



Contents lists available at ScienceDirect

Environmental Pollution

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

Anthropogenic noise disrupts use of vocal information about predation risk[☆]

Julie M. Kern^{*}, Andrew N. Radford

School of Biological Sciences, Life Sciences Building, 24 Tyndall Avenue, University of Bristol, BS8 1TQ, United Kingdom

ARTICLE INFO

Article history:

Received 27 April 2016

Received in revised form

28 July 2016

Accepted 20 August 2016

Available online 29 August 2016

Keywords:

Anthropogenic noise

Environmental change

Vocal communication

Predation

Risk assessment

Sentinel behaviour

ABSTRACT

Anthropogenic noise is rapidly becoming a 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 exhibited a lessened response to surveillance calls in traffic-noise compared to ambient-sound playback, increasing 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 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 dominance 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, an acoustic-transmission experiment showed that while surveillance calls were potentially audible during approaching traffic noise, they were probably inaudible during peak traffic intensity noise. 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.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

Anthropogenic 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; Morley et al., 2014). Although background sound is an inherent feature of the environment, the properties of noise generated by humans are such that its impression on the acoustic environment is considerable (Hildebrand, 2009). Studies have investigated 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 et al., 2013; Wale et al., 2013a; 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 (Slabbekoorn and Peet, 2003; Wood and Yezerinac, 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

[☆] This paper has been recommended for acceptance by Dr. Chen Da.

^{*} Corresponding author.

E-mail addresses: Julie.Kern@bristol.ac.uk (J.M. Kern), Andy.Radford@bristol.ac.uk (A.N. Radford).

exclusive (Kight and Swaddle, 2011). Noise could inhibit vocal communication via acoustic masking, which affects the perception of signals with frequencies overlapping background sound; in the case of anthropogenic noise, predominantly low frequencies (Klump, 1996; Lohr et al., 2003; 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; Recio et al., 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). 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 et al., 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., 2013; 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; Meillère 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 optimise 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 that 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 hearing surveillance calls from dominant compared to subordinate groupmates (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 exposed to traffic noise compared to ambient sound, 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. Second, we use an acoustic-transmission experiment to consider whether surveillance calls might be masked by traffic noise, thus causing the increase in vigilance.

2. Materials and methods

2.1. Study site and population

This study took place on Sorabi Rock Lodge Reserve, a 4 km² 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. Adult group members were classified as either 'dominant' (male and female pair) or 'subordinate' (the remaining individuals) (as in Kern et al., 2016). The dominant pair could be identified through observations of aggression, feeding displacement, scent marking and greeting behaviour (Rasa, 1977).

2.2. 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). The frequency response of the recording system was flat within 3 dB from 500 to 10 000 Hz. Surveillance calls from individuals on sentinel duty were recorded opportunistically from a distance of 0.5–10 m during behavioural observations (Fig. 1a). Ambient sound 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, 4 × 4, minibus and truck) and their frequency of occurrence recorded during 10 1-h traffic counts (Rogerson, 2014). The maximum amplitude of surveillance calls, ambient sound and traffic noise (passing vehicles) was measured using a HandyMAN TEK1345 Mini Sound Level Meter (Metrel UK Ltd., Normanton, West Yorkshire, UK).

2.3. 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 sound, (ii) their group's dominant male during traffic noise, (iii) a subordinate adult male group member during ambient sound, and (iv) the same subordinate adult male group member during traffic noise ($N = 32$ trials). The four treatments took place across two days at similar times of day, with two treatments per day separated by a minimum of 1 h. Playback order was counterbalanced between groups. Trials were conducted when the entire group was foraging in the same habitat type under calm conditions. Playbacks took place when there was no natural sentinel present, and no natural sentinel had been 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 sound, 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 sound 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-sound and traffic-noise tracks were used for each of the two relevant treatments to a given group, but eight different ambient-sound and traffic-noise tracks were used in the experiment as a whole to ensure that each group received unique tracks. Both ambient-sound and traffic-noise tracks started 20 s before the 3 min sentinel bout, an arbitrary time period aimed at minimising 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 normally occurring noise levels (ambient sound: 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-sound 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 sound or traffic noise. All tracks were the same as those used in the

