



Contents lists available at ScienceDirect

Environmental Pollution

journal homepage: www.elsevier.com/locate/envpol

Anthropogenic noise alters dwarf mongoose responses to heterospecific alarm calls[☆]

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ARTICLE INFO

Article history:

Received 21 November 2016
Received in revised form
17 January 2017
Accepted 17 January 2017
Available online xxx

Keywords:

Eavesdropping
Environmental change
Noise pollution
Predation risk
Vocal communication

ABSTRACT

Anthropogenic noise is an evolutionarily novel and widespread pollutant in both terrestrial and aquatic habitats. Despite increasing evidence that the additional noise generated by human activities can affect vocal communication, the majority of research has focused on the use of conspecific acoustic information, especially sexual signals. Many animals are known to eavesdrop on the alarm calls produced by other species, enhancing their likelihood of avoiding predation, but how this use of heterospecific information is affected by anthropogenic noise has received little empirical attention. Here, we use two field-based playback experiments on a habituated wild population of dwarf mongooses (*Helogale parvula*) to determine how anthropogenic noise influences the response of foragers to heterospecific alarm calls. We begin by demonstrating that dwarf mongooses respond appropriately to the alarm calls of sympatric chacma baboons (*Papio ursinus*) and tree squirrels (*Paraxerus cepapi*); fleeing only to the latter. We then show that mongoose foragers are less likely to exhibit this flee response to tree squirrel alarm calls during road-noise playback compared to ambient-sound playback. One explanation for the change in response is that noise-induced distraction or stress result in maladaptive behaviour. However, further analysis revealed that road-noise playback results in increased vigilance and that mongooses showing the greatest vigilance increase are those that do not subsequently exhibit a flee response to the alarm call. These individuals may therefore be acting appropriately: if the greater gathering of personal information indicates the absence of an actual predator despite an alarm call, the need to undertake costly fleeing behaviour can be avoided. Either way, our study indicates the potential for anthropogenic noise to interfere with the use of acoustic information from other species, and suggests the importance of considering how heterospecific networks are affected by this global pollutant.

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1. Introduction

Over the last century, noise pollution has increased globally as a result of human activities such as urban development, resource extraction and transportation networks (Barber et al., 2010; Slabbekoorn et al., 2010). The acoustic characteristics of man-made sounds are often very different to those emitted from biotic and abiotic sources (Hildebrand, 2009), and there is a growing body of research documenting noise-induced effects in a variety of taxa, across a range of scales; from individual behaviour to ecosystem and community ecology (reviewed in: Barber et al., 2010;

Slabbekoorn et al., 2010; Radford et al., 2014; Shannon et al., 2015). Perhaps the greatest focus to date has been on acoustic communication, but there has been a bias towards avian species and sexual signals in this regard (Morley et al., 2014; Read et al., 2014; Shannon et al., 2015).

Anthropogenic noise can interfere with acoustic communication in four main ways which are not mutually exclusive: by masking information either completely or partially (Brumm and Slabbekoorn, 2005); by diverting an individual's finite attention away from detecting or responding to a signal (Chan and Blumstein, 2011); by inducing physiological stress that results in inappropriate responses (Kight and Swaddle, 2011); or by increasing perceived threat levels and thus indirectly affecting behaviour (Frid and Dill, 2002). The consequences of masking for signallers has received considerable research attention, with numerous studies showing that anthropogenic noise can lead to adjustments in the acoustic parameters of vocalisations via behavioural plasticity, ontogenetic

[☆] This paper has been recommended for acceptance by David Carpenter.

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changes or adaptation (Slabbekoorn and Ripmeester, 2008; Gross et al., 2010; Luther and Baptista, 2010; Roca et al., 2016). Equally important, but relatively understudied, is the potential disruption to receiver responses (Halfwerk et al., 2012; McMullen et al., 2014; Kern and Radford, 2016).

Alarm calling, the production of particular vocalisations to warn others of danger, is a key anti-predator strategy in many species (Klump and Shalter, 1984; Hollén and Radford, 2009). The few studies exploring the impact of anthropogenic noise on alarm-call behaviour have mostly considered conspecific communication, particularly how the acoustic parameters of the alarm calls themselves differ depending on noise conditions (Lowry et al., 2012; Potvin et al., 2014; Templeton et al., 2016), but also how responses may be disrupted (Rabin et al., 2006; McIntyre et al., 2014; Templeton et al., 2016). However, many animals are known to eavesdrop on heterospecific alarm calls, responding appropriately to warnings of danger and even the additional information often contained within such vocalisations (Magrath et al., 2015). To our knowledge, only one study has examined the impact of anthropogenic noise on heterospecific alarm-call use: Grade and Sieving (2016) showed that eavesdropping on tufted titmouse (*Baeolophus bicolor*) alarm calls by northern cardinals (*Cardinalis cardinalis*), which is apparent in areas far from roads, did not occur in noisier sites closer to roads.

