View metadata, citation and similar papers at core.ac.uk

brought to you by CORE

provided by Explore Bristol Research

This electronic thesis or dissertation has been downloaded from Explore Bristol Research, http://research-information.bristol.ac.uk

Author:
Richens, Emily P L

Title:
The effects of variation in anthropogenic noise on anti-predator behaviours in dwarf mongooses (Helogale parvula)

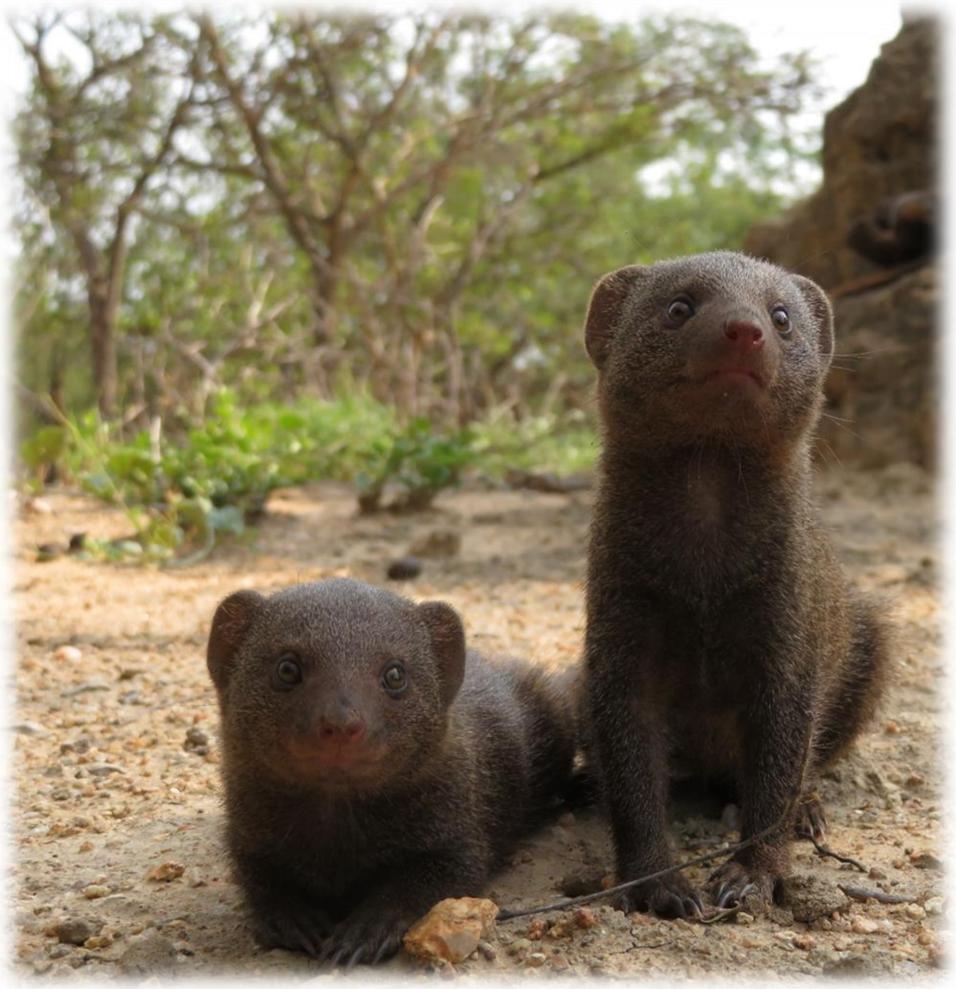
General rights
Access to the thesis is subject to the Creative Commons Attribution - NonCommercial-No Derivatives 4.0 International Public License.   A copy of this may be found at https://creativecommons.org/licenses/by-nc-nd/4.0/legalcode This license sets out your rights and the restrictions that apply to your access to the thesis so it is important you read this before proceeding.

Take down policy
Some pages of this thesis may have been removed for copyright restrictions prior to having it been deposited in Explore Bristol Research. However, if you have discovered material within the thesis that you consider to be unlawful e.g. breaches of copyright (either yours or that of a third party) or any other law, including but not limited to those relating to patent, trademark, confidentiality, data protection, obscenity, defamation, libel, then please contact collections-metadata@bristol.ac.uk and include the following information in your message:

- Your contact details
- Bibliographic details for the item, including a URL
- An outline nature of the complaint

Your claim will be investigated and, where appropriate, the item in question will be removed from public view as soon as possible.

The effects of variation in anthropogenic noise on anti-predator behaviours in dwarf mongooses (*Helogale parvula*)



Emily Richens

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Master of Science in the Faculty of Science.

July 2019

Biological Sciences   Word count: 18,052

Summary

Anthropogenic noise is an evolutionarily novel but now ubiquitous source of pollution and a growing environmental and health concern. Road networks are a major feature of our increasingly urbanised world and detrimental effects are commonly linked to collisions and habitat fragmentation. However, in the last decade it has become increasingly clear that traffic noise alone can have a negative impact on animals, although little is known about whether variation in noise characteristics affects behavioural responses. In this study, I use field-based playback experiments to investigate whether traffic noise affects anti-predator behaviours, specifically vigilance, in foraging dwarf mongooses (*Helogale parvula*). I consider whether variation in a temporal aspect (continuous vs intermittent) of noise results in different responses and, in a second experiment, I explore the group-level impacts when continuous traffic playback is conducted at sleeping burrows. First, I demonstrate that both variants of traffic noise result in significantly greater vigilance during playback than an ambient control, as measured by the frequency and duration of headscans and sentinel bouts (where individuals adopt a raised position to scan for danger). Individuals were also displaced more often from foraging patches in traffic noise compared to the ambient control, suggestive of a disturbance effect. No significant difference in vigilance measures was observed between intermittent and continuous traffic noise over the course of playback. However, sentinel bout frequency increased following continuous traffic noise, but a decrease was observed following intermittent traffic. This could be due to a greater cumulative noise exposure in the continuous treatment, resulting in longer-lasting effects. If noise poses a ‘threat’, then longer periods of noise may equate to a higher threat level and therefore an increase in sentinel activity after the ‘threat’ has passed could be an adaptive response to assess the surroundings for lingering danger. In my second experiment, I found that continuous traffic-noise playback resulted in a significant delay in group emergence and departure from burrows to forage, as well as an increase in grooming rates among groupmates. If such noise effects persisted, there could be detrimental consequences to condition and survival. Altogether, these findings show that even small differences in noise characteristics can have differing effects on behaviour, even after noise exposure ceases. Furthermore, they highlight the importance of considering different contexts when investigating the impacts of anthropogenic noise. Future work should incorporate multiple measures and conduct trials over longer periods in order to assess whether individuals are able to compensate for costs incurred by noise and to explore potential changes in tolerance.

For my Grandpa ~

> who once kept a mongoose in Malaya and would have loved to hear my tales about the dwarf mongooses, and whose cheeky sense of humour and adventurous spirit remain my source of inspiration.

Acknowledgements

First and foremost, I would like to extend my deepest gratitude to Andy Radford for his constant support and guidance from inception right to the final throes of thesis writing! Even when wading through exam marking or preparing numerous manuscripts for publication, he still managed to find the time to ensure I was on track and check my work with an exceptional eye for detail. I am so grateful for all your expertise and unwavering assurance even if things got wobbly and thank you for always having an open door. I may not say it enough but thank you so much for everything!

I could not write any further without offering my deepest gratitude to Julie Kern who had the vision and ambition to set up the Dwarf Mongoose Project in 2011. Without Julie this whole project or the amazing research that has subsequently spawned from it would not exist. I can't thank you enough Julie for your infectious enthusiasm, your passion for research and your effortless ability to radiate a positive and calming attitude. It has been such a privilege to share time with you in South Africa, and I wish you all the very best for the future and hope we will cross paths again!

I would like to thank Amy Morris-Drake for always being there, both in the field and back in Bristol. You have always shown an optimistic and considerate attitude which I admire, and I am grateful for your generosity and support throughout this Masters. My time in the field would not have been the same without Amy, Sophie Manson, Emily Grout, Josh Arbon and Jenny Linden with whom I shared countless memorable experiences, from the mud, sweat and tears of the Rhino Warrior Challenge to "Thursday's musical nights", not to mention the numerous braais and trips to Kruger for a 'Big Five' fix!

Last but certainly not least, I would like to thank my family for their wholehearted support of my various endeavours. My parents especially, for allowing me to undertake this Masters and for coming to visit me in the field – I never thought they would cross the world to visit me and it meant a lot to be able to introduce them to the 'gooses' and share my research with them. And thank you to my big sister and brother, who rarely question my enthusiasm for wildlife but who provide a constant source of criticism, love and inspiration.

Author's declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

Signed: Emily Richens

Date: 31st July 2019

Table of contents

Chapter 1: General Introduction

1.1 Human population growth and pollution

Our planet is becoming increasingly urbanised, globalised and polluted by humans. The global population is projected to increase from the current 7.5 billion people (https://www.census.gov/popclock/) to 9.8 billion by 2050 (United Nations, 2017). Coupled with this unprecedented growth rate is an inevitable increase in exploitation of natural resources; one-third to one-half of the global land surface area is already exploited by humans and we consume over half of all available freshwater (Crutzen, 2002). Modern industrial societies also use far more energy than earlier societies; a combination of greater demand and available knowledge and technologies (Steffen, Crutzen and Mcneill, 2007). The current geological epoch has thus been dubbed the “Anthropocene”; a term that acknowledges the scale and degree of impact our activities have had, and will continue to have, on our planet (Crutzen, 2002; Steffen, Crutzen and Mcneill, 2007, but see Zalasiewicz *et al.*, 2011; Lewis and Maslin, 2015 for discussion on defining this geological term).

Our widespread activities place increasing pressure on the natural balance of ecosystems (Lewis and Maslin, 2015). Tropical deforestation and urbanisation are two main drivers of habitat fragmentation and biodiversity loss (Pimm *et al.*, 1995; Steffen, Crutzen and Mcneill, 2007; Güneralp and Seto, 2013; Hughes, 2017). Our impacts extend to major changes to climatic composition and ocean chemistry as a consequence of pollutants generated by our activities. Nearly half of the human-induced rise in atmospheric CO_2 has occurred in the last 30 years (Steffen, Crutzen and Mcneill, 2007) and Earth’s oceans are suffering from acidification and rising temperatures as a result, causing imbalances to chemical processes, water currents and ecological communities (Doney *et al.*, 2009; Zalasiewicz *et al.*, 2011). Our activities also give rise to a variety of other pollutants which threaten wildlife.

The abundance and longevity of plastics pose a major threat to ecosystem health and this pollutant is of international concern (see UNEP, 2018). Plastics can contribute up to 95% of marine debris in some areas (Moore, 2008) and have even been found in remote regions including Easter Island (Thiel *et al.*, 2018), the Artic and in deep-sea sediments (Thompson *et al.*, 2009; Van Cauwenberghe *et al.*, 2013; Woodall *et al.*, 2014). Across taxa, direct impacts of plastic include entanglement and ingestion, both of which can cause fatalities from albatrosses to sea turtles and cetaceans (Moore, 2008; Wright, Thompson and Galloway, 2013; Vegter *et al.*, 2014; Thiel *et al.*, 2018). Additionally, the adsorption of metals to plastic litter (Holmes, Turner and Thompson, 2012; Brennecke *et al.*, 2016) and leaching of toxic contaminants (e.g. bisphenol A) can disrupt endocrine pathways (Cole *et al.*, 2011; Wright, Thompson and Galloway, 2013; Wang *et al.*, 2016).

Strongly associated with man-made landscapes, artificial light is a widespread pollutant (Davies *et al.*, 2014; also see www.lightpollutionmap.info). Many species have evolved circadian rhythms whereby behavioural and physiological processes may be synchronised with cyclic patterns of natural light (Davies *et al.*, 2014). Over 60% of all invertebrates and 30% of vertebrates are nocturnal (Hölker *et al.*, 2010) and may have specialised senses for foraging under low-light conditions; exposure to artificial light could impact biological processes. Artificial light at night (ALAN) can reduce sex pheromone production in nocturnal moths (Van Geffen *et al.,* 2015), disorientate sea turtle hatchlings (Tuxbury and Salmon, 2005; Dimitriadis *et al.*, 2018) and migrating birds (Poot *et al.*, 2008), and disrupt ecological services such as pollination (Knop *et al.*, 2017; Macgregor *et al.*, 2019). As light can vary in spectral composition, temporal pattern and intensity (by reflection or scattering), the effects of light pollution on wildlife can be complex.

Anthropogenic noise, although often underestimated, is now recognised as a global pollutant. Anthropogenic noise pervades almost all environments, yet this 'unwanted sound' has only received substantial research attention in recent decades (Radford, Morley and Jones, 2012; Brouček, 2014). Noise pollution is now incorporated in international reports and legislation, such as the European Environmental Agency's Environmental indicator report 2018[1], the World Health Organisation's Environmental Noise Guidelines[2], Convention on Migratory Species' Marine Noise Assessment Guidelines and the International Maritime Organisation's Marine Environmental Protection Committee (MEPC). The importance of understanding and mitigating the effects of anthropogenic noise – for the benefit of human health and wildlife – is increasingly recognised, and the complexity of noise and its impacts make research in this field even more critical.

---

[1] See Mourelatou, 2018

[2] See Eriksson, Pershagen and Nilsson, 2018

1.2 Anthropogenic noise

1.2.1 Sources of anthropogenic noise

Noise is a natural feature in nature, be it from biotic (e.g. animal vocalisations) or abiotic (e.g. waves breaking on a reef or beach) sources (Radle, 2007; Peng, Zhao and Liu, 2015; Dunlop, 2016). However, anthropogenic noise refers to sound originating from man-made sources, representing an evolutionarily novel noise source (Radford, Morley and Jones, 2012; Dooling and Popper, 2016a). On land, these sources include transportation networks, construction, military activities, resource extraction (e.g. quarrying and pile-driving) and wind turbines (Radford, Morley and Jones, 2012). Anthropogenic noise in the marine environment comes from shipping, recreational boating, ice-breaking, pile-driving (e.g. for construction of oil platforms, wind turbines), seismic exploration surveys (often using air guns) and military sonar (Nowacek *et al.*, 2007; Slabbekoorn *et al.*, 2010). Noise may be intentional (e.g. military sonar, seismic surveys, acoustic deterrents) or a by-product of activities (e.g. vehicle engines or vessel propulsion) (Shannon, McKenna, *et al.*, 2016).

Recreational activities are particularly concentrated around coastal and in-shore areas (Slabbekoorn *et al.*, 2010), whilst shipping and road networks are more ubiquitous sources in marine and terrestrial environments respectively (Forman and Alexander, 2002; Nowacek *et al.*, 2007; Barber, Crooks and Fristrup, 2010). Shipping alone has caused a noise increase of 12 dB in our oceans (Hildebrand, 2009), a 10–100 fold increase in ambient sound levels in many places (Tyack, 2008). Transportation networks are one of the most widespread terrestrial sources of anthropogenic noise and continue to grow; for instance, over 80% of land in the US is within 10.6 km of a road (Barber, Crooks and Fristrup, 2010). By its nature, noise extends far beyond its source and pervades even in our most ‘wild’ areas (Barber, Crooks and Fristrup, 2010; Buxton *et al.*, 2017).

1.2.2 Acoustic variation

The medium in which sound is transmitted will influence aspects of the acoustic signal between source and receiver (Shannon, McKenna, *et al.*, 2016). Sound travels up to five times faster and over greater distances in water than in air, due to lower attenuation (Nowacek *et al.*, 2007; Kight and Swaddle, 2011). Sound energy weakens (attenuates) by spherical spreading losses as waves travel away from the source. Additional attenuation may occur due to scattering and absorption, both of which are affected by the environment in which the sound-waves propagate (Marten and Marler, 1977; Radle, 2007). Shielding by objects with absorption properties, such as vegetation, can significantly reduce transmission (Warren *et al.*, 2006; Dooling and Popper, 2016a). The density of surrounding habitat affects attenuation of sound waves; Marten and Marler (1977) found that attenuation of acoustic energy was greatest in open habitats at ground-level, suggesting a possible effect of temperature-mediated air currents and turbulence. Above ground-level, attenuation generally increases with frequency and decreases with source height (Marten and Marler, 1977). Human-altered habitats such as cities affect transmission and propagation of sound waves; flat surfaces such as buildings can reflect acoustic energy. Reflection, or ricocheting, can cause sound to be scattered in multiple directions (other than that in which it was propagated), reduce attenuation and increase the likelihood or degree of interference (Warren *et al.,* 2006).