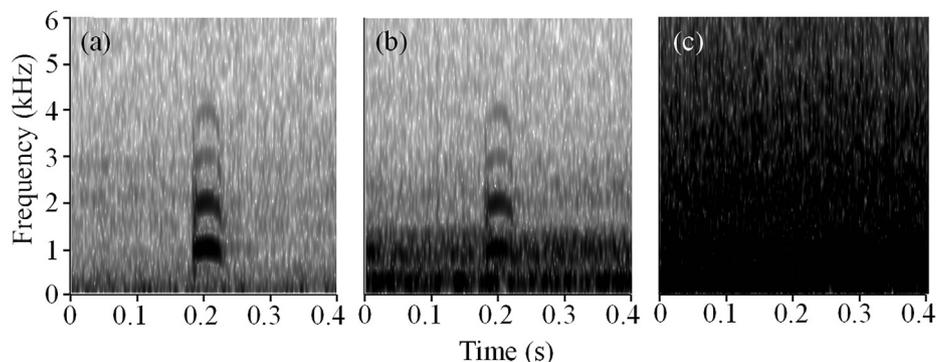


Fig. 1. Illustrative spectrograms of dwarf mongoose surveillance calls: (a) in ambient sound, (b) in approaching traffic noise, and (c) in peak traffic intensity noise. Spectrograms were created using Raven Pro 1.5 (FFT length 1024, Hann window, 75% overlap, 1.45 ms time resolution, 43 Hz frequency resolution).

first experiment. The same focal forager in each of the eight groups was exposed to the two treatments: (i) ambient sound and ambient sound, and (ii) ambient sound and traffic noise ($N = 16$ trials). 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.

2.4. Acoustic-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 sound; (ii) the group's dominant male during traffic noise; (iii) a subordinate adult male group member during ambient sound; 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 sound or traffic noise. Each traffic-noise track comprised two vehicle passes. Surveillance calls were broadcast from an mp3 player (Apple Inc., Cupertino, California, USA) 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 (as above) 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). Raven's manual selection tool was used to select the time and frequency range of the surveillance calls to be analyzed and recordings measured for root-mean-squares amplitude (dB) (RMS). SNR were calculated from recordings as the ratio between RMS amplitudes of vocalisation (E_y) to background noise (ambient sound or traffic noise) for each re-recorded stimulus, using the formula $SNR = 10 \log ((E_y - E_n)/E_n)$ (as in LaZerte et al., 2015). Background-sound amplitudes (E_n) were measured from a section of the recording which was of equal duration 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-sound measurements were made from the closest possible section of the same recording. During traffic noise, two surveillance calls were measured: the first at 2 s into traffic noise during the approach of traffic (hereafter approaching traffic); the second at 10 s coinciding with peak intensity of traffic noise (hereafter peak traffic intensity). During periods of peak

traffic intensity, 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. Measurements were taken from spectrograms of the first surveillance call per individual in ambient sound ($N = 16$; 8 dominant, 8 subordinate). Raven's manual selection tool was used to select the time and frequency range of the lowest harmonic of each visually distinct element to be analyzed.

2.5. 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. 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 the 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' (Pinheiro et al., 2012). 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 by order of least significance and models compared using likelihood ratio tests. Removed terms were returned to the minimal model individually to confirm that they were not significant. Presented χ^2 and P -values for significant terms were obtained by comparing the minimal model with models in which the term of interest had been removed. Presented χ^2 and P -values for non-significant terms were obtained by comparing the minimal model with models in which the term of interest had been added. Presented effect sizes (\pm 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. For categorical variables containing more than two levels, post hoc comparisons of each pair of levels were conducted using paired t -tests and subsequent Bonferroni corrections (Rice, 1989).