Here, we use experimental playbacks to examine the effect of road noise on the anti-predator responses of dwarf mongooses (*Helogale parvula*) to heterospecific alarm calls. Dwarf mongooses are vocal, cooperatively breeding, diurnal carnivores that live in large (5–30 individuals) mixed-sex groups (Rasa, 1977). Since they frequently forage in a head-down position, dwarf mongooses rely on the auditory transfer of information about predator presence, and have evolved a complex alarm-call system which conveys information on the type of predator and urgency of the threat (Beynon and Rasa, 1989; Collier et al., in review). Additionally, they join mixed-species foraging parties, eavesdropping on heterospecific alarm calls produced from a range of animals (Rasa, 1983, 1985; Sharpe et al., 2010). Previous experimental work has demonstrated that anthropogenic noise can disrupt dwarf mongoose use of information about predation risk, including that provided by the surveillance calls of conspecific sentinels (Kern and Radford, 2016; Morris-Drake et al., 2016).

In this study, we first demonstrate that dwarf mongooses respond similarly to tree squirrel (*Paraxerus cepapi*) alarm calls as to conspecific alarm calls; tree squirrels are a sympatric species which, due to their small size and terrestrial foraging, are vulnerable to the same suite of predators as dwarf mongooses (Rasa, 1985). We then investigate whether dwarf mongooses continue to respond to these heterospecific calls during road noise and whether the nature of the response is affected. Finally, we consider a possible vigilance-related explanation for the difference in response found to heterospecific alarm calls during road-noise playback.

2. Materials and methods

2.1. Study site and population

This study was conducted on Sorabi Rock Lodge Reserve, South Africa, a 4 km² private game reserve in north-eastern South Africa (24°11'S, 30°46'E); full details are available in Kern and Radford (2013). The reserve borders a tar road (R530), thus anthropogenic noise from this source is ecologically relevant (Kern and Radford, 2016), and is home to a wide range of terrestrial and aerial predators (Sharpe et al., 2010; Kern, 2012). Data were collected in February–May 2014 and April–June 2015 from seven wild dwarf

mongoose groups (mean group size \pm SE: 10.9 \pm 0.9, range: 5–13) habituated to close observation (<5 m) on foot (Kern and Radford, 2013, 2014; Kern et al., 2016). Monitoring of the population has occurred since 2011, therefore the age of most individuals is known. All individuals are uniquely identifiable through small blonde dye marks on their fur (Wella UK Ltd, Surrey, UK; applied using an elongated paintbrush) or distinctive physical markings (e.g. a scar or missing body part). Individuals are sexed through observing anogenital grooming sessions.

2.2. Playback experiment 1

To investigate the anti-predator responses of dwarf mongooses to heterospecific alarm calls, seven adults (one from each study group) each received four playback treatments: alarm calls from two heterospecifics – a tree squirrel and a chacma baboon (*Papio ursinus*) – a conspecific alarm call given to aerial predators (Collier et al., in review), and a conspecific close call as a non-alarm control ($N = 28$ trials in total). Both heterospecifics occupy the same habitat as dwarf mongooses, but while tree squirrels share the same suite of predators, chacma baboons (hereafter baboons) are generally vulnerable to different predators.

Original sound recordings were made at a sampling rate of 44.1 kHz with a 16-bit resolution, using a Marantz PMD660 professional solid-state recorder (Marantz America, Mahwah, NJ, USA) and a handheld ME 66 shotgun directional microphone (Sennheiser UK, High Wycombe, Buckinghamshire, UK) with a Rycote Softie windshield (Rycote Microphone Windshields, Stroud, Gloucestershire, UK). The frequency response of the recording system was flat within 3 dB from 500 to 10,000 Hz. Recordings were stored on a Transcend SD card (Transcend, Taipei, Taiwan). Dwarf mongoose aerial alarm calls were recorded from dominant males when heard during observation sessions or elicited by throwing a Frisbee over those individuals when they were slightly apart from the rest of the group and were being vigilant (Rogerson, 2014). Close calls, given throughout foraging bouts (Kern and Radford, 2013), were recorded *ad libitum* from the same individuals. Baboon and tree squirrel alarm calls were also recorded *ad libitum* on the reserve. Spectrograms of example calls are provided in Fig. 1. To standardise playbacks across groups, the peak sound-pressure amplitude of different calls (in dB) was measured using a HandyMAN TEK 1345 sound meter (Metrel UK Ltd., Normanton, UK).