Sound can vary along spatial gradients. In general, low-frequency sounds will transmit greater distances (Marten and Marler, 1977) and attenuate less than higher frequencies (Hildebrand, 2009). Sound intensity also decreases by around 6 dB with a doubling of distance from point sources, but only 3 dB from line sources due to cylindrical rather than spherical spreading (Dooling and Popper, 2007, 2016a; Radle, 2007; Francis and Barber, 2013). Although, as mentioned above, a mix of factors will influence the quality and transmission of sound waves. Many transportation networks, such as roads or marine shipping routes, act as line sources due to the movement of numerous vehicles or vessels (Dooling and Popper, 2016a). Together with the fact that low frequencies tend to dominate sound profiles from road and marine traffic (Nemeth and Brumm, 2009; Radford, Morley and Jones, 2012), the radius of sound perception can be much greater compared to stationary point sources. By comparison, high-intensity military blasts or mining explosions are more localised.

Noise from human activities is evolutionarily novel and inherently highly variable. Importantly, noises from identical sources can vary in spectral, spatial and temporal characteristics (Clark *et al.*, 2009). Naturally produced noise from wind on water can share a broadband frequency range with vessel noise (around 500 Hz) but wind speed can alter the intensity by a range as much as 30 dB (Tyack, 2008; Dunlop, 2016). The type of source has an effect on the noise properties. For instance, pile-driving produces one of the highest noise levels, with intensities around 95 dB from a distance of 15 m (Dooling and Popper, 2016b), whilst noise from roads is typically around 65 dB at 10 m (Kern and Radford, 2016). However, traffic noise comes from a combination of motor engines and interactions of tyres with the road surface, both of which will vary with vehicle type and road conditions (Dooling and Popper, 2016a).

The timing and duration of sound is not always predictable or consistent. Noise from high-impact sources (such as pile-driving or airgun-arrays at sea) has a rapid onset and is often not sustained (Dooling and Popper, 2007). By contrast, noise from motorised or mechanical sources such as wind turbines can be near-continuous. On a broad scale, areas with a high density of human activities – such as cities – are hardly ever quiet due to numerous, complex noise sources (Gill *et al.*, 2015). Even places with lower human population density, such as global Protected Areas (PAs), do not escape noise altogether as roads border or bisect reserves and possible occurrence of illegal activities (Mcdonald *et al.*, 2009; Buxton *et al.*, 2017). Temporally unpredictable noise is likely to cause different effects or different levels of effects than exposure to consistent noise. Anthropogenic noise may overlap in time with biologically relevant sounds or key behaviours such as intraspecific communication during breeding, foraging or navigation. If noise of a given type has an effect on a species, the temporal ‘window’ between periods of noise exposure may be an important factor to consider (Francis, 2015). Considering the temporal aspects of sound occurrence and transmission is therefore important if we are to understand the implications (Halfwerk *et al.*, 2011).

1.3 Impacts of anthropogenic noise

Anthropogenic-noise sources worldwide have been expanding and diversifying since the Industrial Revolution, but it is only in recent years that there has been substantial research in this field (for reviews, see Williams *et al.*, 2015; Shannon, McKenna, *et al.*, 2016; Dutilleux, 2017). With continued human population growth and inevitable expansion of human-dominated environments, exposure to anthropogenic noise pollution is likely to increase, as noise-free habitats become scarcer. Therefore, a thorough understanding of both the consequences and mechanisms by which noise affects humans and animals alike is vital to ensure appropriate protection of vulnerable populations and maintain healthy, functional ecosystems.

Additional noise has substantial effects on human health, ranging from sleep disturbance (one in five people) to mental health disorders (WHO Regional Office for Europe, 2011). Around 100 million people in the EU are estimated to be exposed to levels of road noise above 55 dB, which is the indicator threshold for day, evening and night-time (L_{den}) at and above which these health consequences are reported (Mourelatou, 2018). According to a WHO report, an estimated one million healthy life years are lost in western Europe due to traffic noise alone (WHO Regional Office for Europe, 2011).

Due to the inherent variability in noise, the impacts can be equally as varied. These range from short-term, minor behavioural disturbances to permanent physiological changes (Blickley and Patricelli, 2010; Dooling and Popper, 2016b). Research in recent decades, considering exposure to noise both experimentally and *in situ*, has documented effects from an individual to population and community level across a range of non-human taxa. In some cases, positive changes have been observed, and we should acknowledge the often highly specific nature of exposure to noise and the potential consequences.

1.3.1 Community-level impacts

It can be challenging to isolate noise from other disturbances associated with a noise source, such as chemical pollution or habitat fragmentation (Barber, Crooks and Fristrup, 2010; Blickley and Patricelli, 2010; Morley, Jones and Radford, 2014). Additional complications arise when monitoring ecosystem-wide responses due to numerous confounding factors such as variation in habitat structure, community composition and behavioural patterns (e.g. migration and breeding seasons). Despite this, several studies have attempted to investigate how noise impacts ecological communities.

Anthropogenic noise alone has been linked to changes in community composition. An influential field experiment, taking advantage of noisy operating gas compressors and quiet inactive gas wells (which controlled for potential confounding factors such as physical infrastructure and associated disturbances), documented changes in the local avian community; species richness was over one-third lower at noisy sites (Francis, Ortega and Cruz, 2009). However, the responses observed were species-specific. Three species were found only at noisy sites and two indicator species – black-chinned hummingbirds (*Archilochus alexandri*) and house finches (*Carpodacus mexicanus*) – accounted for over 30% of all nests, compared to only 3% at control sites. These species may have benefited from a decline in their primary nest predator, the western scrub-jay (*Aphelocoma californica*). By contrast, mourning doves (*Zenaida macroura*) and black-headed grosbeaks (*Pheucticus melanocephalus*) showed a stronger association with control sites (Francis, Ortega and Cruz, 2009). Bayne, Habib and Boutin (2008) provide similar evidence for reduced bird abundance in habitat surrounding noisy gas well compressors.

Similarly, a phantom road created by McClure *et al.* (2013, 2016) experimentally demonstrated that abundance of songbirds was reduced by a quarter in habitats differing only in the addition of road noise (via a linear arrangement of loudspeakers in an otherwise road-free area). Again, the effects were species-specific, with two species (cedar waxwings, *Bombycilla cedrorum* and yellow warblers, *Setophaga petechia*) showing complete avoidance of the noise, whilst Cassin's finches (*Haemorhous cassinii*) showed a greater tolerance for noise (McClure *et al.*, 2013). Furthermore, effects on abundance and body condition were more pronounced in younger individuals (Ware *et al.*, 2015; McClure *et al.*, 2016). Such changes could not only reduce the fitness (ability to survive and reproduce) of individuals present but potentially shift the age-structure of a population.

Critical ecological services can be altered as a consequence of anthropogenic noise affecting community composition. In the gas-well study, a greater abundance of black-chinned hummingbirds at noisy sites resulted in a five-fold increase in pollination rate of scarlet gilia (*Ipomopsis aggregata*) flowers (Francis *et al.*, 2012). Additionally, *Pinus edulis* seed predation and dispersal were differentially affected by the higher levels of predation by *Peromyscus* (deer) mice at noisy sites, whilst the western scrub jay, a key seed disperser, completely avoided noisy areas (Francis *et al.*, 2012). These studies serve to highlight the complexity of species interactions and how noise alone can initiate ecosystem-wide changes which may, ultimately, begin at an individual level.

1.3.2 Individual-level impacts: non-behavioural

Though the responses may be more cryptic than observable behaviours, noise is considered a stressor and has been shown to impact on auditory and neuroendocrine systems, with growing evidence for effects on fitness (Kight and Swaddle, 2011; Brouček, 2014). Exposure to loud noise can cause temporary or permanent hearing damage. Hearing in vertebrates (and some invertebrates) relies on detection of pressure waves via specialised structures in tympanal ears (e.g. sensory hair cells) (Dooling and Popper, 2007; Morley, Jones and Radford, 2014). Direct damage to these hearing organs can result in a temporary threshold shift (TTS) or permanent threshold shift (PTS) (Clark, 1991; Nowacek *et al.*, 2007). PTS is mostly likely to occur in close proximity to high-intensity noise, above the hearing threshold of a given individual. TTS and noise intensity show a linear relationship in fish and terrestrial vertebrates (Smith, 2004a, 2004b) but the onset of TTS may occur at lower amplitudes when animals are exposed to frequencies to which they are most sensitive (Nowacek *et al.*, 2007).

Frequency of noise is important; generally, higher frequencies will induce higher TTS than low frequencies of the same level and duration (Smith, 2004b; Finneran, 2015). However, hearing abilities differ substantially between species; for instance, European eels (*Anguilla anguilla*) can detect infrasound and bottlenose dolphins (*Tursiops truncates*) have highly evolved ultrasonic vocalisations far outside our own hearing range (Slabbekoorn *et al.*, 2010). Fin whales (*Balaenoptera physalus*) can hear across a wide frequency range, from 0.01 kHz to 10 kHz, whilst fathead minnows (*Pimephales promelas*) a hearing specialist, are most sensitive to frequencies between 0.8 kHz and 2 kHz (Peng, Zhao and Liu, 2015). Goldfish (*Carassius auratus*), another hearing specialist, showed a significant threshold shift when exposed to white noise, whilst tilapia (*Oreochromis niloticus*), a cichlid fish with poorer hearing, showed little change in auditory threshold (Smith, 2004a, 2004b). Toadfish (*Halobatrachus didactylus*) have a low-frequency hearing range; ship-noise playback caused a drop in auditory sensitivity which was more marked at the lowest frequencies (Vasconcelos, Amorim and Ladich, 2007). Over time, an asymptotic threshold shift may be reached (Smith, 2004b), but high noise levels or prolonged periods of exposure may also affect recovery (Dooling and Popper, 2016a). Hearing impairment can have fitness consequences for a range of species that use sound; for example, where sound is used as a detection cue to locate predators or prey, or as a primary mode of communication about potential threats (Slabbekoorn *et al.*, 2010).

Anthropogenic noise is also regarded as a stressor; an often unpredictable, harmful stimulus that elicits a stress response (Wright *et al.*, 2007). This refers to the release of glucocorticoid (GC) hormones (e.g. cortisol, corticosterone; CORT) which can trigger an adaptive behavioural response – a re-distribution of metabolic resources to optimise energy availability for flight in relation to an immediate threat, such as predation (Sapolsky, Romero and Munck, 2000). Extraneous noise presents an additional source of stress in increasingly anthropogenic landscapes and has been found to increase GC levels in a number of taxa including birds (Blickley *et al.*, 2012; Davies, Haddad and Ouyang, 2017), fish (Anderson *et al.*, 2011) and whales (Rolland *et al.*, 2012). However, contradictory evidence has also been demonstrated (e.g. Crino *et al.*, 2013; Potvin and MacDougall-Shackleton, 2015; Nedelec *et al.*, 2016; Guralnick *et al.*, 2018).

Importantly, the duration of and previous exposure to noise (especially at critical stages of development) may be associated with adaptation or changes in response over time (Nedelec *et al.*, 2016; Parks *et al.*, 2018). For example, frogs that hatched from eggs originating from noisy ponds showed no difference in CORT levels in traffic-noise or control treatments, contrary to conspecifics from quiet sites (Parks *et al.*, 2018). If individuals experience noise during plastic stages of development, they may be better equipped – physiologically – to tolerate noise later in life (Kight and Swaddle, 2011). Additionally, responses may be condition-dependent, with individuals in poorer condition more susceptible to noise than members of the population in better condition (Purser *et al.*, 2016). Sustained elevation of baseline GC levels may be detrimental to fitness (Kight and Swaddle, 2011; Creel *et al.*, 2013). For instance, frogs had a lower likelihood of expressing antimicrobial peptides following traffic-noise playback compared to a quiet control, potentially increasing their risk of disease (Parks *et al.*, 2018). Adverse effects on the immune response have also been shown experimentally in chickens (Jankowski *et al.*, 2010).

Geographical and individual differences in responses to noise could ultimately have downstream effects on a population. ‘Noise tolerant’ western bluebirds (*Sialia mexicana*) experienced lower hatching success at nestboxes near noisy gas wells compared to control sites, yet other species studied did not appear to be affected in this way (Guralnick *et al.*, 2018). Similarly, Halfwerk *et al.* (2011) reported smaller clutches in great tits (*Parus major*) closer to roads. This highlights a common misunderstanding that the presence of a species in noisy habitats suggests it is unaffected by noise. Although noise may not have been the sole contributing factor in Halfwerk *et al*.'s study, it provides reasonable evidence that noise can have cryptic effects. A traffic-noise playback experiment reported a reduction in telomere length in house sparrows (*Passer domesticus*) despite corticosterone levels, growth and fledging success remaining unaffected (Meillère *et al.*, 2015).

1.3.3 Individual-level impacts: behavioural

Behavioural responses to anthropogenic noise have been widely studied, with efforts to quantify changes in acoustic communication, foraging and anti-predator behaviours most prevalent in the literature.

1.3.3.1 Acoustic communication

A large proportion of literature (over one-fifth) investigating anthropogenic noise impacts on animal behaviour has focused on acoustic communication (Shannon, McKenna, *et al.*, 2016). For many animals, vocalisations play a vital role in daily activities including foraging (Luo, Siemers and Koselj, 2015), detection of prey/predators (Clark *et al.*, 2009), territory defence (McMullen, Schmidt and Kunc, 2014), mate choice (Swaddle and Page, 2007; Schmidt, Morrison and Kunc, 2014; de Jong *et al.*, 2018) and parental care (Schroeder *et al.*, 2012; Lucass, Eens and Müller, 2016). Anthropogenic noise presents an evolutionarily novel challenge and animals are required to adapt or compensate, otherwise they may suffer the costs of degraded information networks (Barber, Crooks and Fristrup, 2010).

Urban areas can be around 9 dB louder than rural locations (Hu and Cardoso, 2010; Potvin, Parris and Mulder, 2011) reducing the active space (the maximum distance over which a conspecific can detect an acoustic signal; Slabbekoorn *et al.*, 2010) over which animals can communicate (Potvin, Mulder and Parris, 2014). Birds have been extensively studied in the context of noise impacts on song (Slabbekoorn and den Boer-Visser, 2006; Pohl *et al.*, 2012) with increases in amplitude (the "Lombard effect") widely reported. For example, Brumm and Todt (2002) exposed male nightingales (*Luscinia megarhynchos*) to experimental white (broadband) noise at 55–75 dB (in 5 dB intervals). Birds increased song amplitude in all noise treatments compared to an ambient control. Although only four birds were analysed in this experiment, a subsequent study on wild nightingales corroborated the results; Brumm

(2004) reported that male nightingales sang at average levels of 77 and 91 dB (A) on the quietest and noisiest territories (40 and 64 dB) respectively. Eastern bluebirds (*Sialia sialis*) also increased the amplitude of their songs in high levels of ambient noise (Kight and Swaddle, 2015) and great tits increased alarm-call amplitude in traffic-noise playback (Templeton, Zollinger and Brumm, 2016). Although these changes appear to be simple adaptations to counteract a reduction in active space, less visible impacts such as chromosomal changes (Meillère *et al.*, 2015) and associated energy costs of altering vocal communication may reduce fitness (Read, Jones and Radford, 2014)

Spectral characteristics of noise, such as frequency, can also impact significantly on the ability to communicate. Masking is one such mechanism by which noise can affect acoustic communication in animals (Barber, Crooks and Fristrup, 2010; Rosa and Koper, 2018) increasing the threshold for signal detection or discrimination (Clark *et al.*, 2009). In some instances, individuals may be able to compensate by altering the frequency of their vocalisations (Francis, Ortega and Cruz, 2011b). Typically, an upward shift is observed as urban noise overlaps most with lower frequencies (Hu and Cardoso, 2010; Francis and Barber, 2013); traffic noise, for instance, is usually around 3 kHz (Radford, Morley and Jones, 2012). Such frequency shifts have been reported in silvereyes (*Zosterops lateralis*) (Potvin, Mulder and Parris, 2014), great tits (Slabbekoorn and den Boer-Visser, 2006) and white-crowned sparrows (*Zonotrichia leucophrys nuttalli*) (Luther and Derryberry, 2012). By recording vocalisations of 12 different bird species at urban and non-urban sites, Hu and Cardoso (2010) found that the average minimum frequency was higher for all species in the urban populations. Similarly, eight of nine tropical passerines studied by Tolentino, Baesse and Melo (2018) showed an increase in dominant frequency of vocalisations in forest fragments closer to urban sites. Although this fits with other studies, it also highlights the fact that not all species respond in the same way. A Principal Component Analysis revealed that male eastern bluebirds increased song frequency in high ambient noise levels. Since low-pitched calls may be an indicator of larger body size (or maturity; Nemeth *et al.*, 2012) and thus an attractive signal for females (Laiolo, 2010), considering morphological measures in such studies is important. Alteration of call characteristics could directly impact reproductive success (Read, Jones and Radford, 2014; Dutilleux, 2017). At the community level, acoustic masking may in turn affect diversity and abundance of species in noisy areas (Katti and Warren, 2004).

