndall Avenue, University of Bristol, BS8 1TQ.

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Corresponding author: Julie M. Kern, School of Biological Sciences, Life Sciences Building, 24 Tyndall Avenue, University of Bristol, BS8 1TQ, julie.kern@bristol.ac.uk, +447790645939, no fax number

Statement of authorship

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

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

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

INTRODUCTION

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

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

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

Our aim was to investigate how anthropogenic noise affects responses to surveillance calls produced by sentinels, using the cooperatively breeding dwarf mongoose (*Helogale parvula*) as a model system. Sentinel behaviour, where an individual adopts a raised position, scanning for predators and warning others of danger, has been documented in a range of social species (reviewed in Bednekoff 2015). Sentinels publicise threats using specific alarm calls, providing receivers with crucial information about immediate danger (Bednekoff 2015). In several species, sentinels also produce low-amplitude surveillance calls, providing essential information about sentinel presence, identity, satiation level and height (Manser 1999; Hollén et al. 2008; Bell et al. 2009, 2010; Radford et al. 2009, 2011; Kern et al. 2016), and an estimate of current risk levels (Bell et al. 2009; Kern and Radford 2013). Surveillance calls provide tangible benefits to groupmates, helping to mitigate indirect predation effects by enabling receivers to optimize the foraging–vigilance trade-off (Manser 1999; Hollén et al. 2008; Bell et al. 2010; Kern et al. 2016). If receiver detection of surveillance calls is disrupted by masking or distraction, or their responses lessened as a result of other noise-related effects, then receivers may have to increase reliance on personal information, negating at least some of the benefits of sentinel presence.

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

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

MATERIALS AND METHODS

(a) Study site and population

This study took place on Sorabi Rock Lodge Reserve, a 4 km^2 private game reserve in Limpopo Province, South Africa (24°11'S, 30°46'E), part of southern Africa's Savanna Biome (see Kern and Radford 2013 for full details). Data were collected from eight groups of wild dwarf mongooses (mean group size = 8.3; range = 3–17), habituated to close observation (<5 m) on foot (Kern and Radford 2013). All animals are individually identifiable either from markings of blonde hair dye (Wella UK Ltd, Surrey, UK), applied with an elongated paintbrush, or from natural features such as scars or facial irregularities. The population has been monitored since 2011, thus the age of most individuals is known; individuals can be sexed through observations of ano-genital grooming.

(b) Acoustic recordings

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

(c) Playback experiments

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

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

Noise-treatment tracks consisted of 220 s of ambient or traffic noise. Each traffic-noise track comprised 13 vehicle passes, constructed using a combination of all four vehicle types in proportion to their frequency of road use. The same ambient-noise and traffic-noise tracks were used for each of the two relevant treatments to a given group, but eight different ambient-noise and traffic-noise tracks were used in the experiment as a whole to ensure that each group received unique tracks. Both ambient-noise and traffic-noise tracks started 20 s before the 3 min sentinel bout, to minimise any disruption to vigilance resulting from initial startle effects of loud noise. Noise-treatment tracks were broadcast from a second mp3 player (IBrightspot, Manchester, UK) connected to a second SME-AFS portable field speaker placed on the ground, 2–5 m from the focal forager and approximately 1 m to the side of the speaker playing surveillance calls. Playback amplitude was standardised according to the amplitude of naturally occurring noise levels (ambient noise: peak amplitude = 40 dB SPLA at 1 m; traffic noise: peak amplitude = 65 dB SPLA at 10 m).

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

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

(d) Transmission experiment

To investigate the impact of traffic noise on the signal-to-noise ratio (SNR) of surveillance calls, a transmission experiment was conducted in September 2014. All experimental trials were performed at the same time of day, in calm weather conditions. Playbacks took place at a site approximately in the centre of each group’s territory, where groups had previously been observed foraging. At each site, playbacks were conducted of surveillance calls from: (i) the group’s dominant male during ambient noise; (ii) the group’s dominant male during traffic noise; (iii) a subordinate adult male group member during ambient noise; and (iv) the same subordinate adult male group member during traffic noise. Surveillance calls were the same as those used in the first playback experiment. All playbacks per site were carried out during a single visit to ensure conditions were as similar as possible.