Each trial consisted of a 20-s playback of ambient sound (recorded in the territory of the focal mongoose) with the relevant call played from the same loudspeaker 10 s after the start of the trial. Playback tracks were constructed from recordings of good signal-to-noise ratio using Raven Lite 1.0 (Cornell Lab of Ornithology, Ithaca, NY). Different ambient-sound and call exemplars were used for every trial and all sounds were played back at natural amplitudes (ambient sound: peak amplitude = 40 dB sound-pressure level A (SPLA) at 10 m; all alarm-calls: peak amplitude = 55 dB SPLA at 1.5 m; control close calls: peak amplitude = 45 dB SPLA at 1.5 m). Playbacks were from an Excel Audio loudspeaker (Guangzhou, China) placed on the ground and connected to a Kubic Evo EV8B mp3 player (ARC UK). Two trials were conducted to each focal individual in the morning (0800–1200) on each of two days (separated by 1–3 days); trials on the same day were separated by at least 1 h, and treatment order was counterbalanced between individuals. Trials were conducted in calm conditions when the focal individual had been foraging in a relatively open area for at least 5 min prior to playback, and at least 10 min after any natural disturbance, such as a natural alarm call, encounter with a predator, or inter-group interaction (Kern and Radford, 2013; Kern et al., 2016). The immediate response of the focal individual to each vocalisation (no response, look up or flee)