Alteration of vocalisations in response to noise in the marine environment has largely focused on cetaceans, since long-distance communication is both possible (due to lower attenuation) and important for many species (Slabbekoorn *et al.*, 2010). Shipping alone has caused a 10–100 fold increase in ambient noise levels within the 20–200 Hz frequency band, overlapping with the frequencies used by many baleen whales for communication (Tyack, 2008). North Atlantic right whales (*Eubalaena glacialis*) showed a short-term response to increased background noise (overlapping with their call frequency) by raising their call amplitude (Parks *et al.*, 2011). Similarly, killer whales (*Orcinus orca*) increased the amplitude of their calls by 1 dB for every 1 dB rise in background noise due to shipping (Holt *et al.*, 2009). An observational study on 37 humpback whales (*Megaptera novaeanglia*) found that groups responded to increased wind noise by using more non-vocal behaviours (e.g. 'surface-generated' sounds from breeching and pectoral slaps) and increasing vocal amplitude by 1.5 dB for every 1 dB increase in wind-generated noise. Contrary to predictions, the whales did not further increase their vocal or non-vocal behaviours in response to passing vessels. The authors highlight that detection thresholds are unknown for humpback whales and that changes reported here are short-term responses (Dunlop, 2016). Combining empirical data with modelling approaches (e.g. Clark *et al.*, 2009) may allow more reliable conclusions to be formed that can be generalised and applied to numerous species. The functional significance of acoustic signals and hearing thresholds are unknown for many species, so being able to make accurate assessments and predictions about the long-term consequences of noise exposure for populations at risk are vital.

1.3.3.2 Foraging

Anthropogenic noise can affect foraging behaviours in multiple ways. Since foraging is an essential behaviour in most species, impairment to foraging efficiency or success can ultimately impact fitness (Francis and Barber, 2013; Luo, Siemers and Koselj, 2015). Noise can incur direct impacts such as reducing food detection or indirectly through re-allocation of effort (time and energy) for vigilance or other anti-predator behaviours (Francis and Barber, 2013).

In the past decade, several laboratory studies have strived to assess how anthropogenic noise impacts foraging behaviours. Using a simple choice experiment, Schaub, Ostwald and Siemers (2008) showed that greater mouse-eared bats (*Myotis myotis*) reduced their foraging effort in noisy areas compared to quieter locations. In a later study, playback of computer-generated 'traffic' noise (corresponding to noise levels 7.5 m from a highway) reduced successful prey capture by nearly 50% and search time increased fivefold compared to a silent control (Siemers and Schaub, 2011). Even in a lower level of noise relating to a distance of 50 m from a highway, search time was significantly greater (150%) than the control (Siemers and Schaub, 2011). The authors suggested masking as the likely mechanism, although only seven bats were tested. Daubenton's bats (*Myotis daubentonii*) also showed a decline in foraging success when exposed to traffic-noise playback with overlapping or non-overlapping spectral elements (Luo, Siemers and Koselj, 2015).

Field studies on various taxa have supported some of these earlier findings, namely that anthropogenic noise disturbs foraging behaviour. For example, great tits increased vigilance at the expense of lost foraging time during periods of passing aircraft, almost doubling their level of vigilance during peak noise levels (Klett-Mingo, Pavón and Gil, 2016). There are fewer marine studies focused on foraging compared to other behavioural aspects of marine organisms. However, using acoustic data from remote tags on nine humpback whales, Blair *et al.* (2016) investigated the impact of ship noise on sub-surface foraging behaviours. As the level of ship noise increased, whales showed slower descent rates (by 14.5%) and fewer bottom-feeding side-roll behaviours, typical of humpbacks in the study area. This suggests a disturbance effect of noise leading to a possible decrease in foraging efficiency, although compensatory behaviours were not observable. It does, however, demonstrate that we should consider temporal variation in animal behaviours and noise exposure as impacts could substantially differ.

1.3.3.3 Anti-predator behaviours

Predation is a strong evolutionary force and anti-predator behaviours are therefore commonplace in the natural world. Anti-predator behaviour can be defined as any proactive or reactive action performed in response to a predation risk (Gaynor *et al.*, 2019). Typical responses to immediate threats include fleeing to safety and vigilance – appropriate responses to avoid attack and assess level of risk, respectively (Lima and Dill, 1990). Vigilance may precede flight behaviour. Anthropogenic noise can elicit responses analogous to the presence of a predator; for example, Daubenton's bats will avoid noise (Luo, Siemers and Koselj, 2015). Despite this, empirical research isolating the effects of anthropogenic *noise* on anti-predator behaviours is scarce (Templeton, Zollinger and Brumm, 2016).

Detection of alarm calls, conspecific or heterospecific, plays an important role in initiating anti-predator behaviours, such as a fleeing or heightened vigilance response (Francis and Barber, 2013). Alarm calls may encode information relating to the urgency or type of threat (Ficken, 1990); for instance, predator-specific calls in dwarf mongooses (*Helogale parvula*) (Collier *et al.*, 2017) and Mexican chickadees (*Parus sclateri*) (Ficken, 1990). Therefore, detection and discrimination of these calls can directly affect likelihood of survival. Alternatively, information regarding predation risks can be attained from sympatric species that may share similar predators, by eavesdropping on heterospecific alarm calls (e.g. Sharpe, Joustra and Cherry, 2010; Huang, Sieving and Mary, 2012). For instance, the bright green Madagascan giant gecko (*Phelsuma kochi*) darkens in colour in response to alarm calls of the sympatric paradise flycatcher (*Terpsiphone mutata*). The authors suggest this is likely an adaptive, short-term anti-predator response; darker colouration may reduce conspicuousness, although this may partially be stress-induced (Ito, Ikeuchi and Mori, 2014).

There are two main ways in which noise can impact on survival via anti-predator behaviour: by eliciting unnecessary anti-predator behaviours (due to a perceived increased risk), thus increasing energetic costs; or by reducing responsiveness to real threats. For instance, noise delays startle responses to predators (e.g. Simpson, Purser and Radford, 2015; Petrelli *et al.*, 2017). Since alarm calls act as an early warning system, a lack of response may increase the likelihood of attack by a predator and thus directly impact on survival (Zhou, Radford and Magrath, 2019). Wild great tits failed to respond to conspecific alarm calls in traffic noise (Templeton, Zollinger and Brumm, 2016) and wild dwarf mongooses were less likely to flee in response to tree squirrel alarm calls during traffic-noise playback than a control treatment (Morris-Drake *et al.*, 2017). A field study demonstrated a lack of response in northern cardinals (*Cardinalis cardinalis*) to playback of tufted titmice (*Baeolophus bicolor*) alarm calls in noisy areas (Grade and Sieving, 2016). Disruption of these information networks could therefore potentially impact the wider community, and research should not focus on one species but interspecific interactions.

1.3.3.3.1 Risk-perception

Appropriate anti-predator behaviour depends on accurate risk assessment. The ‘risk-allocation hypothesis’ (Lima and Bednekoff, 1999a) posits that the optimal allocation of effort in anti-predator behaviours should relate to the perceived level of risk, as well as the frequency and duration of the threat; individuals should allocate more time to anti-predator behaviours in frequent and prolonged high-risk situations. However, beyond a threshold, investment in anti-predator behaviours diminishes to reduce excessive energy loss (Sirot, 2010).

Noise can influence an individual’s ability to assess and respond to risks appropriately. Noise may affect anti-predator behaviours through being perceived as a direct threat, analogous to a predator (Shannon, McKenna, *et al.*, 2016). This is explained by the ‘increased threat hypothesis’ (Owens, Stec and O’Hatnick, 2012) which builds on the ‘risk-disturbance hypothesis’ (Frid and Dill, 2002); both state that anthropogenic noise can result in increased reactive anti-predator behaviours. Support for these hypotheses come from field and laboratory-based studies. For example, black-tailed prairie dogs (*Cynomys ludovicianus*) showed heightened vigilance and flee responses at greater distances to human observers during playback of road noise compared to a no-noise control; this indicates increased sensitisation rather than habituation (Shannon *et al.*, 2016). However, it would be interesting to see if varying the frequency with which prairie dogs are exposed to noise or human observers alters the results.

An alternative theory states that anthropogenic noise can distract individuals, causing attention shifts away from behaviours such as foraging. The ‘distracted prey hypothesis’ (Chan *et al.*, 2010) suggests that a noise stimulus can prevent or delay appropriate responses to approaching threats. European eels (*Anguilla anguilla*) suffered increased risk of predation as a result of distraction by playback of ship noise (Simpson, Purser and Radford, 2015). A study by Chan *et al.* (2010) revealed that hermit crabs (*Coenobita clypeatus*) delayed their response to a simulated predator approach (human or ‘looming object’) in boat-motor playback compared to silent controls. Furthermore, the flight initiation distance (the distance at which the crab seeks shelter in its shell) significantly decreased and to a greater magnitude with the addition of flashing lights to the noise stimulus. A set of experiments by Simpson *et al.* (2016) provides simultaneous support for this hypothesis as well as evidence that responses can affect predator–prey dynamics, by favouring one or the other. Passing motorboats significantly reduced the likelihood of a startle response in Ambon damselfish (*Pomacentrus amboinensis*) to a simulated predator, and the responses were 22% slower, allowing the 'predator' to get much closer. Dusky dottybacks (*Pseudochromis fuscus*) made more successful prey captures in boat-noise playback compared to ambient-sound controls. Complementary laboratory-based and open-water experiments showed that significantly more damselfish were depredated during playback of boat noise and passing motorboats respectively, compared to control treatments in each case (Simpson *et al.*, 2016).

Far from just visual assessment of predation risk, cues from other modalities may indicate presence of predators (Lima and Dill, 1990). Noise has been shown to affect assessment of olfactory cues too; in wild dwarf mongooses, for instance, detection and interaction with predator faeces were lessened by playback of traffic noise. Furthermore, vigilance was lower in noise than expected following detection of a predator cue, potentially increasing likelihood of a predator attack (Morris-Drake, Kern and Radford, 2016). Shifts to a different sensory modality may compensate for interference by noise (Partan, 2017).

1.3.3.3.2 Foraging–vigilance trade-offs

Time and energy are finite; individuals must invest in essential behaviours appropriately. Foraging and vigilance are both time-consuming and are often mutually exclusive, resulting in a key behavioural trade-off (Lima and Bednekoff, 1999a). For example, wild elk (*Cervus elaphus*) significantly increased vigilance when wolves (*Canis lupus*) were in the vicinity (Creel *et al.*, 2008). This trade-off applies to the majority of species, including predators (e.g. Pangle and Holekamp, 2010). As noise can affect risk-perception, either as a threat or by distracting attention, this puts greater pressure on an individual exposed to noise to allocate resources optimally. An increased predation risk requires greater effort be put toward anti-predator behaviours. However, social circumstances such as group size and interspecific information-gathering also influence investment in vigilance (Lima and Bednekoff, 1999b; Sharpe, Joustra and Cherry, 2010; Owens, Stec and O'Hatnick, 2012). Additionally, a common assumption of many studies is that an animal with its head down has near-zero ability to detect predators (Rasa, 1989; Fortin *et al.*, 2004). However, partial (if obscured) views or cross-modal cues will likely play a role in an individual's foraging–vigilance trade-off, especially in species with laterally placed eyes and thus wide fields of vision (Lima and

Bednekoff, 1999b). Furthermore, animals often do not receive perfect information, so how an animal optimises this trade-off will vary between contexts.

Although laboratory studies can be restrictive in the ecological relevance of their conclusions, they allow isolation of the effects of noise on foraging–vigilance trade-offs. Ship-noise playback disrupted foraging in shore crabs (*Carcinus maenas*) and increased time taken for crabs to reach shelter (Wale, Simpson and Radford, 2013). Using a simple choice experiment with two noise treatments (at 70 dB and 50 dB SPLA), Evans, Dall and Kight (2018) found that zebra finches (*Taeniopygia guttata*) allocated more time to vigilance than foraging when under the noisier condition. In a subsequent trial vigilance was unchanged, but time spent foraging was greater. This suggests some compensatory behaviour under repeated exposure to noise.

A number of studies have employed naturally occurring anthropogenic noise or experimental noise to investigate effects on this trade-off. At sites with noisy wind turbines, California ground squirrels (*Spermophilus beecheyi*) showed increased alertness, despite a lower predator abundance, compared to control sites (Rabin, Coss and Owings, 2006). Wild-caught chaffinches (*Fringilla coelebs*) foraging in white-noise treatments increased their vigilance by increasing the number (but not the duration) of head-up scans, with a consequential decrease in food intake (Quinn *et al.*, 2006). If compensation for lost foraging time cannot be achieved, energy losses may threaten survival. However, further empirical work on wild populations would help substantiate these findings and investigate whether individuals alter food choice or handling, as well as noise-induced changes in predator behaviours which may offset the negative impacts on prey species, via ‘predator-release’ (Rytwinski and Fahrig, 2013). Additionally, there is little work on the long-term impacts of these responses; whether and how animals compensate is vital to understanding how anthropogenic noise impacts on populations.

1.4 Variation in noise: Impacts

Anthropogenic noise has high spatial and temporal variation (Dooling and Popper, 2016a). As discussed above, the impacts of spectral and amplitude differences have been fairly widely researched in relation to behavioural parameters and several studies looking at temporal variation have focused on physiological measures (e.g. Wysocki, Dittami and Ladich, 2006; Nichols, Anderson and Širović, 2015) or physical damage (e.g. Kastelein *et al.*, 2014, 2015). But to my knowledge, few empirical studies have investigated the effects of temporal characteristics on foraging or vigilance behaviours specifically.

Some studies have used noise from different sources to examine the effects of temporal variation, despite the inherent variability in numerous aspects and thus not just temporal structure. Blickley, Blackwood and Patricelli (2012) used playback of recorded road noise and gas-drilling as exemplars of short-term and chronic noise. Abundance of male greater sage grouse (*Centrocercus urophasianus*) at leks was nearly three-quarters lower at road-noise sites and nearly one-third lower at drilling noise sites compared to paired controls, but this cannot be wholly attributed to temporal variation. Additionally, female abundance was reportedly highly variable and is certain to influence male behaviour, yet this was not implicated in the conclusions. Age and physical condition are likely to impact on such behaviours (Blickley, Blackwood and Patricelli, 2012; Purser *et al.*, 2016) and must be considered in studies aiming to investigate impacts of noise variation. The presence of roads in the study area may have contributed to the observed differences, as birds may associate these with a direct threat and therefore learnt to avoid road noise.

Neo *et al.* (2014) exposed European seabass (*Dicentrarchus labrax*) to artificially generated intermittent and continuous noise at different amplitudes. Groups became more cohesive and swimming depth increased during noise exposure, compared to baseline measures. Initial startle responses (sudden changes in swimming speed and direction) were similar in both noise types. However, the recovery rate from this change in depth during exposure was significantly longer following intermittent noise compared to continuous noise. Behavioural and physiological baseline changes may occur in relation to time of day; diurnal seabass swim significantly slower and nearer the surface at night (Neo *et al.*, 2018). When exposed to artificial noise, increases from baseline swimming speed and depth were more significant at night (Neo *et al.*, 2018). This highlights how understanding the behavioural patterns of a species, even on a local scale, has an important influence on our assessment of the magnitude and long-term impacts of noise exposure.

Beyond the obvious variations in noise itself, differences in the time intervals between periods of noise exposure can have more lasting effects. Masini, Day and Campeau (2008) demonstrated how longer or shorter intervals between periods of noise exposure (spaced vs massed) had differing effects on long-term habituation in laboratory rats. Rats receiving noise with either massed or spaced intervals showed stress hormone levels comparable to no-noise controls after six exposure periods. However, on noise re-exposure 48 hours after the six days, rats in the massed noise treatment had CORT levels comparable to individuals receiving noise treatment for the first time, whilst rats from the spaced group retained lower levels suggesting longer-term habituation. This study shows that aside from noise type or total duration of exposure, the duration of no-noise intervals can have significant impacts on physiological measures, with potentially negative implications for long-term fitness.

Although laboratory studies allow isolation of noise effects on physiological measures, a contained environment limits the full range of behavioural responses (Popper and Hastings, 2009). Empirical field studies using consistent methods with wild animals and ecologically relevant noise sources are needed to investigate key behaviours affected by noise varying in temporal characteristics. Quiet intervals between periods of noise exposure is also important to consider in terms of immediate responses and recovery rates (see Finneran, 2015).