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

Spectrograms of re-recorded stimuli were created in Raven Pro 1.5 using a 1024 point fast Fourier transformation (Hann window, 75% overlap, 1.45 ms time resolution, 43 Hz frequency resolution; Fig. 1). Recordings were measured for average signal power (dB). Raven’s manual selection tool was used to select the time and frequency range of the surveillance calls to be analyzed. SNR were calculated from recordings as the average power of background noise (ambient or traffic) subtracted from the average power at the time of the vocalisation (as in LaZerte et al. 2015). Background-noise amplitudes were measured from a section of the recording which was of equal length to the stimulus. Where possible, these sections were immediately adjacent to that containing the stimulus, but if these sections were overlapped by other sounds, background-noise measurements were made from the closest possible section of the same recording. Two surveillance calls from each recording were measured: the first at 2 s into background noise during the approach of traffic; the second at 10 s coinciding with peak traffic noise. In peak traffic noise, the surveillance call of interest was not always visible on the spectrogram, in which case a time stamp was used to select the area where the call was known to be. To compare the surveillance calls of dominant and subordinate sentinels, peak frequency of the fundamental (kHz), defined as the frequency at which maximum power occurs within the lowest formant, was also measured from spectrograms of the first surveillance call per individual in ambient noise ($N = 16$; 8 dominant, 8 subordinate). Raven's manual selection tool was used to select the time and frequency range of the element to be analyzed.

(e) Statistical analysis

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

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

To investigate focal forager response to surveillance-call playback in different noise conditions, two LMMs were used following transformation of the data (number of vigilance scans was square-root transformed, duration of vigilance scans was log 10+1 transformed). For both models, the fixed effects of noise treatment (traffic or ambient), dominance status (dominant or subordinate), treatment order and the interaction between noise treatment and dominance status were fitted, and focal individual was included as a random term. To investigate differences in SNR of surveillance calls in noise (from the transmission experiment), a further LMM was conducted following log 10+100 transformation as the data contained negative values; SNR was calculated by subtracting the average power of background noise (ambient or traffic) from the average power at the time of vocalisation. The fixed effects of noise treatment (traffic or ambient), call position (approaching traffic or peak traffic), dominance status (dominant or subordinate), treatment order and the interactions between noise treatment and call position, and between noise treatment and dominance status were fitted, and caller identity nested in group was included as a random term.

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

RESULTS

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

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

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

DISCUSSION

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

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

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

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

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

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

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Figure legends

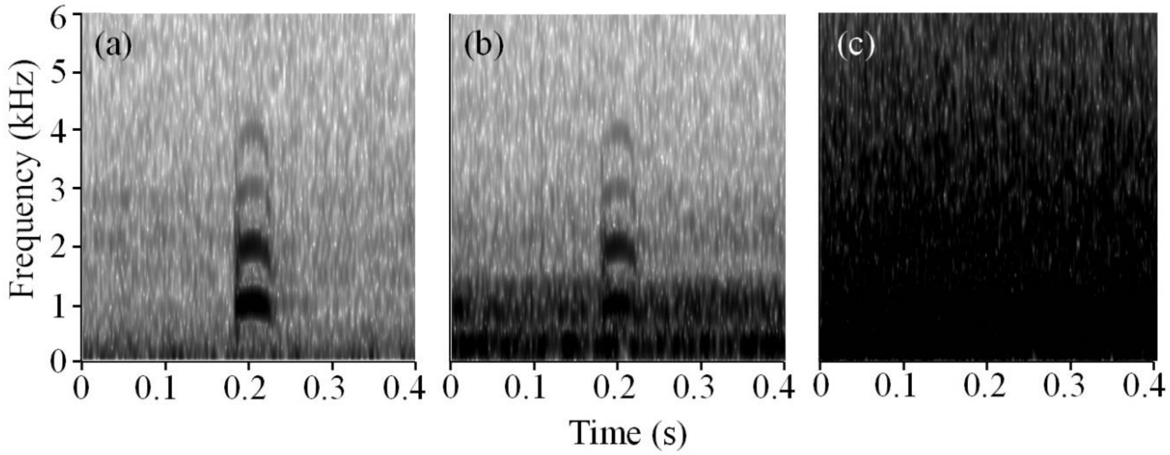

Figure 1. Illustrative spectrograms of dwarf mongoose surveillance calls: (a) in ambient noise, (b) in approaching traffic noise, and (c) in peak traffic noise. Spectrograms were created using Raven Pro 1.5 (FFT length 1024, Hann window, 75% overlap, 1.45 ms time resolution, 43 Hz frequency resolution).