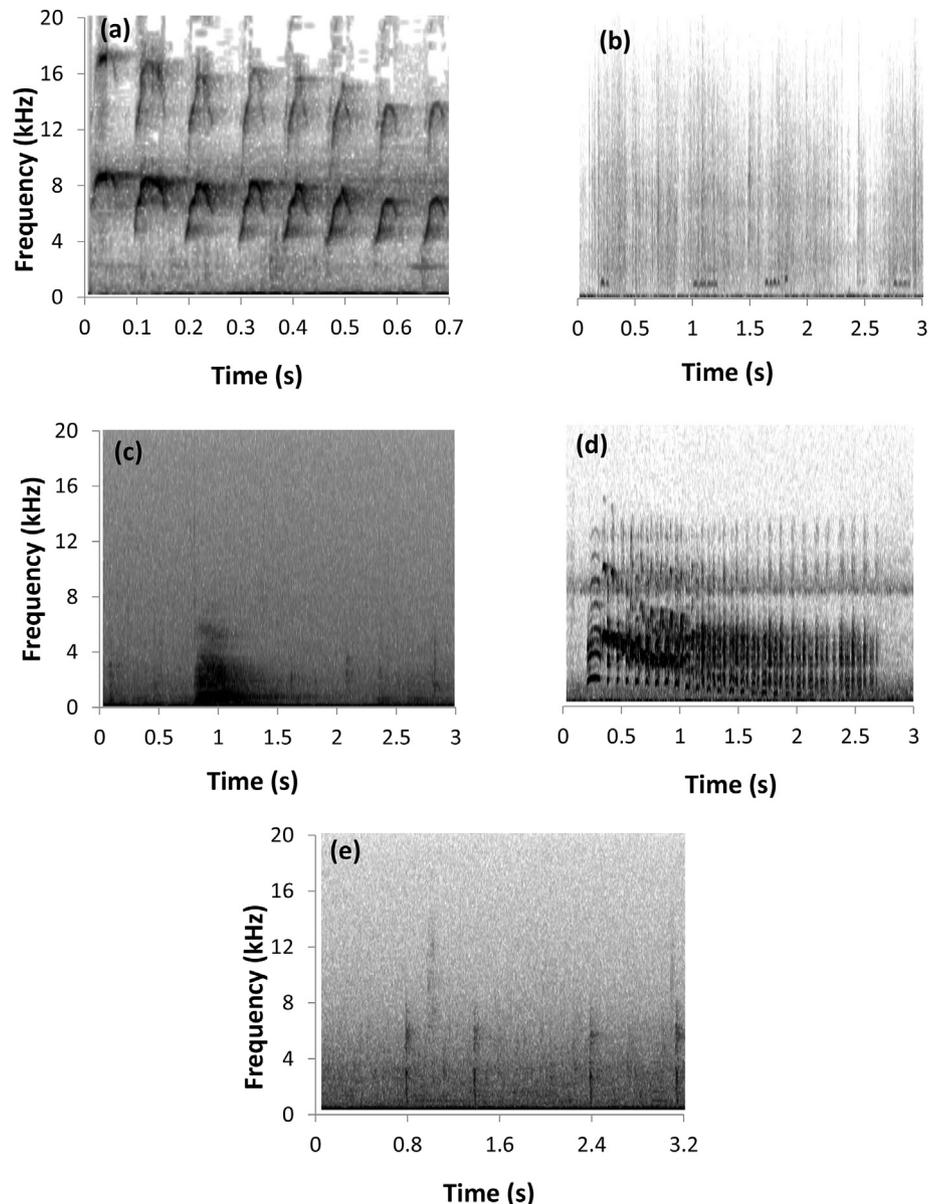


Fig. 1. Illustrative spectrograms of a: (a) dwarf mongoose aerial alarm call; (b) dwarf mongoose close call; (c) chacma baboon alarm call; (d) tree squirrel alarm call; and (e) tree squirrel control call. Spectrograms were created using Raven Pro 1.5 (FFT length 1024, Hann window, 75% overlap, 1.45 ms time resolution, 43 Hz frequency resolution) from playback tracks used in experiments.

was recorded. The overall group response (the response of the majority of individuals within sight at the time of call playback) was recorded in similar fashion.

2.3. Playback experiment 2

To assess how road noise affects vigilance behaviour and responses to heterospecific alarm calls, 14 adult female dwarf mongooses (two from each study group) each received three playback treatments: (i) tree squirrel non-alarm (control) call in ambient sound; (ii) tree squirrel alarm call in ambient sound; and (iii) tree squirrel alarm call in road noise ($N = 42$ trials in total). Tree squirrel vocalisations were chosen as dwarf mongooses were found to respond strongly to their alarm calls in Experiment 1 (see Results). Original sound recordings were made using the equipment described above. Tree squirrel alarm calls were available from Experiment 1. By observing tree squirrel behaviour, a specific non-

alarm vocalisation, associated with tail-wagging, was selected for use as a control call (Fig. 1e); these vocalisations were recorded *ad libitum* on the reserve. Ambient sound was recorded from the centre of each dwarf mongoose group's territory at a similar time of day in calm conditions, after checking that no dwarf mongooses were present. The microphone was positioned in the opposite direction to the R530 at a height of 10 cm (to replicate the head height of dwarf mongoose). Road-noise recordings from the R530 were used from another study (Kern and Radford, 2016). For these recordings, the microphone was positioned 10 m from the road at a height of 10 cm. The peak sound-pressure amplitudes of ambient sound and road noise were recorded (in dB), the latter during the passing of vehicles, using a HandyMAN TEK 1345 sound meter (Metrel UK Ltd., Normanton, UK).

Playback tracks were constructed in Praat 5.3.55 (Phonetic Sciences, University of Amsterdam, Amsterdam, The Netherlands), with four different tracks created for each mongoose group:

ambient-sound track, road-noise track, control-call track, and alarm-call track. Any undesirable sounds (for instance, air traffic and other heterospecific alarm calls) were cut out of the ambient-sound recordings, while road-noise recordings were modified to contain the same number and type of vehicle relative to the frequency they were observed on the R530 during 10 1-h traffic counts (Rogerson, 2014; Kern and Radford, 2016). Each treatment consisted of a 1-min pre-playback period before the start of a 3-min ambient-sound or road-noise playback track from one loud-speaker; the relevant call was played back from a second loud-speaker, 30 s after the start of the ambient or road-noise playback (this 30 s period is subsequently referred to as the initial playback period). Each call was timed to overlap with the peak amplitude of a passing vehicle in the road-noise treatment. Different sound and call exemplars were used for every trial and all sounds were played back at natural amplitudes (as above; road noise: peak amplitude = 65–75 dB SPLA at 10 m). Tracks were played back from two portable SME-AFS field speakers (Saul Mineroff Electronics Inc., New York), connected to Kubic Evo EV8B mp3 players (ARC UK). The speaker playing the sound treatment (ambient or road) was hidden in vegetation along the predicted foraging route, approximately 10 m from the focal individual. The speaker broadcasting the call-type (control or alarm) was attached to the side of the experimenter at a height of 1 m (to imitate the raised position of a tree squirrel), with ca. 5 m between the focal mongoose and the speaker. Ipsilateral acoustic stimulation was also taken into consideration, with the speaker and the focal individual always in the same orientation.