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 $\log 10 + 10$ transformation as the data contained negative values. The fixed effects of noise treatment (ambient, approaching traffic or peak traffic intensity) and dominance status (dominant or subordinate), and the interaction 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

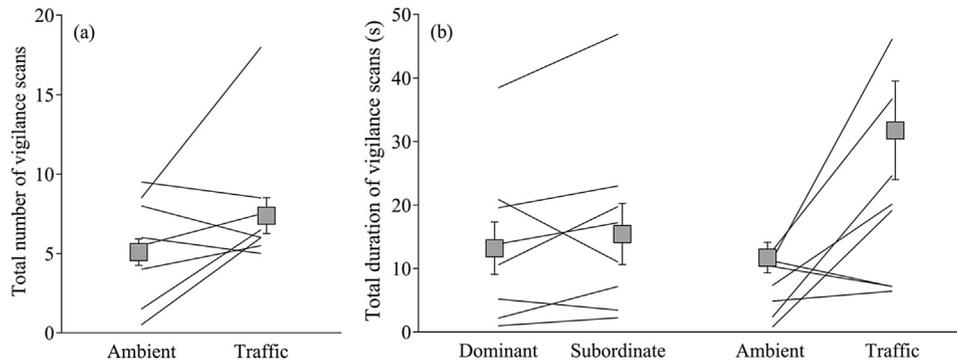


Fig. 2. Response – (a) total number of vigilance scans and (b) total duration of vigilance scans – of foraging dwarf mongooses to the playback of sentinel surveillance calls in different noise treatments ($N = 8$). Shown are the mean values for the same focal individuals in the two treatments (solid lines) and the overall treatment mean (solid squares) \pm SE.

different dominance class, peak frequencies of the fundamental were analyzed using a Wilcoxon signed-rank test.

3. 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 sound. 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-sound playback (Table 1).

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) ($N = 32$ trials, 8 groups). Significant fixed terms shown in bold; variance \pm SE reported for random terms.

	Fixed effect	Effect \pm SE	χ^2	P
(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		
(b) 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		

During the second playback experiment (noise-only testing), 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 sound (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 ($Z = 15$, $N = 8$, $P = 0.742$).

The SNR of surveillance calls was significantly affected by noise treatment (Table 2; Fig. 4).

Surveillance calls in ambient sound had a significantly greater SNR than calls in traffic noise (ambient vs approaching traffic; paired-samples t -test: $t_{15} = 8.59$, $P < 0.0001$, ambient vs peak traffic intensity; $t_{15} = -9.35$, $P < 0.0001$). Surveillance calls in approaching traffic noise also had a significantly greater SNR than calls in peak traffic intensity ($t_{15} = -4.93$, $P = 0.0002$). 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 \pm SE: 1044 \pm 38 Hz) were significantly lower in peak frequency of the fundamental than those of subordinates (1195 \pm 38 Hz; Wilcoxon signed-rank test: $W = 10$, $N = 16$, $P = 0.023$).

4. Discussion

Dwarf mongoose foragers exposed to playback of surveillance calls were more vigilant when also experiencing traffic-noise playback compared to ambient-sound playback, increasing both the total number and the total duration of vigilance scans. By engaging in more vigilance behaviour in noisy conditions, dwarf

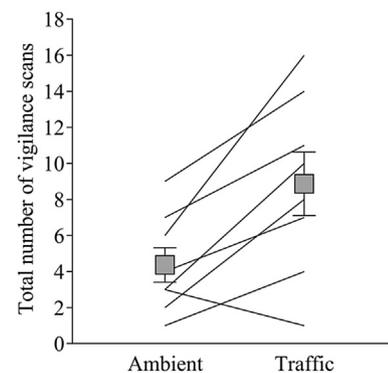


Fig. 3. Total number of vigilance scans by foraging dwarf mongooses ($N = 8$) in response to the playback of different noise treatments without mongoose vocalisations. Values for the same focal individuals in the two treatments are joined by solid lines and the overall treatment mean shown as solid squares \pm SE.