1.5 Dwarf mongooses

1.5.1 Study species

The dwarf mongoose is a social carnivore, the smallest species in the family Herpestidae (250–350 g; Rood, 1986, 1987). Widespread across sub-Saharan Africa, these mammals inhabit open woodland and savannah habitats from north-east South Africa to Ethiopia (Sharpe, Kern and Linh San, 2015).

Dwarf mongooses live in stable, mixed-sex groups numbering up to 30 individuals (mean group size = 9; Rood, 1990; Creel and Waser, 1994) consisting of a dominant breeding pair, subordinate helpers and pups (Rasa, 1977; Schneider and Kappeler, 2014). Home ranges incorporate numerous refuges – often termite mounds, which are used as den sites – and overlap with neighbouring groups, especially where population density may be high (Hiscocks and Perrin, 1991; Schneider and Kappeler, 2014). Population densities are likely influenced by habitat quality, including availability of food and refuges, and predation pressures; Rood (1987) noted densities of up to 31 individuals/km^2 at the onset of the breeding season. Groups show cooperative defence of their territories by regular scent-marking using cheek and anal glands (Rasa, 1977). Physical intergroup interactions may be observed at latrine sites (often at territory boundaries) and shared den sites (Rasa, 1987; Schneider and Kappeler, 2014; Christensen *et al.*, 2016; Richens, pers. obs).

Dwarf mongooses have a linear dominance hierarchy, with dominant individuals generally being the oldest group members (Creel and Waser, 1994; Creel *et al.*, 1995). Mongooses reach sexual maturity at a year old, although reproduction is monopolised by the dominant pair (Rood, 1987; Schneider and Kappeler, 2014). During the more favourable conditions of the wet season between November and May, dominant females can give birth to up to three litters of between one and six pups (Rood, 1990; Creel *et al.*, 1995). Aggressive interactions, normally initiated by dominants and directed at subordinates, determines dominance status and reinforce reproductive suppression of subordinates (Creel *et al.*, 1992). Although subordinate males are physiologically capable of reproducing, greater aggression shown by the dominant male during mating periods restricts mating opportunities for subordinate males (Creel *et al.*, 1992).

Subordinate adults assist in cooperative care of the young to gain inclusive fitness (Creel and Waser, 1994; Creel *et al.*, 1995) and due to high costs of dispersing or breeding alone (Jennions and Macdonald, 1993; Creel and Waser, 1994). 'Babysitting' of pups, whereby adults remain at the den with young pups, is one such helping behaviour to which subordinate adults contribute the most (Rasa, 1977; Creel and Waser, 1994). Pups will remain in the safety of den sites for their first weeks, so while the rest of the group are elsewhere foraging, babysitters of both sexes will stay to protect and provision the pups (Rasa, 1977, 1987; Waser *et al*. 1995). In larger groups, subordinate females may allolactate, reducing energetic costs for the dominant female (Rood, 1990). During this period, the group will more frequently move den site with the pups being carried in the mouths of the adults (Rasa, 1987; Richens, pers. obs.).

Due to their small size and diurnal behaviour, dwarf mongooses are vulnerable to a range of terrestrial and aerial predators (Rood, 1987; Waser *et al.* 1995; Veron *et al.*, 2004). These include: banded mongooses (*Mungos mungo),* black-backed jackals (*Canis mesomelas),* martial eagles (*Polemaetus bellicosus*), tawny eagles (*Aquila rapax*), snake eagles (*Circaetus pectoralis,*), puff adders (*Bitis arietans),* Mozambique spitting cobras (*Naja mossambic)* (Rood, 1990) and servals (*Felis serval)* (Richens, pers. obs). Whilst foraging for insects or small vertebrates, groups can cover over 1 km in a day (Rasa, 1989), though this may be an underestimate particularly during dry winter months when prey is more scattered. Group cohesion is maintained with short 'contact' calls between neighbouring foragers and longer, higher-pitched 'lost' calls given by individuals that have become separated from the group (Rasa, 1986, 1989; Sharpe, Hill and Cherry, 2013).

Since foraging and vigilance are mutually exclusive activities, sentinel duty is an important anti-predator measure for dwarf mongooses (Rasa, 1986). A sentinel is defined as an individual who adopts a vigilant attitude on a raised post; termite mounds and trees make useful lookout posts (Rasa, 1989; Hoffmann, Roberts and Kern, 2014; Richens, pers. obs.). Subordinate males tend to perform the majority of sentinel behaviour (Rasa, 1977, 1987, 1989). Whilst on duty, the sentinel often gives a 'Watchman's song', which informs other group members of their position, dominance status and imminent dangers (Kern and Radford, 2013). On detection of a threat, sentinels emit specific alarm calls alerting foragers to terrestrial or aerial predators (Collier *et al.*, 2017; Kern, Laker and Radford, 2017). As group size increases, the likelihood of there being a sentinel present also increases, and typical bout duration decreases, optimising foraging–vigilance trade-offs (Rasa, 1986, 1987). However, the dominance status of the sentinel also affects this trade-off, with foragers showing lower levels of vigilance in the presence of dominant sentinels compared to subordinates or juveniles (Kern, Sumner and Radford, 2016). Additionally, vegetation density, risk-perception and group activity influence the likelihood and duration of sentinel bouts, as well as individual satiation level and presence of existing sentinels (Rasa, 1983; Kern and Radford, 2014).

1.5.2 Study site

This study was conducted on Sorabi Rock Lodge reserve, a 4 km^2 private game reserve in South Africa's Limpopo Province (24° 11'S, 30° 46'E), 388–514 m above sea level. The climate is characterised by two distinct seasons: cool, dry winters (May–August) and hot, wet summers (September–April). The majority of annual rainfall (mean 467 mm; Sept 1998 –

May 2012) typically falls within the summer months. Average daily temperatures can reach a maximum of 34.6°C in the hottest month (Feb) and 25.7°C in the coolest month (July) (Kern, 2012; Kern and Radford, 2013).

As part of the Savannah biome, the land is predominantly lowveld and grassland, although Sorabi's history of cattle grazing is evident from the current floral community, consisting of rapid colonisers. The most common tree species on the reserve include marula (*Sclerocarya birrea*), red bush willow (*Combretum apiculatum*), velvet corkwood (*Commiphora mollis*) and several acacias: blue thorn (*Acacia erubescens*), knob thorn (*Acacia nigrescens*) and flaky thorn (*Acacia exuvialis*). Several large specimens of rock fig (*Ficus abutilifolia*) and fever tree (*Vachellia xanthophloea*) are also present. True grassland is scarce on the reserve but *Aristida* and *Eragrostis* species are common. Shrub species include *Abutilon angulatum*, *Heliotropium steudner* and *Ocimum canum*.

The reserve is home to a range of fauna, largely dominated by grazers. Ungulates included impala (*Aepyceros melampus*), giraffe (*Giraffa camelopardalis*), blue wildebeest (*Connochaetes taurinus*), waterbuck (*Kobus ellipsiprymnus*), bushbuck (*Tragelaphus scriptus*), zebra (*Equus burchellii*), greater kudu (*Tragelaphus strepsiceros*), common duiker (*Sylvicapra grimmia*), klipspringer (*Oreotragus oreotragus*) and warthog (*Phacochoerus africanus*). Chacma baboons (*Papio ursinus*), vervet monkeys (*Chlorocebus pygerythrus*), cape porcupines (*Hystrix africaeaustralis*) and banded mongooses are also present. Numerous species represent potential predators to dwarf mongooses, including black-backed jackals, African civets (*Civettictis civetta*), honey badgers (*Mellivora capensis*), servals, caracals (*Caracal caracal*) and slender mongooses (*Galerella sanguinea*). Reptilians encountered were rock monitors (*Varanus exanthematicus*), Mozambique spitting cobras, puff adders and black mambas (*Dendroaspis polylepis*). Raptors common to the area include African fish-eagles (*Haliaeetus vocifer*), brown snake-eagles (*Circaetus cinereus*), African hawk-eagles (*Hieraaetus spilogaster*), tawny eagles and dark-chanting goshawks (*Melierax metabates*).

1.5.3 Study population

Since the Dwarf Mongoose Research Project was founded in 2011, this study population has been under near-continual observation, and as such the age, sex and life-history of most of the mongooses is known. During this study period from January to July 2018, the population consisted of 96 individuals across seven groups, ranging from 8 to 21 per group (mean ± SE: 13.7 ± 1.6). The number of adults in each group ranged from 5 to 13; the proportion of pups within each group ranged from 0.25 to 0.54. Each group had two litters born in November and January. Pups were classified as individuals less than 6 months old and adults were at least one year. One group was only recently habituated (October 2017) so individuals were not used for the focal-forager experiment; the group as a whole was included in the burrow experiment.

All groups were habituated to human presence and followed on foot for at least two full consecutive days (dawn to dusk) with a maximum of 12 days without human presence. It was possible to observe individuals in close proximity (<5 m) without disturbance. Individuals were identifiable by natural distinguishable features (e.g. stumpy tails, facial scars) or by blonde hair-dye (Wella UK Ltd, Weybridge, Surrey, U.K) marks applied to their pelt. This study was conducted under permission from the Department of Environmental Affairs and Tourism, Limpopo Province (permit number: 001-CPM403-00013) and the Ethical Review Group, University of Bristol (University Investigator Number: UB11/038).

1.6 Thesis aims

Our current knowledge of how anthropogenic noise affects vigilance behaviours, particularly in terrestrial mammals, is relatively poor. Field-based playback experiments investigating anthropogenic noise only accounted for 15% of over two decades of literature reviewed by Shannon *et al.* (2016). This study therefore aims to contribute toward this paucity of research and provide a replicable methodology for further studies. Dwarf mongooses, as small-bodied carnivores, have numerous direct and indirect interactions with a range of other species; understanding how noise effects this species provides a small step towards broadening our knowledge of the anthropogenic impacts on wildlife and ecosystems.

This study is an attempt to explore the effects of temporal variation in noise from the same source, specifically continuous and intermittent traffic noise. The wild, habituated study population provides a fantastic opportunity to study behavioural responses in detail within a natural setting. I first use a playback experiment to investigate whether continuous and intermittent traffic noise affect the foraging and vigilance behaviour of wild dwarf mongooses differently and in comparison to ambient-sound controls. I then use a second experiment to determine if traffic-noise playback had further effects on the group at the sleeping burrow, normally a place of safety. If responses to intermittent and continuous traffic noise differ substantially, this could alter our understanding of the ultimate effects of anthropogenic noise on non-human species.

Chapter 2: Effects of experimental traffic noise on individual and group behaviours of wild dwarf mongooses (*Helogale parvula*)

2.1 Abstract

Escalating urbanisation and globalisation of our planet is placing increasing pressure on nature. Anthropogenic noise, an increasingly widespread pollutant, is becoming a key concern. Extraneous noise is known to have detrimental effects on human health and although there is growing recognition of the impacts of noise on wildlife, research has largely focused on acoustic communication with field-based studies comprising only a minor proportion. Here, I address some shortfalls in the current literature by way of field-based experimental playbacks to investigate whether variation in temporal characteristics of noise differentially affects foraging–vigilance trade-offs in wild dwarf mongooses (*Helogale parvula*). I show that during playback of either intermittent or continuous traffic-noise, foragers show increased vigilance (headscans and sentinel behaviour) compared to an ambient-sound control. There was no difference in vigilance levels between intermittent or continuous traffic-noise. However, sentinel bout frequency increased following playback of continuous traffic noise but decreased after playback of intermittent noise. These responses could be due to differences in overall noise exposure, with continuous noise presenting a greater stimulus or 'threat.' If noise is analogous to a predation threat, greater investment in vigilance may be adaptive as individuals assess their surroundings for danger. However, if noise persists, or if noise distracts individuals from real threats, survival could be compromised. Additionally, playback of traffic noise at sleeping burrows significantly delayed group emergence and departure. In this context, entire groups may suffer lost foraging time with associated declines in individual fitness. Grooming rates were also influenced by noise, with greater frequency but not duration observed in traffic noise. Further research would benefit from using several behavioural measures and conducting longer-term studies to investigate changes in responses over time and to assess where individuals may be able to compensate for costs incurred by noise exposure.

2.2 Introduction

Unprecedented growth in the human population has led to increased pressure on the natural world. The direct consequences of some of our activities, such as deforestation and the spread of transportation networks, may be readily evident, but associated pollutants are also a growing concern. Anthropogenic noise is an evolutionarily novel and widespread pollutant (WHO Regional Office for Europe, 2011) originating from various sources including industrial energy extraction, military and recreational activities (Shannon, McKenna, *et al.*, 2016). Global transportation networks are the most common source of anthropogenic noise, with traffic and shipping contributing to a substantial increase in ambient noise levels (Tyack, 2008; Barber, Crooks and Fristrup, 2010). Anthropogenic noise is known to affect human health adversely (Passchier-Vermeer and Passchier, 2000; Hammer, Swinburn. and Neitzel., 2014; Eriksson, Pershagen and Nilsson, 2018), but the impacts on non-human species have only recently received detailed study (for reviews, see Williams *et al.*, 2015; Shannon, McKenna, *et al.*, 2016; Dutilleux, 2017).

The impacts of anthropogenic noise on wildlife can be complex and long-lasting. At a community-level, changes to species diversity and abundance have been documented in field studies using either naturally occurring (Francis, Ortega and Cruz, 2009, 2011a) or broadcasted (McClure *et al.*, 2013; Ware *et al.*, 2015) noise. More broadly, urban homogenisation of avian communities has been reported in urban areas (Clergeau *et al.*, 2006), although noise pervades even our most 'wild' areas (Buxton *et al.*, 2017). Absence of evidence is not evidence of absence; although some organisms may not overtly avoid noisy areas (in some instances even show a positive response; Francis *et al.*, 2012), this may be due to limitations on movement (e.g. due to discrete territories or food resources) (Wright *et al.*, 2007). Individuals that remain may suffer physical damage or shifts in hearing thresholds, masking of acoustic cues and signals, and/or changes in physiology or behaviour (Barber, Crooks and Fristrup, 2010; Shannon, McKenna, *et al.*, 2016). Physical damage may be most likely to occur in close proximity to high-intensity noises, whilst communication and behaviour can be affected at far greater distances from the noise source (see Fig. 4 in Dooling and Popper, 2016a), although these effects are not mutually exclusive. Ultimately, there can be consequences for fitness (Read, Jones and Radford, 2014; Simpson *et al.*, 2016).

Anti-predator behaviours play a vital role in survival for a variety of species (Blumstein, 2006; Caro, 2005) and anthropogenic noise has been shown to have a negative impact on these behaviours in several ways. Individuals may respond to immediate threats by increasing their vigilance (and thus improving their ability to assess risk) or fleeing (Shannon, Crooks, *et al.*, 2016). Such behaviours are adaptive and are often provoked by alarm calls from conspecifics or heterospecifics (Hollén and Radford, 2009; Magrath *et al.*, 2015), which can be masked by extraneous noise resulting in a deterioration in detection and discrimination (Zhou, Radford and Magrath, 2019). For example, wild great tits (*Parus major*) failed to respond to conspecific alarm calls in traffic-noise playback (Templeton, Zollinger and Brumm, 2016), and dwarf mongooses (*Helogale parvula*) were less likely to flee in response to tree squirrel (*Paraxerus cepapi*) alarm calls during traffic-noise playback (Morris-Drake *et al.*, 2017). Additionally, vigilance and flee responses can be directly affected by anthropogenic noise, which may be perceived as a threat in itself ('increased threat hypothesis'; Owens, Stec and O'Hatnick, 2012) and result in responses analogous to a predation threat (Shannon, Crooks, *et al.*, 2016). Exhibiting costly behaviours when no real threat is present could have negative impacts on individual fitness if foraging opportunities are lost and compensatory behaviour is not possible. Alternatively, some studies support the 'distracted prey hypothesis' (Chan *et al.*, 2010), which suggests that acoustic stimuli may act as a distractor causing a lack of or delayed response as individuals may be unable to detect a threat. For example, in open-water experiments, Ambon damselfish (*Pomacentrus amboinensis*) showed a delayed response toward both simulated and real predators when exposed to boat noise, resulting ultimately in increased mortality by predation (Simpson *et al.*, 2016).