Trials to the same focal individual were conducted on separate days, but at a similar time of day (always between 0800 and 1200) and when foraging group size was the same; treatment order was counterbalanced between individuals. Trials to the same two individuals in a given group were separated by at least 1 h; treatment order differed for the two individuals in the same group. Playbacks took place in calm conditions when the focal individual had been foraging in a relatively open area. A minimum of 10 min was left before playbacks commenced following a conspecific or heterospecific alarm call, or any other group disturbance, such as predatory encounters or inter-group interactions (Kern and Radford, 2013; Kern et al., 2016). Trials were abandoned if the focal individual went on sentinel duty (adopted a raised position at least 10 cm above the ground; Kern and Radford, 2013) or paused to scan the surroundings immediately before the call-type (control or alarm) was broadcast. Similarly, if a natural alarm call was produced, if the individual stopped foraging to interact socially with another group member (e.g. playing, grooming), or if the subject was lost from sight, trials were discarded. In these circumstances, 24 h passed before repeating the trial. Trials were recorded with a HD video camera (Panasonic DMC-XS3EB-R, Panasonic House, Berkshire, UK); later video analysis resulted in a continuous focal watch during each 4-min trial, which was used to determine time spent vigilant and number of vigilance scans, and the immediate response to the tree squirrel vocalisation (no response, look up or flee).

2.4. Statistical analysis

All analyses were performed using R version 3.2.4 (R Development Core Team, 2016). 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; non-parametric tests were otherwise used. For both experiments, focal mongoose responses to the playback vocalisation were analysed using Cochran Q and McNemar tests. A first analysis in each case considered whether there

was any response (look up or flee vs no response); a second analysis (where there was variation) used the subset of response occasions to compare the type of response (look up vs flee). For Experiment 1, group-response data were analysed in similar fashion, as well as using a Friedman test and post-hoc Wilcoxon tests, with response categories given a continuous score (1 = no response, 2 = look up, 3 = flee).

For Experiment 2, Linear Mixed Models (LMMs) with individual nested in group as a random term were used to consider treatment-based differences in the change in proportion of time spent vigilant and scan rate between the pre-playback period and the initial period of ambient-sound or road-noise playback. LMMs were conducted using the lme4 package (Bates et al., 2014). Random-effects models with a common subject slope but different intercepts were used, since observations were not replicated (Barr et al., 2013). Model simplification was conducted using Likelihood Ratio Tests, comparing the change in deviance on removal of a term (ANOVA model comparison, Chi-squared test), in conjunction with the Akaike Information Criterion (Crawley, 2005). Consequently, the minimal model only contained terms that explained significant variation in the data and whose removal reduced the explanatory power of the model. Non-significant terms were returned to the minimal model to obtain correct significance levels, while significant terms were confirmed by comparing the term of interest to a null model. In all models, visual examination of residual plots did not reveal any obvious deviations from homoscedasticity or normality. Presented effect sizes \pm SE are shown in model tables and were acquired from the minimal model, as was the variance component for the random term (\pm SD). Mann-Whitney U-tests were used to compare differences in pre-alarm-call playback vigilance on the response type shown to the alarm call.

3. Results

3.1. Playback experiment 1

The immediate response of the focal dwarf mongoose to call playback was significantly affected by the call type (Cochran Q test: $Q = 21.00$, $df = 3$, $P < 0.001$). While all individuals fled on hearing both the conspecific alarm call and that from a tree squirrel, no individuals showed a response following playback of a baboon alarm call or a conspecific close call. Qualitatively similar findings were apparent when considering the group response (categorical response term: $Q = 12.50$, $df = 3$, $P = 0.006$; continuous response score, Friedman test: $\chi^2 = 19.60$, $df = 3$, $P < 0.001$; Fig. 2). That is, there was a similar response to the alarm calls of both conspecifics and tree squirrels, a heterospecific with similar predators.

3.2. Playback experiment 2

Playback treatment significantly affected the likelihood of a tree squirrel vocalisation initiating a response (look up or flee vs no response) from the focal dwarf mongoose (Cochran Q test: $Q = 24.15$, $df = 2$, $P < 0.001$). That was because, compared to a tree squirrel control call, dwarf mongooses were more likely to respond to a tree squirrel alarm call whether it was in ambient sound (McNemar test: $\chi^2 = 11.08$, $df = 1$, $P < 0.001$) or road noise ($\chi^2 = 10.08$, $df = 1$, $P = 0.001$). There was no significant difference in the likelihood of response to a heterospecific alarm call in ambient-sound or road-noise playbacks ($\chi^2 = 0$, $df = 1$, $P = 1$).