Table 2

Model output from LMM investigating SNR 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	P
Minimal model	(Intercept)	1.06 \pm 0.00		
	Noise treatment		73.02	<0.0001
	Noise			
	Ambient	0.00 \pm 0.00		
Dropped terms	Approaching traffic	-0.05 \pm 0.00		
	Peak traffic intensity	-0.06 \pm 0.00		
	Dominance status		0.30	0.583
Random terms	Noise:Dominance status		0.86	0.836
	Caller ID nested in group	0.00 \pm 0.01		

mongooses compromise time that would otherwise be available for foraging. Additional 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), traffic noise may negatively affect the key starvation–predation trade-off (Lima and Dill, 1990). Although increasing vigilance may be an adaptive method to 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-sound playback. This may have produced conservative results given the double-playback of ambient sound during the ambient-noise treatment; natural ambient-sound levels would be lower. Anthropogenic noise itself may be seen as threatening, causing individuals to respond as if under a true predatory threat (Rabin et al., 2006; Owens et al., 2012; Shannon et al., 2014). As a result, individuals may show inappropriate startle responses (Francis and Barber, 2013), or an unnecessary increase in vigilance. Alternatively, if anthropogenic noise 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 adaptively increasing use of the visual medium (Beale and Monaghan, 2004; Shannon et al., 2016). Several

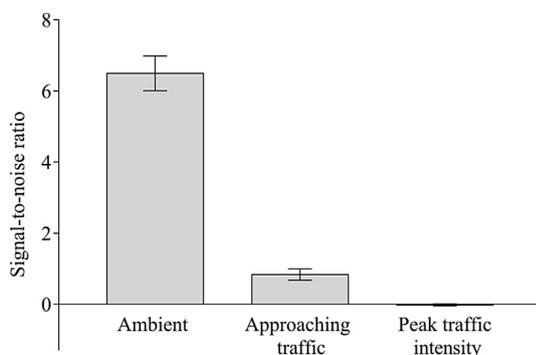


Fig. 4. The effect of noise treatment on the signal-to-noise ratio of surveillance calls ($N = 24$). Means and standard errors calculated from raw data are shown.

previous studies have reported an increase in vigilance in anthropogenic noise (Rabin et al., 2006; Larsen et al., 2014; Lynch et al., 2014; Meillère et al., 2015; Shannon et al., 2016). However, increased vigilance in direct response to noise does not provide a full explanation for the results from our first playback experiment, as only one aspect of vigilance behaviour (total number of scans) was affected.

One other possibility is that the observed increase in vigilance in the first playback experiment could be a consequence of partial masking; a lessened response to the surveillance calls themselves. Despite the increased vigilance behaviour during traffic-noise playback, foragers maintained the ability to discriminate acoustically between surveillance calls of sentinels of different dominance status, probably using differences in fundamental frequency (see also Kern et al., 2016). 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. Thus, surveillance calls could not have all 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. SNR suggests that surveillance calls were probably completely masked during periods of peak traffic intensity, although this cannot be confirmed without information about hearing sensitivity in this species. By contrast, although SNR was also reduced during vehicle approach, it was considerably greater than during peak traffic intensity and thus surveillance calls were likely to be audible during these periods. This would mean that receivers could potentially still detect sentinel presence and identity during traffic-noise playbacks, depending on the timing of surveillance calls. However, there may be implications for perceived call rate. That is, if surveillance calls were masked only during peak traffic intensity periods of playback, call rate would effectively have been reduced compared to during ambient-sound 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). 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 the noise does not represent an actual threat (Scholik and Yan, 2001; Popper et al., 2005; Wale et al., 2013a; Nedelec et al., 2015; Radford et al., 2016). 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.