Although noise is often highly variable, particularly in spatial and temporal aspects (Dooling and Popper, 2016a), there is a relative paucity of empirical research which considers this when assessing the impacts on animal behaviour. Several studies, focusing on physiological changes, have utilised the inherent temporal variation in different noise sources (e.g. Wysocki, Dittami and Ladich, 2006; Radford *et al.*, 2016) although these will also vary in other characteristics (Clark *et al.*, 2009) such as rise time (Dooling and Popper, 2016a). Non-continuous noises had greater negative effects than continuous noise sources on the abundance of greater sage grouse (*Centrocercus urophasianus*) at leks (Blickley, Blackwood and Patricelli, 2012) and on stress (Radford *et al.*, 2016) and anti-predator behaviours (Spiga, Aldred and Caldwell, 2017) in European seabass (*Dicentrarchus labrax*). A study on wild house wrens (*Troglodytes aedon*) found that traffic noise caused heightened levels of corticosterone in both rural and urban birds, whilst a ‘pink’ noise control did not; the authors suggested that the variability of traffic noise may have contributed to these findings (Davies, Haddad and Ouyang, 2017). It can be inferred from these studies that variation in the characteristics of noise can result in substantial variation in responses. However, responses may also differ in relation to natural patterns of behaviour over time in some species; through experiments with seabass, Neo *et al.* (2014, 2018) found that swimming behaviour during noise exposure was more pronounced at night. Additionally, investigating possible recovery in quiet intervals between periods of noise exposure (e.g. Masini, Day and Campeau, 2008) could prove important with regard to improving our understanding of the long-term effects on behaviour.

Here, we used experimental playbacks to investigate the effect of temporal variants of traffic noise on vigilance behaviours in dwarf mongooses, and also to consider how traffic noise affects group behaviours. Dwarf mongooses are small, diurnally active carnivores and live in groups ranging from 5 to 30 individuals (Rasa, 1977; Kern and Radford, 2014). As they are vulnerable to a range of predators, vigilance – both whilst foraging and as sentinels (raised guards) – is crucial but must be traded-off against foraging; effort invested in behaviours which directly impact fitness must be allocated optimally. Anthropogenic noise has been shown to increase vigilance behaviour in foraging mongooses (Kern and Radford, 2016), even influence detection of secondary predator cues (Morris-Drake, Kern and Radford, 2016). A habituated wild population was used for this study, allowing experimental manipulation and close observations (<5 m on foot) of wild individuals without disrupting natural behaviours.

Specifically, the experiments described here involved playback of traffic noise recorded from the busy tar road (R530) which borders the reserve inhabited by the study population. Traffic noise was either intermittent or continuous (corresponding to the frequency of passing vehicles) and the aim of this study was to examine if this temporal variation results in different responses. Playback was conducted to focal foragers and a subsequent experiment carried out at the sleeping burrow aimed to explore if exposure to traffic noise had effects on group behaviours. It was predicted that foragers would increase their vigilance and sentinel activity in traffic noise compared to an ambient control and may show greater vigilance during intermittent noise compared to continuous noise. This latter prediction is based on the ‘increased threat hypothesis’ (Owens, Stec and O’Hatnick, 2012) and the findings of the few empirical studies which have explored this type of variation in noise exposure. Regarding traffic noise at the burrow, it was predicted that this might result in a delayed emergence and departure time, and/or increased vigilance if additional noise is perceived as a threatening stimulus.

2.3 Methods

2.3.1 Study site and population

The study was conducted at Sorabi Rock Lodge, a 4 km^2 private game reserve situated in Limpopo Province, South Africa (24° 11’S, 30° 46’E). As part of the Savanna biome, this area is characterised by relatively low annual rainfall (mean 467 mm, Sept 1998 – May 2012), most of which falls in the summer months from October to March (Kern and Radford, 2013), allowing grasses and shrubs to dominate this region. For full details of the study site, see Kern and Radford (2013).

Since 2011, the Dwarf Mongoose Research Project (DMRP) at Sorabi has collected behavioural and life-history data on the wild population of dwarf mongooses, which are habituated to close human presence (<5 m on foot) (Kern and Radford 2003, 2004). All data for this study were collected between March and July 2018 and included a single pupping season. As pups are confined to a burrow with ‘babysitters’ while the rest of the group may be away foraging, experiments were only carried out once the pups were consistently involved in the group’s daily foraging. Six habituated mongoose groups (mean group size = 13.7; range = 8–21) were used for the focal-forager experiment, and a seventh group was included for the burrow experiment. Individuals were identifiable by blonde dye markings applied to their pelt or distinguished by natural features or scars (e.g. a missing ear or foreleg). Groups had discrete territories which were mapped using handheld GPS devices (Garmin Etrex H GPS; Garmin Europe Ltd., Southampton, Hampshire, UK) and MapSource (software version 6.16.3, Garmin Ltd), and their burrows were identifiable by distinct physical features and GPS waypoints. Adults were classed as individuals older than one year of age, and pups were those younger than six months old. Groups contained a ‘dominant’ breeding pair and ‘subordinate’ adult helpers of both sexes.

2.3.2 Acoustic recordings and composition of playback tracks

Ambient sound was recorded from the core of each group’s territory using a Marantz solid-state recorder (PMD661 *MKII*, Marantz America, Mahwah, NJ, USA; DC 5V 1.4A) with a Sennheiser ME66 shotgun microphone (Sennheiser UK, High Wycombe, Buckinghamshire, UK). The microphone was directed away from the R530 road and positioned at a height of 10 cm to imitate mongoose head height (as in Morris-Drake *et al.*, 2017). This set-up was then left to record at least 50 m away from any human or mongoose activity, at a similar time of day (around noon) for all groups and during calm weather conditions. Peak amplitude of ambient sound was recorded using a HandyMAN TEK1345 Mini Sound Level Meter (Metrel UK Ltd., Normanton, West Yorkshire, UK). These ambient-sound recordings were then edited in Audacity (v 2.2.1, GNU GENERAL PUBLIC LICENSE, Boston, USA, 1991); any conspecific or heterospecific vocalisations – such as alarm calls – and any human or road-related noises were cut out. A 6-min ambient-sound track for each group was then created, with an additional 1 min of silence included at the start to allow for baseline observations.

Traffic-noise tracks used for playback experiments were created using recordings made as part of the study by Kern and Radford (2016). A Sennheiser ME66 microphone was set up perpendicular from the R530 road and 10 m from the road edge to record passing traffic; the peak amplitude (65–75 dB SPLA at 10 m) was measured using a HandyMAN TEK1345 Mini Sound Level Meter (Metrel UK Ltd., Normanton, West Yorkshire, UK). Recordings were edited in Audacity to create unique tracks. Due to differing group sizes, the number of individuals tested within each group ranged from two to eight. For this reason, eight unique tracks for each traffic-noise playback treatment were produced. Within a given treatment, each track contained equal numbers of each vehicle type, previously classified in Kern and Radford (2016). For the intermittent-traffic tracks, gaps of 15 s were inserted using the “generate silence” command in Audacity. Each traffic track was mixed and rendered with the appropriate ambient-sound recording for each group and made to be 6 min in duration, again with 1 min of silence added to the start.

2.3.3 Data collection

2.3.3.1 Playback to foragers

To investigate the effects of different characteristics of traffic noise on individual forager vigilance, a playback experiment was carried out between March and July 2018. Six groups were used as the individuals in the seventh group were not habituated sufficiently for this experiment. Individuals were chosen for focal-forager trials if they were adult and if they were suitable to follow on foot within 2–5 m. There were some individuals who demonstrated lower habituation to observer presence and would therefore not have been suitable to achieve a 6-min playback with post-playback observations at the stated distance. Both dominant and subordinate individuals were used, including at least one dominant from each group. Similar numbers of males (N = 16) and females (N = 12) were used.

Each individual received three trials in total: ambient-sound (as a control), intermittent-traffic and continuous-traffic playback. Each individual received only one playback trial per day, to minimise potential carry-over effects. Subsequent trials to the same individual were conducted 1–7 days later, to reduce the possibility that changes in group dynamics (e.g. group size or dominant pairing) or individual health might affect responses between trials. Trials to the same individual were conducted at a similar time of day (within 2 h if possible) and in similar habitat density. Trials to different individuals within the same group were separated by at least 30 min and treatment order was counterbalanced (to control for the sequence of playback trials received) so no two individuals trialled on the same day received the same playback treatment. Playback trials were started once the group had been foraging for at least 30 min under calm conditions and as long as there had been no major intergroup interactions, latrine events or snake mobs; there also needed to have been no alarm calls (conspecific or heterospecific) for the preceding 15 min. If an alarm call occurred during a trial or the focal individual became a sentinel during the pre-playback period, the trial was abandoned and re-attempted at least 30 min later.

Playback tracks were broadcast via mobile phone (Motorola moto G) through a single SME-AFS portable field loudspeaker (Saul Mineroff Electronics Inc., New York, USA) held at a height of 1 m and 3–5 m from the focal forager. Playback was at natural amplitude at a distance of 5 m (ambient: 46 dB; traffic: 81 dB) tested prior to trials using a HandyMAN

TEK1345 sound-level meter. The start and end of all headscans and sentinel bouts were dictated to a digital camera (Powershot SX720 HS, Canon UK Ltd, Reigate, Surrey, UK) for 1 min prior to the start of playback (to obtain a baseline measure of vigilance), during the 6 min of playback and for 2 min post-playback. A headscan was defined as when the foraging individual stopped foraging and scanned for danger with its head above the horizontal; a sentinel bout was defined as when the individual adopted a raised position on a substrate such as a rock or tree (with its feet ≥10 cm above the ground). For all focal-forager trials, data were collated on the following responses: i) frequency of headscans; ii) duration of headscans; iii) frequency of sentinel bouts; iv) duration of sentinel bouts; and v) whether the individual moved foraging patch (>10 m from their current position and/or crossing an open patch of ground).

2.3.3.2 Playback at sleeping burrows

To investigate the effects of traffic-noise playback at the group sleeping burrows, trials were conducted between April and July 2018. Each group (*N* = 7) received two treatments: playback of ambient sound or continuous traffic noise first thing in the morning on consecutive days. The continuous-traffic track played to a group was one which had not been used previously on any group member for the focal-forager experiment. Treatment order was counterbalanced, and within each group both trials were received at the same burrow and under calm weather conditions. In all cases, trials were only conducted at burrows with visible entry points and clear lines of sight to ensure that emergence times and other responses could be observed and recorded as accurately as possible.

A SME-AFS portable field loudspeaker was placed 3–5 m from the main burrow entrance before any mongooses first emerged in the morning. The observer sat approximately 3 m from the loudspeaker, which was connected to a mobile phone (Motorola Moto G) from which the mp3 audio track was played. Playback was at natural amplitude at 5 m determined before each trial using a HandyMAN TEK1345 sound-level meter (ambient: 46 dB; traffic: 81 dB). Once the first individual had fully emerged from the burrow, the playback track was started and responses were recorded onto a Dictaphone (Sony IC Recorder ICD-PX440, Sony Corp., Tokyo, Japan) until the last individual departed from the burrow area to start foraging. For each trial, data on the following behaviours were collected and calculated: i) latency to re-emerge (if the first individual returned inside the burrow); ii) latency for 50% of the group to leave the burrow to start foraging; iii) sentinel bout frequency and iv) duration of time on sentinel; v) grooming rate; and vi) proportion of time spent grooming at the burrow. The data for sentinel and grooming behaviours were recorded *ad libitum* and all times were recorded to the nearest second using a stopwatch function on a digital watch (Model no. R2383HX9, SEIKO U.K. Ltd., Maidenhead, Berkshire, U.K).

2.3.4 Data analysis

2.3.4.1 Effects of traffic-noise playback on foragers

The duration (in seconds) of headscans and sentinel bouts in the 1-min pre-playback period, the first 2 min of the playback period and the first 2 min of the post-playback period were calculated for each trial. The change between the pre-playback and playback periods was used to assess the immediate effects of exposure to different sound treatments; the difference between the post-playback and playback periods and the difference between the post- and pre-playback periods were used to assess the occurrence of any lasting effects of playback.

Statistical analyses were carried out in RStudio (R version 3.4.2; R Core team 2017). Mixed models with random effects were chosen due to the matched-design nature of this experiment; there were repeated trials to the same individual and several individuals per group. For all models, fixed effects included were treatment (ambient-sound and continuous and intermittent traffic-noise playback), sex, rank (dominant or subordinate) and treatment order (1–3). Individual and group identities were included as random effects.

For each response variable, the data and residuals were plotted to check visually that they met the assumptions of normality and homoscedasticity required for parametric tests; Linear Mixed Models (LMMs) were used where data conformed to these assumptions. For non-normal distributions of data, and where transformation was ineffective, Generalized Linear Mixed Models (GLMMs) were used. The lmer and glmer functions in the R package ‘lme4’ (Bates *et al*. 2015) were used for LMMs and GLMMs respectively. All reported p values are two-tailed, and results were considered significant at an alpha value of 0.05.

For each response variable, a maximal model with all measured explanatory terms was produced. Fixed terms were dropped, in order of effect size, by backward stepwise elimination (Crawley 2015), until any further loss of terms led to a significant decrease in explanatory power. Models were ranked using Akaike's Information Criterion (AIC; Akaike, 1974). To confirm model fit and significance of terms, pairs of models were compared using the Likelihood Ratio test (LRT) with the anova function in lme4; the minimal model was chosen for the lowest AIC (Crawley 2015) and where AIC values differed by < 2, by parsimony of terms. Chi-square (χ^2) and *p*-values presented for non-significant terms were obtained by comparison of the minimal model with another model differing only in the term of interest. For significant terms, chi-square (χ^2) and *p*-values were obtained by comparison to the null model or the minimal model with the term in question removed.

To test for the likelihood of moving foraging patch and likelihood of sentinel bouts, Cochran's Q and McNemar related-samples tests were carried out in SPSS Statistics for Windows version 24.0 (IBM Corp., Armonk, NY, 2016).

2.3.4.2 Effects of traffic-noise playback at sleeping burrows

The duration (in seconds) of any sentinel bouts and grooming bouts that occurred over the course of the playback were calculated for each trial. Wilcoxon Signed-ranks tests were carried out using the function 'wilcoxsign_test' in the R package 'coin' (Hothorn *et al.* 2006) to test for differences in group-level responses between ambient-sound and traffic-noise playback. All tests were two-tailed, and results were considered significant at $p < 0.05$.

2.4 Results

2.4.1 Focal-forager experiment

2.4.1.1 Does traffic noise affect forager vigilance behaviour?

Sound treatment had a significant effect on headscan frequency of foraging individuals (Table 2.1a; Figure 2.1a). A greater increase in vigilance level (compared to the baseline pre-playback period) was shown in continuous (Tukey contrasts: 4.00 ± 0.48, $p < 0.001$) and intermittent (-4.36 ± 0.48, $p < 0.001$) traffic-noise treatments compared to ambient-sound playback, but there was no significant difference between the two traffic treatments (0.36 ± 0.48, $p = 0.736$). Similarly, sound treatment had a significant effect on the proportion of time spent vigilant during playback (Table 2.1b; Figure 2.1b). Again, there was a greater increase in the proportion of time spent vigilant from the pre-playback period in continuous (-0.015 ± 0.03, $p < 0.001$) and intermittent (-0.14 ± 0.32, $p < 0.001$) traffic-noise treatments compared to ambient-sound playback, but no significant difference between the two traffic treatments (-0.01 ± 0.03, $p = 0.956$).

Sound treatment had a significant effect on the likelihood that focal individuals moved foraging patch during playback (Cochran Q test: $Q = 12.10$, $df = 2$, $p = 0.002$; Figure 2.2). Individuals were significantly more likely to move patch during both traffic-noise treatments than during ambient-sound playback (McNemar test: $\chi^2 = 6.67$, $df = 1$, $p = 0.01$ for both comparisons), but there was no significant difference between continuous and intermittent traffic noise ($\chi^2 = 0$, $df = 1$, $p = 1.00$).

Table 2.1 Output from Linear Mixed Models investigating the change in (a) headscan frequency and (b) proportion of time vigilant during the first 2 min of the playback period compared to the pre-playback period. Effect size (± SE) are shown for fixed terms in the minimal model and variance (± SD) is reported for random terms (italicised). Significant fixed terms shown in bold. *N* = 28 individuals in six groups.