Considering only the individuals that responded to both alarm-call treatments ($N = 13$ out of 14 tested in total), there was a significant difference in the type of response elicited (flee vs look up) depending on sound treatment ($\chi^2 = 5.14$, $df = 1$, $P = 0.023$). During playback of ambient sound, individuals always fled to cover on

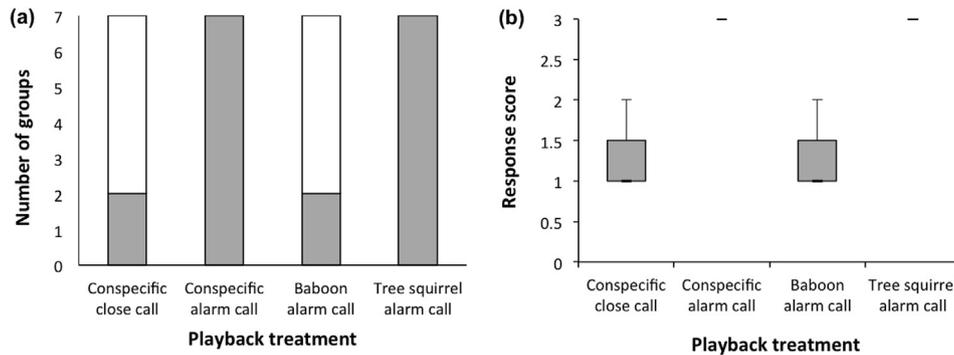


Fig. 2. Group-level responses to playbacks of different conspecific and heterospecific vocalisations. Shown in (a) are the number of groups exhibiting a response (grey bars) vs no response (white bars), and in (b) are the median (and inter-quartile ranges) of response scores (1 = no response, 2 = look up, 3 = flee); in (b) all groups had a response score of 3 for the alarm calls of conspecifics and tree squirrels. $N = 7$ groups.

hearing the tree squirrel alarm call. However, in road-noise playback, over half the individuals instead looked up and scanned the surroundings from a stationary position (Fig. 3a).

Sound treatment significantly affected the change in both the proportion of time spent vigilant (LMM: $\chi^2 = 16.31$, $df = 1$, $P < 0.001$; Table 1a) and the vigilance scan rate ($\chi^2 = 6.67$, $df = 1$, $P = 0.010$; Table 1b) between the pre-playback period (1 min) and the initial playback period (30 s). While there was little change in

vigilance behaviour when the ambient-sound track started, there were increases in the proportion of time spent vigilant and the scan rate following the start of the road-noise track (Fig. 3b and c). Those individuals that responded to the alarm call by looking up had spent significantly more time collecting personal information beforehand than those that responded by fleeing (Mann-Whitney U test, proportion change in vigilance: $Z = 2.36$, $N_{\text{look up}} = 7$, $N_{\text{flee}} = 6$, $P = 0.018$; proportion of time vigilant following start of playback:

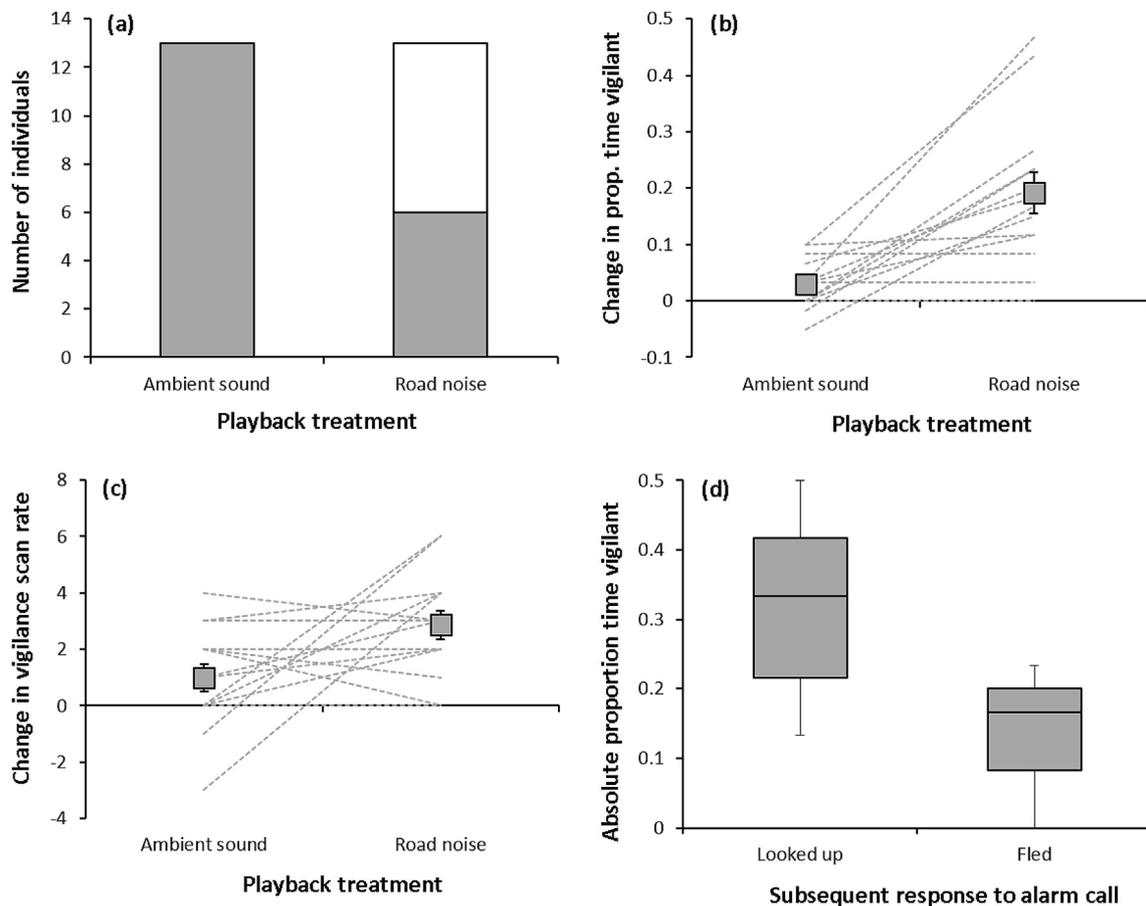


Fig. 3. The effect of sound treatment (ambient-sound or road-noise playback) on (a) the number of dwarf mongoose foragers ($N = 13$) that fled (grey bars) or looked up from a stationary position (white bars) in response to a tree squirrel alarm call, and the change in (b) the proportion of time spent vigilant and (c) the vigilance scan rate between the pre-playback period and the initial playback period ($N = 14$). Shown in (b) and (c) are results for each focal mongoose separately (dotted lines) and the overall treatment mean (solid squares) \pm SE. (d) The effect of the preceding vigilance level on the response shown to alarm-call playback during road-noise playback ($N = 13$). Shown are median and interquartile ranges.

Table 1

Model outputs from two LMMs investigating (a) the change in the proportion of time spent vigilant, and (b) the difference in vigilance scan rate, between the pre-playback period and the initial playback period (once playback of either ambient sound or road noise had started). $N = 28$ trials, 7 groups. The variance (\pm SD) for the random terms (in italics) is reported and significant fixed terms are displayed in bold.

Fixed effect	χ^2	df	P	Effect \pm SE
(a) Change in proportion vigilant				
Sound treatment	16.31	1	<0.001	0.141 \pm 0.030
(Intercept)				0.028 \pm 0.022
Group ID				0.001 \pm 0.001
Individual ID in group				0.001 \pm 0.022
(b) Difference in vigilance scan rate				
Sound treatment	6.67	1	0.010	1.857 \pm 0.702
(Intercept)				1.000 \pm 0.497
Group ID				0.001 \pm 0.001
Individual ID in group				0.001 \pm 0.001

$Z = 2.16$, $N_{\text{look up}} = 7$, $N_{\text{flee}} = 6$, $P = 0.031$; Fig. 3d).

4. Discussion

Dwarf mongoose foragers responded appropriately to the alarm calls of sympatric tree squirrels (with which they share a suite of predators) and baboons (which are generally vulnerable to different predators): they fled on hearing the former, but ignored the latter. Such eavesdropping on heterospecific alarm calls, and the use of relevant information from them, is common across taxa (Magrath et al., 2015). However, the behaviour exhibited by dwarf mongooses in response to tree squirrel alarm calls changed when they were also exposed to road-noise playback compared to ambient-sound playback. Although they still responded (suggesting alarm calls were not completely masked), individuals experiencing playback of road noise were less likely to flee and more likely to look up from their existing position. Our study therefore provides the first experimental evidence that anthropogenic noise can alter the responses of the same individuals to the same heterospecific alarm calls (cf. Grade and Sieving, 2016).

The reduced likelihood of fleeing during road-noise playback could in theory be the result of distraction or a stress-induced cessation of normal locomotor activity. Anti-predator behaviour relies on cognitive processes, including detection, classification and decision-making (Mendl, 1999; Shettleworth, 2010). Stress can reduce the ability of individuals to detect and classify predators or warning signals (Wright et al., 2007), as well as affecting the intensity, duration and frequency of animal behaviour (Broom and Johnson, 1993; Wingfield, 2005). In addition, a stress response could indirectly affect attention (Chan and Blumstein, 2011), as would also be the case if noise were acting as a distracting stimulus (Chan et al., 2010; Purser and Radford, 2011). In the current work, dwarf mongooses may have experienced a limited ability to attend to multiple stimuli, and consequently been less likely to respond accurately to acoustic information about predatory threats. An alternative explanation for the reduced flee response to tree squirrel alarm calls during road-noise playback is that the additional noise partially masked the heterospecific vocalisation, degrading the quality of the information and altering call perception (Naguib et al., 2013; Kern and Radford, 2016). In addition to warning of danger, alarm calls often encode information about, for instance, urgency and predator type (Seyfarth et al., 1980; Evans et al., 1993; Manser, 2001). If such information is lost or distorted in noise, dwarf mongooses may be less effective at interpreting the content, and therefore respond inappropriately.