Statement of authorship

JMK and ANR conceived and designed the study; JMK collected the data; JMK analyzed the data with advice from ANR; JMK wrote the first draft of the manuscript and ANR 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 S. Le Butt and K. Rogerson for invaluable assistance in the field. Three anonymous referees provided valuable comments on the manuscript. This work was supported by a University of Bristol Science Faculty Studentship.

References

- Barber, J.R., Crooks, K.R., Fristrup, K.M., 2010. The costs of chronic noise exposure for terrestrial organisms. *Trends Ecol. Evol.* 25, 180–189.
- Beale, C.M., Monaghan, P., 2004. Behavioural responses to human disturbance: a matter of choice? *Anim. Behav.* 68, 1065–1069.
- Bednekoff, P.A., 2015. Sentinel behavior: a review and prospectus. *Adv. Study Behav.* 47, 115–145.
- Bell, M.B.V., Radford, A.N., Rose, R., Wade, H.M., Ridley, A.R., 2009. The value of constant surveillance in a risky environment. *Proc. R. Soc. Lond. B – Biol. Sci.* 276, 2997–3005.
- Bell, M.B.V., Radford, A.N., Smith, R.A., Thompson, A.M., Ridley, A.R., 2010. Bargaining babblers: vocal negotiation of cooperative behaviour in a social bird. *Proc. R. Soc. Lond. B – Biol. Sci.* 277, 3223–3228.
- Bennett, V.J., Zurcher, A.A., 2013. When corridors collide: road-related disturbance in commuting bats. *J. Wildl. Manag.* 77, 93–101.
- Beynon, P., Rasa, O.A.E., 1989. Do dwarf mongooses have a language? Warning vocalizations transmit complex information. *South Afr. J. Sci.* 85, 447–450.
- Bradbury, J.W., Vehrencamp, S.L., 2011. *Principles of Acoustic Communication*. Sinauer Associates, Sunderland, MA.
- Brumm, H., Slabbekoorn, H., 2005. Acoustic communication in noise. *Adv. Study Behav.* 35, 151–209.
- Burger, J., Gochfeld, M., 1998. Effects of ecotourists on bird behaviour at Loxahatchee National Wildlife Refuge, Florida. *Environ. Conserv.* 25, 13–21.
- Chan, A.A.Y.H., Blumstein, D.T., 2011. Attention, noise, and implications for wildlife conservation and management. *Appl. Animal Behav. Sci.* 131, 1–7.
- Chan, A.A.Y.H., Giraldo-Perez, P., Smith, S., Blumstein, D.T., 2010. Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. *Biol. Lett.* 6, 458–461.
- Crawley, M.J., 2005. *Statistics: An Introduction Using R*. John Wiley & Sons, Ltd, Chichester, UK.
- Cresswell, W., 2008. Non-lethal effects of predation in birds. *IBIS* 150, 3–17.
- Dukas, R., 2004. Causes and consequences of limited attention. *Brain Behav. Evol.* 63, 197–210.
- Francis, C.D., Barber, J.R., 2013. A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Front. Ecol. Environ.* 11, 305–313.
- Francis, C.D., Ortega, C.P., Kennedy, R.I., Nylander, P.J., 2012. Are nest predators absent from noisy areas or unable to locate nests? *Ornithol. Monogr.* 74, 101–110.
- Grade, A.M., Sieving, K.E., 2016. When the birds go unheard: highway noise disrupts information transfer between bird species. *Biol. Lett.* 12, 20160113.
- Gross, K., Pasinelli, G., Kunc, H.P., 2010. Behavioral plasticity allows short-term adjustment to a novel environment. *Am. Nat.* 176, 456–464.