	Fixed effect	Effect ± SE/SD	*df*	χ^2	*P*
(a) Headscan frequency					
Minimal model	(Intercept)	5.36 ± 0.41			
	Treatment		**2**	**58.43**	**<0.001**
	Intermittent	0.36 ± 0.48			
	Ambient	-4.00 ± 0.48			
	Individual	1.45 ± 1.21			
	Group	0.01 ± 0.11			
Dropped terms	Playback order		2	2.38	0.123
	Rank		1	0.75	0.388
	Sex		1	0.09	0.759
(b) Proportion of time vigilant					
Minimal model	(Intercept)	0.22 ± 0.04			
	Treatment		**2**	**24.49**	**<0.001**
	Intermittent	-0.001 ± 0.03			
	Ambient	-0.015 ± 0.03			
	Individual	<0.001 ± 0.005			
	Group	< 0.001 ± 0.001			
Dropped terms	Playback order		2	2.67	0.102
	Rank		1	0.38	0.540
	Sex		1	0.10	0.755

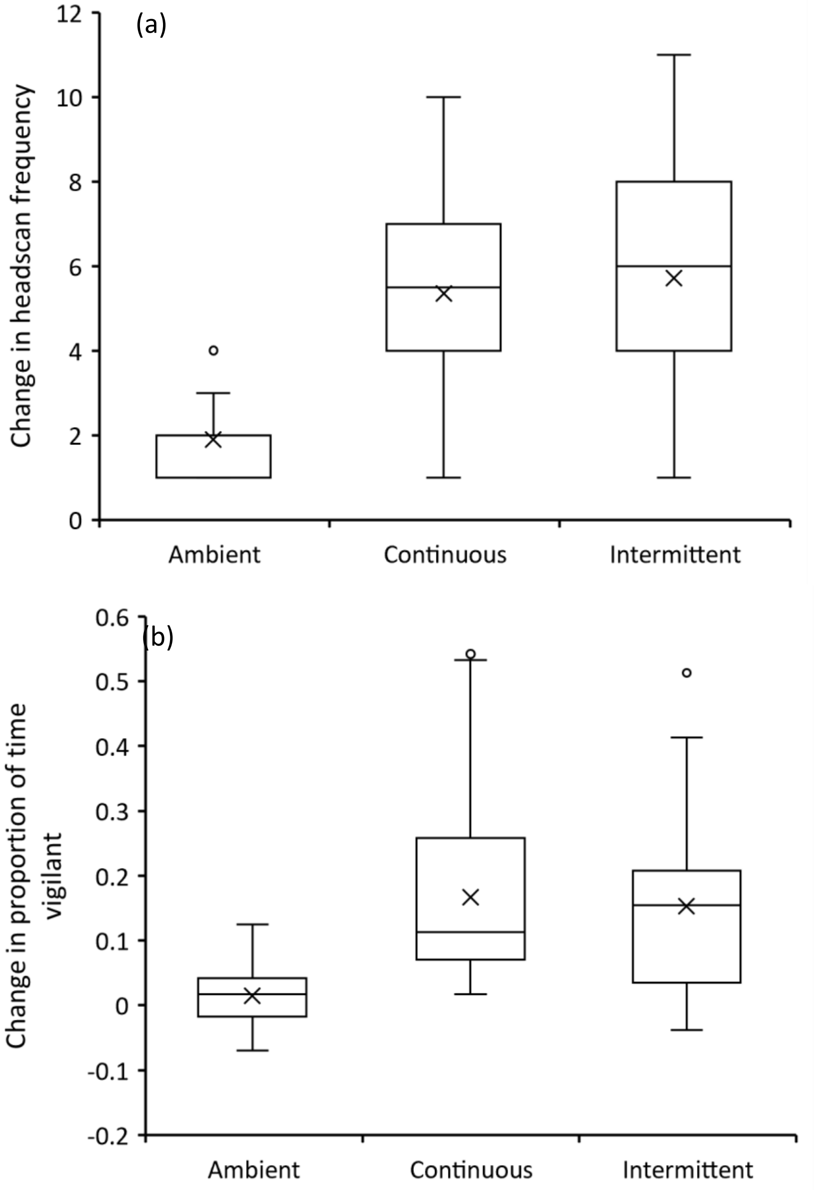


Figure 2.1 The effect of ambient-sound and of continuous and intermittent traffic-noise playback on the change in (a) headscan frequency and (b) the proportion of time focal foragers were vigilant from the pre-playback (baseline) period to the first 2 min of playback. Boxes represent the interquartile range with lines showing the median; mean values represented by X. *N* = 28 individuals, six groups.

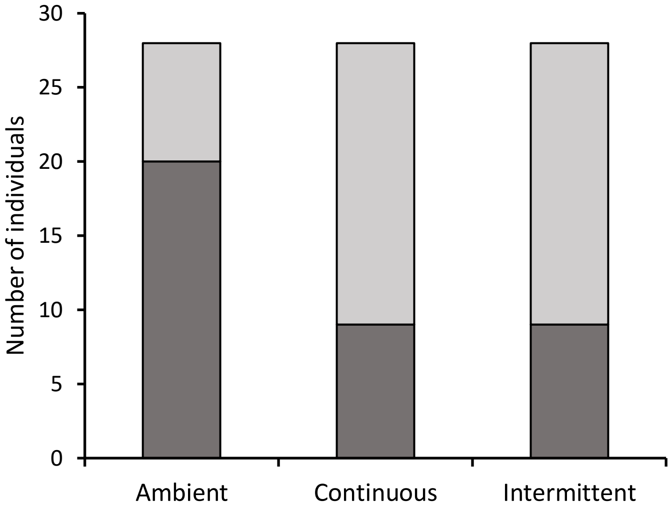


Figure 2.2 Number of individuals who moved (light grey) and did not move (dark grey) foraging patch during ambient-sound and continuous and intermittent traffic-noise trials. N = 28 individuals, six groups.

There was a significant difference between sound treatments in the likelihood of a sentinel bout occurring in the first 2 min of playback (Cochran Q test: Q = 8.77, *df* = 2, *p* = 0.012; Figure 2.3). Sentinel bouts were more likely to occur during either continuous (McNemar test: $\chi^2 = 5.14$, *df* = 1, *p* = 0.023) or intermittent ($\chi^2 = 6.13$, *df* = 1, *p* = 0.013) traffic-noise playback compared to the ambient-sound treatment, but there was no significant difference between the two traffic-noise treatments ($\chi^2 = 0$, *df* = 1, *p* = 1.00). When considering those individuals that acted as a sentinel during playback (traffic-noise trials only), sound treatment did not significantly affect either sentinel bout frequency or the proportion of time spent as a sentinel (Table 2.2).

Table 2.2 Output from Linear Mixed Models investigating (a) sentinel bout frequency and (b) proportion of time as a sentinel during the first 2 min of traffic-noise playback trials. Effect size (± SE) are shown for fixed terms in the minimal model and variance (± SD) reported for random terms (italicised). *N* = 13 individuals in five groups.

	Fixed effect	Effect ± SE/SD	*Df*	χ^2	*P*
(a) Sentinel bout frequency					
Minimal model†	(Intercept)	2.11 ± 0.40			
	Individual	0.02 ± 0.13			
	Group	0.00 ± 0.00			
Dropped terms	Rank		1	2.47	0.12
	Playback order		1	2.30	0.12
	Treatment		1	1.38	0.24
	Sex		1	0.29	0.59
(b) Proportion of time on sentinel					
Minimal model†	(Intercept)	0.26 ± 005			
	Individual	0.00 ± 0.00			
	Group	<0.001 ± 0.01			
Dropped terms	Playback order		1	1.95	0.163
	Rank		1	1.26	0.262
	Sex		1	0.97	0.325
	Treatment		1	0.09	0.760

† Null (intercept and random terms only) model

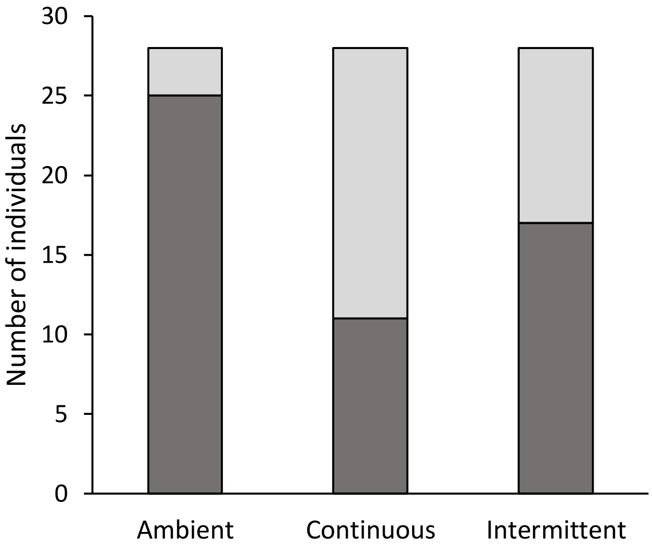


Figure 2.3 Number of individuals who displayed sentinel activity (light grey) and those that did not (dark grey) during ambient-sound, continuous and intermittent traffic-noise trials. *N* = 28 individuals, six groups.

2.4.1.2 Does traffic noise have persistent effects?

Sound treatment had a significant effect on the change in headscan frequency from the playback to the post-playback period (Table 2.3a; Figure 2.4a). There was a significantly greater decrease in headscan frequency following playback of continuous (Tukey contrasts: 3.80 ± 0.60, $p < 0.001$) and intermittent (3.49 ± 0.61, $p < 0.001$) traffic noise compared to ambient sound, but no significant difference between the two traffic-noise treatments (0.30 ± 0.61, $p = 0.87$). Consequently, there was no significant sound-treatment effect on the change in frequency of headscans from the baseline (pre-playback) to the post-playback period (Table 2.3b); headscan frequency in both traffic-noise treatments returned to baseline levels in the 2-min period after the playback was stopped.

Sound treatment also had a significant effect on the change in proportion of time spent vigilant from playback to the post-playback period (Table 2.4a Figure 2.4b). In this case, there was a significant difference between continuous-traffic playback and ambient-sound playback (Tukey contrasts: 0.10 ± 0.04, $p = 0.04$) but not between intermittent traffic and ambient (0.08 ± 0.04, $p = 0.11$) nor between continuous and intermittent traffic (0.02 ± 0.04, $p = 0.89$). The change in proportion of time spent vigilant from pre-playback to post-playback was not significantly affected by sound treatment (Table 2.4b); proportion of time spent vigilant returned to baseline levels once the playback ceased.

Table 2.3 Output from Linear Mixed Models investigating changes in forager headscan responses from (a) the first 2 min of playback to the first 2 min after playback ends (post-playback) and (b) baseline (pre-playback) to post-playback. Displayed are the effect size (± SE) for fixed terms included in minimal models, and variance (± SD) for the random terms (italicised). Significant fixed terms shown in bold. *N* = 28 individuals, six groups.

	Fixed effect	Effect ± SE/SD	*df*	χ^2	*P*
(a) Change in headscan frequency (playback to post-playback)					
Minimal model	(Intercept)	-2.29 ± 0.76			
	Treatment		**2**	**34.99**	**<0.001**
	Intermittent	0.30 ± 0.61			
	Ambient	3.80 ± 0.60			
	Playback order		**2**	**4.29**	**0.038**
	Individual	1.28 ± 1.13			
	Group	0.00 ± 0.00			
Dropped terms	Sex		1	0.38	0.540
	Rank		1	0.03	0.863
(b) Change in headscan frequency (pre- to post-playback)					
Minimal model	(Intercept)	0.89 ± 0.71			
	Individual	0.03 ± 0.06			
	Group	< 0.001 ± <0.001			
Dropped terms	Treatment		2	3.60	0.166
	Playback order		2	1.56	0.212
	Rank		1	0.37	0.545
	Sex		1	0.13	0.720

Table 2.4 Output from Linear Mixed Models investigating change in forager vigilance-proportion responses from (a) the first 2 min of playback to the first 2 min after playback ends (post-playback) and (b) from baseline (pre-playback) to post-playback. Displayed are the effect size (± SE) for fixed terms included in minimal models, and variance (± SD) for the random terms (italicised). Significant fixed terms shown in bold. *N* = 28 individuals, six groups.

	Fixed effect	Effect ± SE/SD	*df*	χ^2	*P*
(a) Change in proportion of time vigilant (playback to post-playback)					
Minimal model	(Intercept)	-0.11 ± 0.03			
	Treatment		**2**	**6.54**	**0.038**
	Intermittent	0.02 ± 0.04			
	Ambient	0.09 ± 0.04			
	Individual	0.00 ± 0.00			
	Group	0.00 ± 0.00			
Dropped terms	Sex		1	2.49	0.114
	Playback order		2	0.48	0.488
	Rank		1	0.05	0.830
(b) Change in proportion of time vigilant (pre- to post-playback)					
Minimal model†	(Intercept)	0.09 ± 0.03			
	Individual	0.00 ± 0.00			
	Group	<0.001 ± 0.03			
Dropped terms	Treatment		2	5.31	0.070
	Sex		1	1.75	0.186
	Playback order		2	0.99	0.319
	Rank		1	0.33	0.565

† Null (intercept and random terms only) model

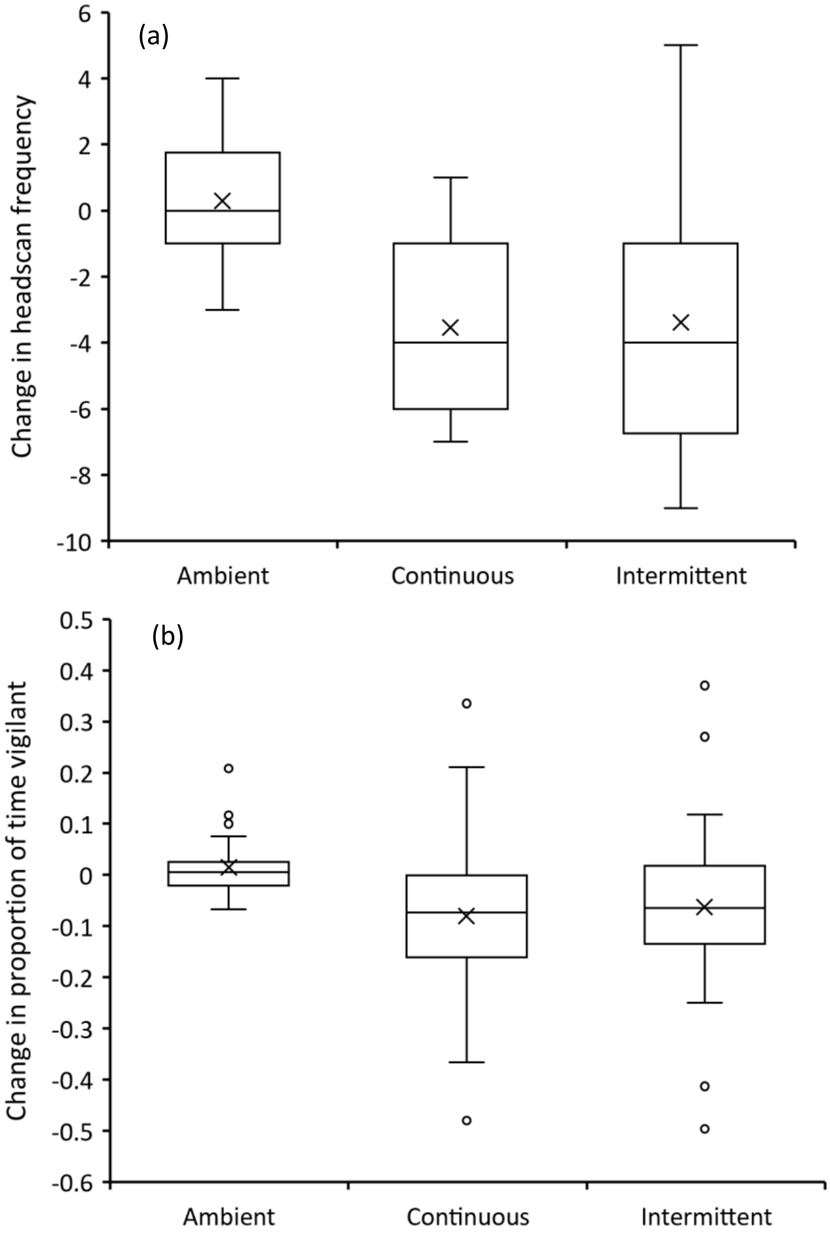


Figure 2.4 The effects of ambient-sound and continuous and intermittent traffic-noise playback on (a) change in headscan frequency and (b) change in proportion of time vigilant from playback to the post-playback period. Boxes represent the interquartile range with the lines showing the median; mean values represented by X. *N* = 28 individuals, six groups.

There was no significant difference between the sound treatments in the likelihood that focal individuals moved foraging patch during the post-playback period (Cochran Q test: Q = 1.44, *df* = 2, *p* = 0.486; Figure 2.5). Movement behaviour had therefore returned to baseline levels once playback ceased.

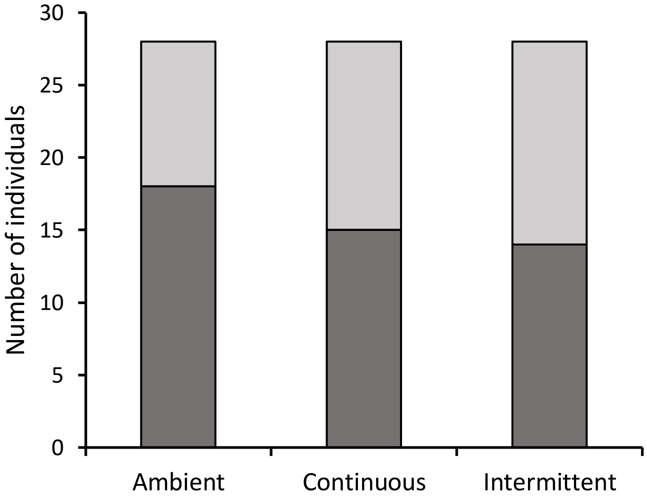


Figure 2.5 Number of individuals who moved (light grey) and did not move (dark grey) foraging patch post-playback in ambient-sound and continuous and intermittent traffic-noise trials. N = 28 individuals, six groups.