Some previous studies have documented earlier detection of,

and heightened responses to, visual predatory stimuli during playback of anthropogenic noise (Meillère et al., 2015; Shannon et al., 2016). However, our results are more in line with other work showing a lessened response to predatory stimuli in such conditions (Chan et al., 2010; Wale et al., 2013a; Simpson et al., 2015, 2016). The common interpretation in the latter cases is that an individual is thus more vulnerable to predation; in the current scenario, that the reduced likelihood of mongooses fleeing to survival-related social information is maladaptive. However, the observed greater vigilance prior to call playback in road-noise trials (Experiment 2) suggests a potential alternative explanation for the changed response to heterospecific alarm calls. A noise-induced increase in vigilance has been commonly found (Rabin et al., 2006; Shannon et al., 2014, 2016; Meillère et al., 2015; Kern and Radford, 2016), and could arise either directly (if noise is itself viewed as threatening; Frid and Dill, 2002; Owens et al., 2012) or indirectly (if animals are compensating for potential loss of acoustic information through masking; Beale and Monaghan, 2004; Rabin et al., 2006). Greater reliance on visual vs acoustic cues in conditions of increased noise represents an example of cross-modal perceptual weighting (Halfwerk and Slabbekoorn, 2015; Gomes et al., 2016); anthropogenic noise may also cause cross-modal interference (Halfwerk and Slabbekoorn, 2015; Morris-Drake et al., 2016). Increased vigilance likely means greater acquisition of accurate personal information about the current situation; social information, such as that arising from heterospecific alarm calls, can be irrelevant, unreliable or outdated (Giraldeau et al., 2002; Dall et al., 2005). Thus, more vigilant individuals could have correctly assessed the current level of risk (no actual predator present, despite the alarm-call playback), and responded appropriately: not engaging in unnecessary escape responses that are energetically costly and also reduce foraging time.

Our work demonstrates an impact of short-term exposure to additional noise, as is the case with much recent research (e.g. Chan et al., 2010; Meillère et al., 2015; Simpson et al., 2015, 2016; Shannon et al., 2016). Longer-term studies are needed to consider such aspects as compensation and changing responses (Bejder et al., 2009), because individuals may become more or less tolerant with repeated exposure (Scholik and Yan, 2001; Wale et al., 2013b; Radford et al., 2016). In terms of vocalisations, there is evidence that anthropogenic noise could lead to signallers adjusting acoustic parameters plastically (Patricelli and Blickley, 2006; Templeton et al., 2016) or alterations occurring across generations (Slabbekoorn and Ripmeester, 2008; Lowry et al., 2012), to improve the effectiveness of communication. However, while there are clear selective pressures with respect to conspecific information transfer in this regard, detrimental consequences for heterospecific eavesdroppers are unlikely to have the same effect.

Roads and the associated noise that they generate are known to result in reduced population densities of at least some species (Forman and Alexander, 1998; McClure et al., 2013); anthropogenic noise in general has consequences for community structure (Francis et al., 2009). Since eavesdropping on heterospecific alarm calls is a widespread biological occurrence, and appropriate anti-predator responses are important for survival (Magrath et al., 2015), the loss of relevant information or disruption of fitness-related behaviour could contribute directly (through increased predation) or indirectly (through prey avoidance) in explaining decreased population densities (see also Grade and Sieving, 2016). But, our study also emphasises the importance of determining whether changes in anti-predator responses resulting from noise exposure are indeed negative. Future research examining direct fitness consequences for individuals (e.g. Simpson et al., 2016) and attempting to provide causal links between anthropogenic noise and population consequences are vital if we are to understand fully,

and potentially mitigate successfully, the impacts of this global pollutant.

Statement of authorship

All authors contributed to the conception and design of the study; AM and AB collected the data; AM and AB analysed the data with advice from JMK and ANR; ANR and AM wrote the first draft of the manuscript, and all authors contributed significantly to revisions.

Acknowledgements

We thank B. Rouwhorst and H. Yeates for granting us access to their land, and F. and E. Louw and C. Esterhuizen for logistical support on site. We thank E. Ackerley, K. Collier, S. Le Butt and K. Rogerson for invaluable assistance in the field, and W. Halfwerk and two anonymous referees for valuable comments during the process. This work was supported by a University of Bristol Science Faculty Studentship.

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