- Habib, L., Bayne, E.M., Boutin, S., 2007. Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. *J. Appl. Ecol.* 44, 176–184.
- Hildebrand, J.A., 2009. Anthropogenic and natural sources of ambient noise in the ocean. *Mar. Ecol. Prog. Ser.* 395, 5–20.
- Hollén, L.L., Radford, A.N., 2009. The development of alarm-call behaviour in mammals and birds. *Anim. Behav.* 78, 791–800.
- Hollén, L.L., Bell, M.B.V., Radford, A.N., 2008. Cooperative sentinel calling? Foragers gain increased biomass intake. *Curr. Biol.* 18, 576–579.
- Karp, D.S., Root, T.L., 2009. Sound the stressor: how hoatzins (*Opisthocomus hoazin*) react to ecotourist conversation. *Biodivers. Conserv.* 18, 3733–3742.
- Kern, J.M., Radford, A.N., 2013. Call of duty? Variation in use of the watchman's song by sentinel dwarf mongooses, *Helogale parvula*. *Anim. Behav.* 85, 967–975.
- Kern, J.M., Radford, A.N., 2014. Sentinel dwarf mongooses (*Helogale parvula*) exhibit flexible decision making in relation to predation risk. *Anim. Behav.* 98, 185–192.
- Kern, J.M., Sumner, S.S., Radford, A.N., 2016. Sentinel dominance status influences forager use of social information. *Behav. Ecol.* 27, 1053–1060.
- Kight, C.R., Swaddle, J.P., 2011. How and why environmental noise impacts animals: an integrative, mechanistic review. *Ecol. Lett.* 14, 1052–1061.
- Klump, G.M., 1996. Bird communication in the noisy world. In: Kroodsma, D.E., Miller, E.H. (Eds.), *Ecology and Evolution of Acoustic Communication in Birds*. Cornell University Press, New York, pp. 321–338.
- Larsen, M.J., Sherwen, S.L., Rault, J.L., 2014. Number of nearby visitors and noise level affect vigilance in captive koalas. *Appl. Animal Behav. Sci.* 154, 76–82.
- LaZerte, S.E., Otter, K.A., Slabbekoorn, H., 2015. Relative effects of ambient noise and habitat openness on signal transfer for chickadee vocalizations in rural and urban green-spaces. *Bioacoustics* 24, 233–252.
- Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68, 619–640.
- Lohr, B., Wright, T.F., Dooling, R.J., 2003. Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. *Anim. Behav.* 65, 763–777.
- Lowry, H., Lill, A., Wong, B., 2013. Behavioural responses of wildlife to urban environments. *Biol. Rev.* 88, 537–549.
- Lynch, E., Northrup, J.M., McKenna, M.F., Anderson, C.R., Angeloni, L., Wittemyer, G., 2014. Landscape and anthropogenic features influence the use of auditory vigilance by mule deer. *Behav. Ecol.* 26, 75–82.
- Magrath, R.D., Haff, T.M., Fallow, P.M., Radford, A.N., 2015. Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biol. Rev.* 90, 560–586.
- Mahjoub, G., Hinders, M.K., Swaddle, J.P., 2015. Using a “sonic net” to deter pest bird species: excluding European starlings from food sources by disrupting their acoustic communication. *Wildl. Soc. Bull.* 39, 326–333.
- Manser, M.B., 1999. Response of foraging group members to sentinel calls in suricates, *Suricata suricatta*. *Proc. R. Soc. Lond. B – Biol. Sci.* 266, 1013–1019.
- McIntyre, E., Leonard, M.L., Horn, A.G., 2014. Ambient noise and parental communication of predation risk in tree swallows, *Tachycineta bicolor*. *Anim. Behav.* 87, 85–89.