Sound treatment (traffic-noise playback only) had a significant effect on the change in sentinel bout frequency from playback to the post-playback period (Table 2.5a). Foragers showed an increase in sentinel bout frequency following continuous-traffic playback, but the opposite was true for intermittent traffic-noise playback (Figure 2.6). However, there was no significant effect of sound treatment on the change in proportion of time acting as a sentinel from the playback to the post-playback period (Table 2.5b).

Table 2.5 Output from Linear Mixed Models investigating changes in (a) sentinel bout frequency and (b) proportion of time on sentinel from the first 2 min of playback to the first 2 min post-playback. Displayed are the effect size (± SE) for fixed terms included in minimal models, and variance (± SD) for the random terms (italicised). Significant fixed terms shown in bold. For (a) *N* = 21 individuals and (b) *N* = 22 individuals in six groups.

	Fixed effect	Effect ± SE/SD	*df*	χ^2	*P*
(a) Change in sentinel bout frequency					
Minimal model	(Intercept)	0.87 ± 0.36			
	Treatment		**1**	**3.85**	**0.050**
	Intermittent	-1.14 ± 0.55			
	Individual	0.03 ± 0.17			
	Group	0.00 ± 0.00			
Dropped terms	Playback order		1	2.08	0.149
	Sex		1	1.64	0.200
	Rank		1	0.64	0.424
(b) Change in proportion of time as a sentinel					
Minimal model†	(Intercept)	0.04 ± 0.09			
	Individual	<0.001 ± 0.02			
	Group	0.02 ± 0.14			
Dropped terms	Sex		1	1.64	0.201
	Rank		1	1.37	0.241
	Treatment		1	0.16	0.692
	Playback order		1	0.08	0.776

† Null (intercept and random terms only) model

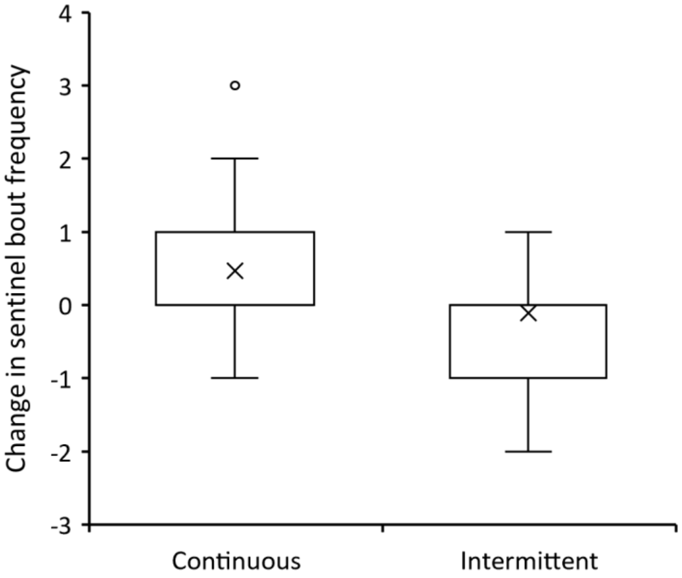


Figure 2.6 The effect of continuous and intermittent traffic-noise playback on the change in sentinel bout frequency from the first 2 min of playback to the first 2 min post-playback. Boxes represent the interquartile range with the mean values represented by X; median lines sit on 0 for both. *N* = 21 individuals, six groups.

2.4.2 Burrow experiment

Individuals took significantly longer to re-emerge from the burrow when there was traffic-noise compared to ambient-sound playback (Wilcoxon signed-rank test: $Z = 2.37$, $N = 7$, $p = 0.016$; Figure 2.7a). Moreover, the group remained at the burrow for significantly longer, before heading off to forage, in the traffic-noise treatment compared to the ambient-sound control ($Z = 2.20$, $N = 7$, $p = 0.031$; Figure 2.7b).

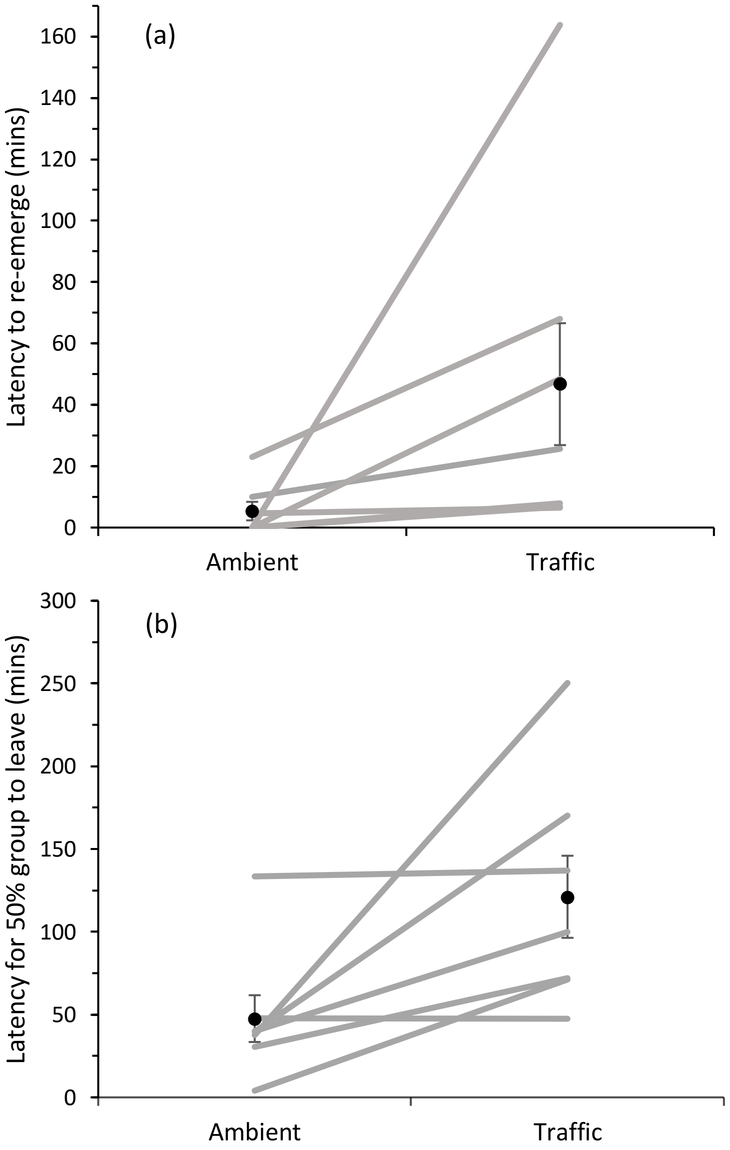


Figure 2.7 The effect of playback (continuous traffic noise or ambient sound) on (a) the latency of mongooses to re-emerge from the burrow and (b) the latency for 50% of the group to leave the burrow, following initiation of playback. Grey lines each correspond to a single group (N = 7) and the black dot with error bars represents the mean ± SE across groups.

The rate of sentinel bouts did not differ significantly between sound treatments (Wilcoxon signed-rank test: Z = -0.42, N = 7, p = 0.750). However, grooming rate was significantly lower in traffic-noise playback than the ambient-sound control (Z = -2.03, N = 7, p = 0.047; Figure 2.8a); the proportion of time grooming was not significantly different between sound treatments (Z = 1.52, N = 7, p = 0.156; Figure 2.8b).

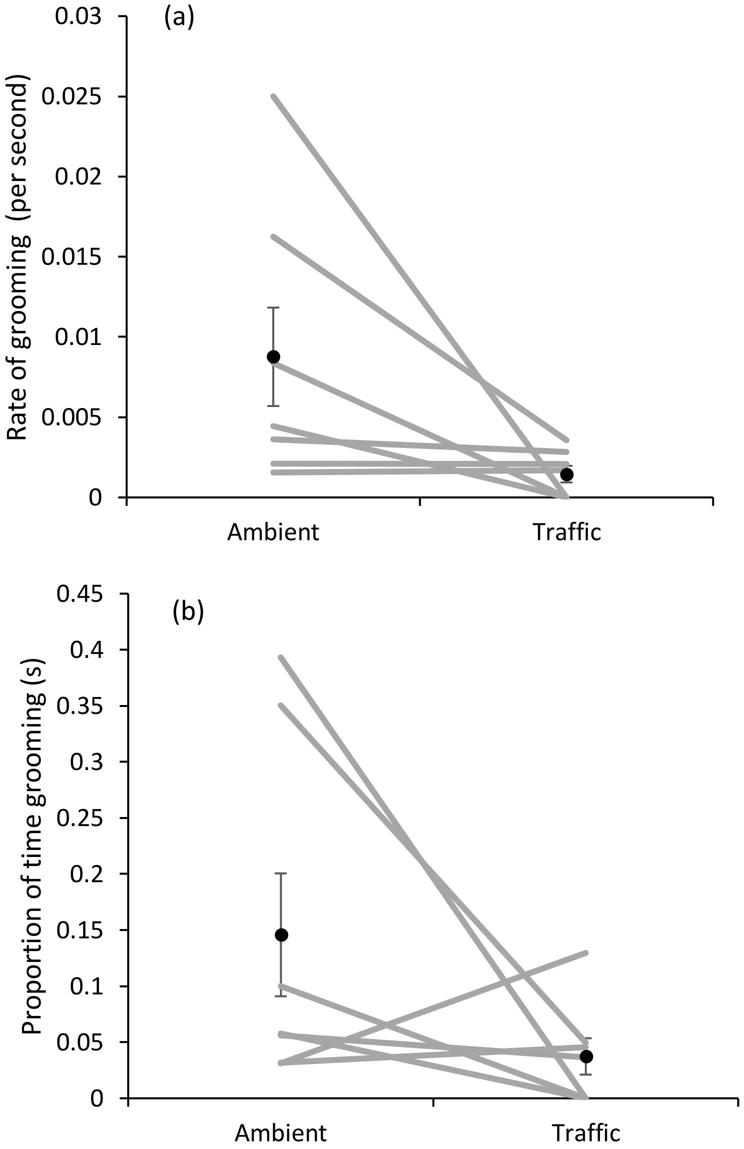


Figure 2.8 The effect of playback (continuous traffic noise or ambient sound) on (a) rate of grooming bouts and (b) proportion of time spent grooming, recorded from the initiation of playback to the time when 50% of the group left the burrow. Grey lines each correspond to a single group (*N* = 7) and the black dot with error bars represents the mean ± SE.

2.5 Discussion

Traffic-noise playback had substantial effects on mongoose vigilance behaviours during the period of noise exposure. During traffic-noise trials, foragers showed greater vigilance, both in terms of frequency and proportion of time spent scanning their surroundings, compared to in ambient-sound trials. Sentinel bouts were more frequent and longer in duration in traffic-noise trials compared to ambient controls. Individuals were more likely to be displaced from their foraging patches during traffic noise compared to ambient sound. However, there was no difference between continuous and intermittent traffic-noise treatments. Following the end of playback, individuals generally returned to baseline levels of vigilance suggesting a shorter-term behavioural response. However, there was a significantly greater frequency of sentinel bouts following playback of continuous traffic compared to intermittent-traffic noise. In the second experiment, continuous traffic-noise playback at the sleeping burrow significantly delayed group emergence and departure times compared to paired ambient controls. Sentinel rates and the proportion of time grooming were similar in both ambient-sound and traffic-noise trials, but grooming rate was lower in traffic noise compared to ambient sound.

2.5.1 Forager responses to traffic noise

Both traffic-noise treatments elicited a heightened vigilance response in foraging mongooses. This result lends support to the idea that noise may be perceived as a threat – the ‘increased threat hypothesis’ (Owens, Stec and O’Hatnick, 2012) – and is consistent with responses previously observed in dwarf mongooses (Kern and Radford, 2016), as well as in black-tailed prairie dogs (*Cynomys ludovicianus*) (Shannon, Crooks, *et al.*, 2016), California ground squirrels (*Spermophilus beecheyi*) (Rabin, Coss and Owings, 2006), great tits (Klett-Mingo, Pavón and Gil, 2016) and chaffinches (*Fringilla coelebs*) (Quinn *et al.*, 2006). In this way, noise is analogous to a predation threat; here, individuals exposed to the ‘threat’ increase personal vigilance to assess their surroundings visually and respond according to a perceived level of risk. As noise can mask acoustic signals (Barber, Crooks and Fristrup, 2010; Rosa and Koper, 2018), it is possible that this may also play a role here; ‘contact calls’ between foragers or the ‘Watchman’s song’ given by sentinels (Rasa, 1986; Kern and Radford, 2013) may be partially masked by the traffic noise (see Kern and Radford, 2016), requiring the forager to increase their personal vigilance in order to compensate for deterioration of communication networks.

Sentinel behaviour was also observed to increase in both traffic-noise treatments compared to the ambient-sound control. Since sentinels typically take up a raised position to scan for danger, often as an active response to alarm calls (Kern and Radford, 2014), this again provides some support for the ‘increased threat hypothesis’ (Owens, Stec and O’Hatnick, 2012); such a behaviour influences the foraging–vigilance trade-off in favour of vigilance and thus is adaptive in situations where survival may be compromised. Although the physical aspects of roads may directly impact wildlife (e.g. mortality by collisions; Morelli *et al.*, 2014), the results of this study, in line with the growing literature, demonstrate that noise alone can cause substantial effects on behaviour in wild animals, and which may be detrimental to fitness if compensatory behaviour is not possible or insufficient.

There was no difference between the continuous and intermittent traffic noise in either the vigilance or sentinel responses observed during playback. Since animals are more likely to habituate, or acclimate, to stimuli that are frequent and of low magnitude (Wright *et al.*, 2007), any differences in responses may be more likely to emerge if playback was longer, with a decreasing level of vigilance expected during the more predictable continuous traffic noise. However, since the intermittency of noise did not have significant effects, we can infer that, at least *during* the playback, individuals were not affected differently in terms of behaviour. Nichols, Anderson and Širović (2015) reported that giant kelpfish (*Heterostichus rostratus*) exposed to intermittent boat noise exhibited significantly higher stress responses than in continuous noise, and Radford *et al.* (2016) found that European seabass experienced elevated ventilation rate (a secondary measure of stress) in impulsive pile-driving compared to ship noise (a more continuous noise) and ambient controls. Therefore, we cannot rule out the possibility that traffic noise of an intermittent or continuous nature might differentially affect physiological state, although such a measure was beyond the scope of this study. It is also possible that the duration of trials was not sufficiently long to generate observable differences in behaviour.

Further work on foraging mongooses would benefit from longer periods of noise exposure, similar to those conducted in laboratory studies by Wysocki, Dittami and Ladich (2006) and

Radford *et al.* (2016), and particularly in field studies such as the ‘phantom road’ experiment developed by McClure *et al.* (2013, 2016) and Ware *et al.* (2015). Close observation of individual behavioural changes was a key benefit of using this habituated population, but our methods restricted the duration of playback as individuals were followed on foot and had to be within view for the entire trial period. Over a longer period of exposure, different patterns may emerge in relation to this temporal variation if habituation or acoustic masking are important in altering foraging or vigilance behaviours.

2.5.2 Post-playback responses of foragers

Following the end of playback, a return to baseline levels of personal vigilance (headscans) was observed. This suggests that, by this measure, the behavioural effect of exposure to both noise types was immediate and short-term. Recovery to baseline behaviours after short-term noise exposure has been reported in European eels (*Anguilla anguilla*) and seabass (Bruintjes *et al.*, 2016). However, seabass exposed to intermittent noise showed a slower recovery to baseline swimming behaviour relative to a continuous noise treatment (Neo *et al.*, 2014), though the majority of individuals tested recovered within 30 min following noise exposure. Together these findings suggest that in quieter periods, at least following acute noise, individuals can recover behaviourally.

Sentinel bout frequency between the playback and the post-playback periods was the only response measure which significantly differed between the two traffic-noise treatments. There was an increase in the frequency of sentinel bouts following continuous traffic noise, but a decrease was observed after playback of intermittent traffic noise. There is a possibility of a carry-over effect from the playback period, as the contrast in consistent noise level between the playback and the end of playback is less defined when noise is of an intermittent nature. Individuals may therefore display similar levels of sentinel vigilance following this type of exposure, whereas when continuous noise ceases there is a more immediate release from the impacts associated with exposure. In intermittent-noise trials, individuals may still be ‘expecting’ subsequent periods of noise and therefore continue to display similar levels of sentinel activity in the immediate aftermath of noise. A recent study on common gobies (*Pomatoschistus microps*) found that continuous noise had significantly greater negative impacts on reproductive success by delaying female nest inspection and pair spawning behaviour compared to intermittent noise and controls; disruption to acoustic signals is important in the breeding behaviour of this species (Blom *et al.*, 2019). It is not possible to know, from our results alone, whether noise represents a direct threat or acts to mask signals, such as alarm calls or the ‘Watchman’s song’; studies testing different mechanisms for noise effects, such as amplitude and degree of frequency overlap (Zhou, Radford and Magrath, 2019) are needed.