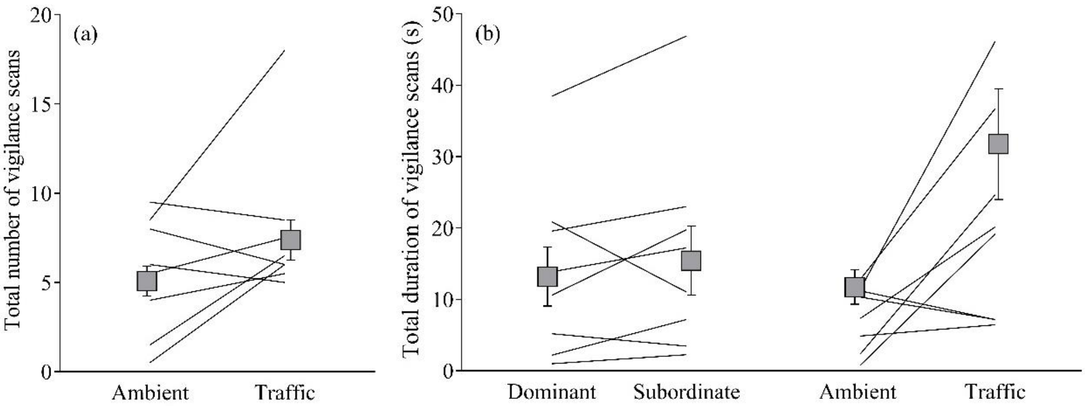

Figure 2. Response – (a) total number of vigilance scans and (b) total duration of vigilance scans – of foraging dwarf mongooses (N = 8) to the playback of sentinel surveillance calls in different noise treatments. For (b), pale grey bars = dominant sentinel; dark grey bars = subordinate sentinel. Means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

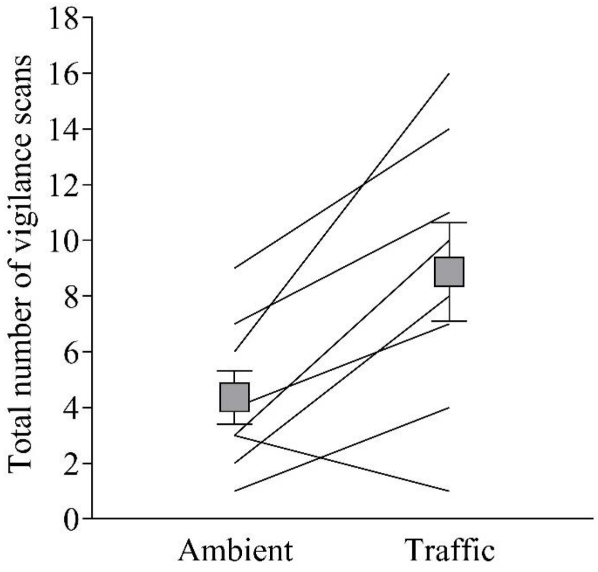

Figure 3. Total number of vigilance scans by foraging dwarf mongooses (*N* = 8) in response to the playback of different noise treatments without mongoose vocalisations. Means and standard errors calculated from raw data are shown.

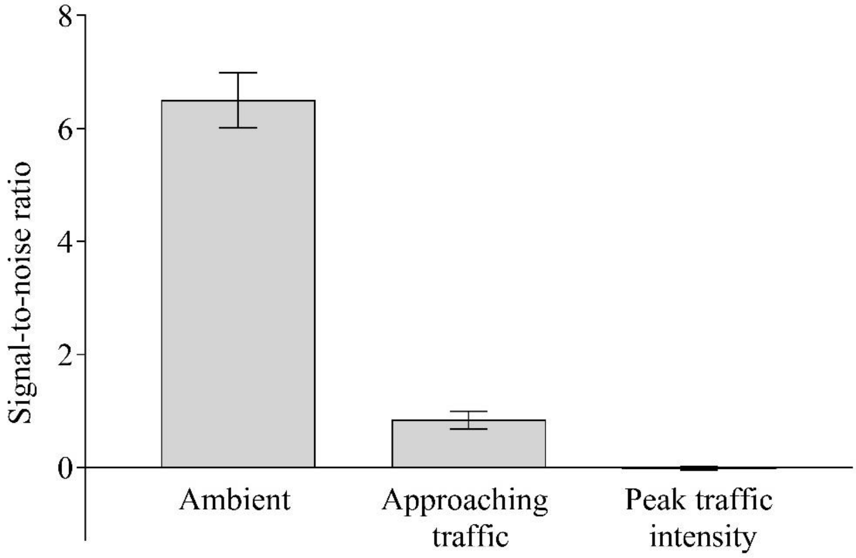

Figure 4. The effect of noise treatment on the signal-to-noise ratio of surveillance calls (*N* = 32). Pale grey bars = call position during ‘approaching traffic’; dark grey bars = call position during ‘peak traffic’. Means and standard errors calculated from raw data are shown.

Tables

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 ± SE reported for random terms.

	Fixed effect	**Effect ± SE**	**χ^2**	***P***
(a) Total number of scans				
Minimal model	(Intercept)	2.14 ± 0.26		
	Noise		**4.17**	**0.041**
	Ambient	0.00 ± 0.00		
	Traffic	0.54 ± 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 ± 0.71		
(a) Total duration of scans				
Minimal model	(Intercept)	0.80 ± 0.14		
	Noise		**6.87**	**0.009**
	Ambient	0.00 ± 0.00		
	Traffic	0.36 ± 0.13		
	Dominance status		**5.81**	**0.016**
	Dominant	0.00 ± 0.00		
	Subordinate	0.32 ± 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 ± 0.36		

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 ± SE reported for random terms.

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