- Meillère, A., Brischoux, F., Angelier, F., 2015. Impact of chronic noise exposure on antipredator behavior: an experiment in breeding house sparrows. *Behav. Ecol.* 26, 569–577.
- Morley, E.L., Jones, G., Radford, A.N., 2014. The importance of invertebrates when considering the impacts of anthropogenic noise. *Proc. R. Soc. Ser. B* 281, 20132683.
- Naguib, M., van Oers, K., Braakhuis, A., Griffioen, M., de Goede, P., Waas, J.R., 2013. Noise annoys: effects of noise on breeding great tits depend on personality but not on noise characteristics. *Anim. Behav.* 85, 949–956.
- Nedelec, S.L., Simpson, S.D., Morley, E.L., Nedelec, B., Radford, A.N., 2015. Impacts of regular and random noise on the behaviour, growth and development of larval Atlantic cod (*Gadus morhua*). *Proc. R. Soc. Lond. B – Biol. Sci.* 282, 20151943.
- Owens, J.L., Stec, C.L., O'Hatnick, A., 2012. The effects of extended exposure to traffic noise on parid social and risk-taking behavior. *Behav. Process.* 91, 61–69.
- Patricelli, G.L., Blickley, J.L., 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. *Auk* 123, 639–649.
- Pinheiro, J., Bates, B., DebRoy, S., Sarkar, D., 2012. nlme: Fit and Compare Gaussian Linear and Nonlinear Mixed-Effects Models. R. Package Version 3.1-104. <http://CRAN.R-project.org/package=nlme>.
- Popper, A.N., Smith, M.E., Cott, P.A., Hanna, B.W., MacGillivray, A.O., Austin, M.E., Mann, D.A., 2005. Effects of exposure to seismic airgun use on hearing of three fish species. *J. Acoust. Soc. Am.* 117, 3958–3971.
- Purser, J., Radford, A.N., 2011. Acoustic noise induces attention shifts and reduces foraging performance in three-spined sticklebacks (*Gasterosteus aculeatus*). *PLoS One* 6, e17478.
- R Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rabin, L.A., Coss, R.G., Owings, D.H., 2006. The effects of wind turbines on anti-predator behavior in California ground squirrels (*Spermophilus beecheyi*). *Biol. Conserv.* 131, 410–420.
- Radford, A.N., Ridley, A.R., 2007. Individuals in foraging groups may use vocal cues when assessing their need for anti-predator vigilance. *Biol. Lett.* 3, 249–252.
- Radford, A.N., Hollén, L.L., Bell, M.B.V., 2009. The higher the better: sentinel height influences foraging success in a social bird. *Proc. R. Soc. B* 276, 2437–2442.
- Radford, A.N., Bell, M.B.V., Hollén, L.L., Ridley, A.R., 2011. Singing for your supper: sentinel calling by kleptoparasites can mitigate the cost to victims. *Evolution* 65, 900–906.
- Radford, A.N., Lèbre, L., Lecaillon, G., Nedelec, S.L., Simpson, S.D., 2016. Repeated exposure reduces the response to impulsive noise in European sea bass. *Glob. Change Biol.* (Online early).
- Rasa, O.A.E., 1977. The ethology and sociology of the dwarf mongoose (*Helogale undulata rufula*). *Z. Tierpsychol.* 43, 337–406.
- Rasa, O.A.E., 1986. Coordinated vigilance in dwarf mongoose family groups: the “watchman's song” hypothesis and the costs of guarding. *Ethology* 71, 340–344.
- Read, J., Jones, G., Radford, A.N., 2013. Fitness costs as well as benefits are important when considering responses to anthropogenic noise. *Behav. Ecol.* 25, 4–7.

- Recio, A., Linares, C., Banegas, J.R., Díaz, J., 2016. Road traffic noise effects on cardiovascular, respiratory, and metabolic health: an integrative model of biological mechanisms. *Environ. Res.* 146, 359–370.
- Rice, W.R., 1989. Analyzing tables of statistical tests. *Evolution* 43, 223–225.
- Rogerson, K.F., 2014. Effect of Anthropogenic Noise on Alarm-call Behaviour of Dwarf Mongooses (*Helogale Parvula*). Master of Science thesis. University of Bristol.
- Rolland, R.M., Parks, S.E., Hunt, K.E., Castellote, M., Corkeron, P.J., Nowacek, D.P., Wasser, S.K., Kraus, S.D., 2012. Evidence that ship noise increases stress in right whales. *Proc. R. Soc. Lond. B – Biol. Sci.* 279, 2363–2368.
- Rood, J.P., 1980. Mating relationships and breeding suppression in the dwarf mongoose. *Anim. Behav.* 28, 143–150.
- Scholik, A.R., Yan, H.Y., 2001. Effects of underwater noise on auditory sensitivity of a cyprinid fish. *Hear. Res.* 152, 17–24.
- Shannon, G., Angeloni, L.M., Wittemyer, G., Fristrup, K.M., Crooks, K.R., 2014. Road traffic noise modifies behaviour of a keystone species. *Anim. Behav.* 94, 135–141.
- Shannon, G., McKenna, M.F., Angeloni, L.M., Crooks, K.R., Fristrup, K.M., Brown, E., Warner, K.A., Nelson, M.D., White, C., Briggs, J., McFarland, S., 2015. A synthesis of two decades of research documenting the effects of noise on wildlife. *Biol. Rev.* (Online early).
- Shannon, G., Crooks, K.R., Wittemyer, G., Fristrup, K.M., Angeloni, L.M., 2016. Road noise causes earlier predator detection and flight response in a free-ranging mammal. *Behav. Ecol.* (Online early).
- Sharpe, L.L., Joustra, A.S., Cherry, M.I., 2010. The presence of an avian co-forager reduces vigilance in a cooperative mammal. *Biol. Lett.* 6, 475–477.
- Siemers, B.M., Schaub, A., 2011. Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. *Proc. R. Soc. Lond. B – Biol. Sci.* 278, 1646–1652.
- Simpson, S.D., Purser, J., Radford, A.N., 2015. Anthropogenic noise compromises anti-predator behaviour in European eels. *Glob. Change Biol.* 21, 586–593.
- Simpson, S.D., Radford, A.N., Nedelec, S.L., Ferrari, M.C., Chivers, D.P., McCormick, M.I., Meekan, M.G., 2016. Anthropogenic noise increases fish mortality by predation. *Nat. Commun.* 7, 10544.
- Slabbekoorn, H., Peet, M., 2003. Ecology: birds sing at a higher pitch in urban noise. *Nature* 424, 267.
- Slabbekoorn, H., Ripmeester, E.A., 2008. Birdsong and anthropogenic noise: implications and applications for conservation. *Mol. Ecol.* 17, 72–83.
- Townsend, S.W., Zöttl, M., Manser, M.B., 2011. All clear? Meerkats attend to contextual information in close calls to coordinate vigilance. *Behav. Ecol. Sociobiol.* 65, 1927–1934.
- Voellmy, I.K., Purser, J., Simpson, S.D., Radford, A.N., 2014. Increased noise levels have different impacts on the anti-predator behaviour of two sympatric fish species. *PLoS One* 9, e102946.
- Wale, M.A., Simpson, S.D., Radford, A.N., 2013a. Size-dependent physiological responses of shore crabs to single and repeated playback of ship noise. *Biol. Lett.* 9, 20121194.
- Wale, M.A., Simpson, S.D., Radford, A.N., 2013b. Noise negatively affects foraging and antipredator behaviour in shore crabs. *Anim. Behav.* 86, 111–118.
- Wood, W.E., Yezerinac, S.M., 2006. Song sparrow (*Melospiza melodia*) song varies with urban noise. *Auk* 123, 650–659.
- Wright, A.J., Soto, N.A., Baldwin, A.L., Bateson, M., Beale, C.M., Clark, C., Deak, T., Edwards, E.F., Fernández, A., Godinho, A., Hatch, L.T., 2007. Do marine mammals experience stress related to anthropogenic noise? *Int. J. Comp. Psychol.* 20, 250–273.