2.5.3 Responses to playback at sleeping burrows

In contrast to the foraging–vigilance trade-offs experienced by foragers, where vigilance comes at the cost of lost foraging time, traffic-noise at the burrow instead results in a delay in group emergence. Although traffic-noise was only presented on a single morning for each group, the impacts are potentially more lasting, particularly if daily foraging time is compromised, with detrimental effects on fitness.

The finding that sentinel behaviour was not affected differentially by sound treatment (unlike in the first experiment) could be explained by the fact that, as with yellow-bellied marmots (*Marmota flaviventris*), mongooses use burrows as refuges (Rasa, 1983, 1987; Monclús, Anderson and Blumstein, 2015). Therefore, if noise is regarded as a threat, as is commonly proposed for explaining the responses of various species to noise (e.g. prairie dogs, Shannon *et al.*, 2016; hermit crabs, Walsh, Arnott and Kunc, 2017), an increase in sentinel activity (in this context at least) may not be beneficial and the most appropriate behaviour would simply be to seek shelter. Unfortunately, we were unable to document behaviours inside the burrows – which would provide an exciting insight not only into dwarf mongoose (nocturnal) social behaviours but also the possibility that they may obtain some foraging opportunities (e.g. termites) when circumstances such as rain can restrict or delay external foraging activity (Thornton, Samson and Clutton-Brock, 2010; Richens, pers. obs.). If noise reduces daily available time to forage, there may be fitness consequences, although these will be lessened if individuals can compensate by food acquisition at the burrow itself.

The finding that grooming rate, but not proportion of time spent grooming, was significantly affected by traffic noise compared to ambient sound could be attributable to noise as a distracting stimulus (‘distracted prey hypothesis’; Chan *et al.*, 2010) or a threat (‘increased threat hypothesis’; Owens, Stec and O’Hatnick, 2012) since both situations may promote vigilance behaviours over secondary behaviours. A reduction in social behaviours has been documented in rats under white-noise conditions at 85 dB (Weyers *et al.*, 1994) and domestic pigs exposed to repeated noise over a month period (Otten *et al.*, 2004) with sensitization to the noise stimulus occurring over time. Without repeating noise trials to mongoose groups we cannot conclude with certainty that this might not occur. Reduced time spent grooming in this study is probably not a result of less time available for such behaviours, as traffic noise increased group latency to leave the burrow. Instead a different trade-off to that experienced by foragers is likely, whereby individuals are able to prioritise anti-predator behaviours to noise over social interactions, without the immediate costs of lost foraging. In light of a recent finding that outgroup conflict can increase affiliative behaviours (including social grooming) within groups (Morris-Drake *et al.*, 2019) we might have expected noise (a potential stressor) to result in increased investment in grooming at the burrow. However, since we were unable to observe behaviours *inside* the burrows, we cannot rule out the possibility that (increased) grooming did occur out of sight in this study.

It is possible that noise effects on dwarf mongooses could have knock-on consequences for other species. Community composition has been shown to be altered by anthropogenic noise, both experimentally (McClure *et al.*, 2013, 2016) and across 'natural' environmental gradients (Polak *et al.*, 2013; Proppe, Sturdy and St. Clair, 2013). In dwarf mongooses, departure time from the burrow has been found to vary with the presence of hornbills (Rasa, 1983), and fork-tailed drongos (*Dicrurus adsimilis*) are known to have a mutual relationship with foraging groups (Sharpe, Joustra and Cherry, 2010). Although the behaviour of species other than dwarf mongooses was not recorded, it is possible that traffic noise might reduce the likelihood of these other species being present in proximity to the group, and therefore the later departure from the burrow could be a result of species-specific effects; the absence of hornbills together with the potential that traffic noise poses a threat, may delay mongooses in their departure to forage.

2.6 Conclusion

Our results show that traffic noise – one of the most ubiquitous sources of noise pollution – incurs costs for individuals in terms of potential losses in foraging time along with associated fitness consequences. This provides possible support for the 'increased threat hypothesis', in line with the growing literature demonstrating that (traffic) noise results in heightened vigilance (Quinn *et al.*, 2006; Kern and Radford, 2016a; Klett-Mingo, Pavón and Gil, 2016; Shannon, Crooks, *et al.*, 2016), although responses here were not long-lasting. We do, however, find differences in the post-exposure responses between two temporally differing noise treatments, which serves to highlight the complexity of noise and how these characteristics can impact on long-term behavioural changes and recovery.

Additionally, we show that group departure to begin foraging was delayed in traffic noise, although there are likely to be numerous factors, including masking effects, that may play a role here. Many studies to-date have only considered impacts in a single context and used only a single type of noise which considerably overlooks the complexity of noise and possible context-dependent effects (Neo *et al.*, 2018). In addition, many tests are under laboratory-controlled conditions so responses cannot be reliably extrapolated to the wild, where the natural range of behaviour is less restricted. Further work investigating possible compensatory behaviour would help substantiate our conclusions as to the magnitude of these noise impacts and the long-term consequences for populations.

Chapter 3. General discussion

3.1 Thesis findings

The main aim of this study was to ascertain whether variation in the temporal aspect of traffic noise (frequency of vehicle passes) might result in differential effects on the anti-predator vigilance of foraging dwarf mongooses. It was important to use the same recorded sound source, as noise is known to be highly variable depending on source type (Clark *et al.*, 2009; Shannon *et al.*, 2016), so only the intermittency of vehicle passes was manipulated here. A second experiment conducted at the burrow involved independent playbacks of continuous traffic and ambient sound. This allowed an exploration of the influence of noise on group behaviours, in a different context where optimal behaviours may differ depending on the primary trade-offs faced during noise exposure. As field studies accounted for only 15% of recently-reviewed literature, the majority of which have focused on birds and marine mammals (Shannon, McKenna, *et al.*, 2016) the present study responds to an imperative need to improve our understanding of the impacts of noise pollution on wildlife and enable better-informed mitigation approaches.

Predation exerts a strong evolutionary force on many species, and as anthropogenic noise has been linked to provoking responses analogous to anti-predator behaviours this ubiquitous pollutant has the potential to have long-lasting ecological, even evolutionary, effects on species. Our findings demonstrate a strong effect on several behavioural measures in free-ranging mongooses. First, vigilance was significantly increased, consistent with the literature (e.g. Quinn *et al.*, 2006; Rabin, Coss and Owings, 2006; Meillère, Brischoux and Angelier, 2015), providing support for the ‘risk disturbance hypothesis’ (Frid and Dill, 2002) and the ‘increased threat hypothesis’ (Owens, Stec and O’Hatnick, 2012). Sentinel behaviour followed a similar pattern: foragers undertook more bouts and spent a greater proportion of time on sentinel during traffic noise. Analysis of post-playback responses revealed that intermittent and continuous traffic-noise followed different trends for this measure, providing evidence that noise variation can affect different responses and that periods after noise exposure are as important, if not more so, when assessing the extent of noise impacts and the speed of behavioural recovery.

3.2 Study limitations and future considerations

Due to limited researchers and a counterbalanced experimental design, it was not possible to conduct trials blind as the researcher was unaccompanied in the field. Ideally, data would be extracted from video trials with the sound muted but, again, the limited personnel meant that this was not possible in the current study. However, this is unlikely to have had major effects on the results as the response variables measured were objective (e.g. frequency of sentinel bouts, headscans etc.).

During each foraging trial, only the behavioural responses of the focal individual were recorded and examined. However, this somewhat disregards the social behaviour of this species; if we were able to assess the behaviour of neighbouring foragers and/or sentinels, this could improve our understanding of group-level impacts in this context. For example, we could examine whether recent sentinel activity influences the likelihood that an individual becomes sentinel and record the proportion of the group that are vigilant during noise playback. Future field experiments would benefit from multiple observers to enable more detailed data collection from several individuals simultaneously. Furthermore, investigating the vocal responses alongside the vigilance behaviours would help us to explore whether variation in traffic noise poses variability in ‘threat’ (‘increased threat hypothesis’; Owens, Stec and O’Hatnick, 2012) or acts to mask ecologically relevant sounds such as alarm calls. In the latter case, vocal activity during vigilance behaviours may be reduced or altered, for instance by increasing amplitude. Building on previous work investigating the effects of traffic-noise on vocal activity (Kern and Radford, 2016b; Morris-Drake *et al.*, 2017), we could explore whether intermittent and continuous noise result in different vocal responses and whether the responses are appropriate.

Due to time limits, it was not possible to investigate any compensatory behaviours in the days following traffic-noise playback at the burrow. Further work, with this longer-term perspective, would enable us to assess whether and how group behaviours change with noise exposure and if any compensatory behaviour is possible; compensatory behaviour could include decreasing time spent on other activities (e.g. grooming or resting) or moving to ‘safer’ refuges. Additionally, GPS tracking would be valuable to explore if territory use changes with noise exposure.

Considering the choice and handling time of food items (such as Purser and Radford, 2011) in future experiments of this type could help us to assess the more cryptic impacts of noise exposure and whether individuals are able to compensate for lost foraging time by switching to a higher calorie prey. With regard to both experiments, recording the presence of other species known to influence the behaviour of the study species could help explain the responses observed. For dwarf mongooses, the presence of fork-tailed drongos and hornbills affects vigilance and group departure from burrows (Rasa, 1983; Sharpe, Joustra and Cherry, 2010). Therefore, considering the behaviour of these species alongside the responses of mongooses could be valuable in understanding the wider impacts of noise on the maintenance of interspecific interactions within ecological communities.

3.3 The future

It is clear from the growing literature that there is an imperative need for a better understanding of the effects of anthropogenic noise on wildlife, particularly with forecasts for future human population growth and climate change, which places increasing pressure on the environment. Noise pollution could have long-term and irreversible impacts, not only on vulnerable, noise-sensitive species but if ecological services are disrupted the consequences could affect humans too.

This study aimed to investigate the behavioural responses of individual dwarf mongooses in relation to traffic-noise playback differing only in temporal characteristics. The responses were measured over a relatively short timescale; further experiments covering a range of time scales would improve our understanding of the longer-term consequences of noise exposure and possible compensatory behaviours at the individual level. Additionally, incorporating physiological measures as part of an interdisciplinary approach (see Wright *et al.*, 2007; Rosa and Koper, 2018) could prove valuable in examining the mechanisms behind the observed responses and the potential for adaptation to noise. Considering previous experience of noise (Radford *et al.*, 2016) and/or exposure during key developmental periods (as in Crino *et al.*, 2013; Potvin and MacDougall-Shackleton, 2015) could also be useful in developing mitigation strategies, for example by reducing noisy activities during certain periods.
On a wider scale, incorporating noise into habitat-selection models (such as Blickley and Patricelli, 2010) would help to understand where populations are most at risk of the impacts of noise and enable us to make predictions about species ranges and movements as well as

potential conflicts with human activities. As attempted in the current study, investigating the impacts of noise on individuals in different contexts is an important consideration when trying to understand the wider implications at a population scale. As behaviours relating to (predation) threats are known to be influenced by knowledge of the environment (Robinson and Merrill, 2013), frequency and prior experience of threats (Nedelec *et al.*, 2016; Radford *et al.*, 2016) and social factors such as group size (Lima and Bednekoff, 1999b), the complexities of noise-induced responses should not be underestimated. Combining modelling with empirical studies would help to establish better-informed conclusions about population-level impacts of noise and how we could mitigate severe impacts.

Many studies so far have not addressed the complexity of noise in the context of a natural ecosystem. Similar to Francis, Ortega and Cruz (2009, 2011), future research should seek to broaden our perspective to investigate the wider ecological impacts of noise by observing multiple species (as in Voellmy *et al.*, 2014) as well as examining changes in the interactions between species (e.g. predator–prey dynamics; Simpson *et al.*, 2016 or responses to (heterospecific) alarm calls; Magrath *et al.*, 2015; Zhou, Radford and Magrath, 2019). Furthermore, filling in the gaps by examining the impacts on a wider range of taxa, including invertebrates (Morley, Jones and Radford, 2014) would further improve our understanding of noise impacts at a community level.

Moving forward, findings from studies investigating the impacts of anthropogenic noise on humans and non-human species alike, should ultimately be used to target conservation – prioritising areas that are particularly sensitive to noise pollution or are inhabited by vulnerable populations – as well as to help develop appropriate mitigation measures, for example through altering timing of activities or creating sound absorbing barriers to reduce exposure levels.

3.4 Conclusion

Anthropogenic noise is an evolutionarily novel pollutant of global concern, but only in recent decades have we begun to appreciate how noise impacts humans and non-human animals alike. Traffic noise is a widespread source of noise pollution (Barber, Crooks and Fristrup, 2010) and the relative dearth of field-based research make this study a relevant and fundamental base on which to investigate the behaviour of animals in their natural environment. The results of this study show that variation in temporal characteristics can afford significant changes in anti-predator behaviour which may consequently affect fitness. Through playback experiments, we show that traffic noise results in heightened vigilance with potential costs to foraging time. However, longer-term experiments would allow better assessment of behavioural changes over time. Additionally, in support of recent research (e.g. Francis *et al.*, 2012), we recommend taking a wider, community-level view and in light of the current study, consider different contexts of noise exposure since this may affect immediate responses and potential tolerance or sensitization over time.

References

Akaike, H., 1974. A new look at the statistical model identification, *IEEE Transactions on Automatic Control,* 19(6), pp.716-723.

Anderson, P. A., Berzins, I. K., Fogarty, F., Hamlin, H. J. and Guillette, L. J. (2011) 'Sound, stress, and seahorses: The consequences of a noisy environment to animal health', *Aquaculture,* 311(1–4), pp. 129–138. doi: 10.1016/j.aquaculture.2010.11.013.

Barber, J. R., Crooks, K. R. and Fristrup, K. M. (2010) 'The costs of chronic noise exposure for terrestrial organisms', *Trends in Ecology and Evolution,* 25(3), pp. 180–189. doi: 10.1016/j.tree.2009.08.002.

Bates, D., Maechler, M., Bolker, B. and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48.doi:10.18637/jss.v067.i01

Bayne, E. M., Habib, L. and Boutin, S. (2008) 'Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest', *Conservation Biology,* 22(5), pp. 1186–1193. doi: 10.1111/j.1523-1739.2008.00973.x.

Blair, H. B., Merchant, N. D., Friedlaender, A. S., Wiley, D. N. and Parks, S. E. (2016) 'Evidence for ship noise impacts on humpback whale foraging behaviour', *Biology Letters,* 12(8). doi: 10.1098/rsbl.2016.0005.

Blickley, J. L., Word, K. R., Krakauer, A. H., Phillips, J. L., Sells, S. N., Taff, C. C., Wingfield, J. C. and Patricelli, G. L. (2012) 'Experimental Chronic Noise Is Related to Elevated Fecal Corticosteroid Metabolites in Lekking Male Greater Sage-Grouse (Centrocercus urophasianus)', *PLoS ONE,* 7(11). doi: 10.1371/journal.pone.0050462.

Blickley, J. L., Blackwood, D. and Patricelli, G. L. (2012) 'Experimental Evidence for the Effects of Chronic Anthropogenic Noise on Abundance of Greater Sage-Grouse at Leks', *Conservation Biology,* 26(3), pp. 461–471. doi: 10.1111/j.1523-1739.2012.01840.x.

Blickley, J. L. and Patricelli, G. L. (2010) ‘Impacts of anthropogenic noise on wildlife: Research priorities for the development of standards and mitigation’, *Journal of International Wildlife Law and Policy*, 13(4), pp. 274–292. doi: 10.1080/13880292.2010.524564.

Blom, E. L., Kvarnemo, C., Dekhla, I., Schöld, S., Andersson, M. H., Svensson, O. and Amorim, M. C. P. (2019) ‘Continuous but not intermittent noise has a negative impact on mating success in a marine fish with paternal care’, *Scientific Reports*, 9(1), pp. 1–9. doi: 10.1038/s41598-019-41786-x.

Blumstein, D. T. (2006) ‘The multipredator hypothesis and the evolutionary persistence of antipredator behavior’, *Ethology*, 112(3), pp. 209–217. doi: 10.1111/j.1439-0310.2006.01209.x.

Brennecke, D., Duarte, B., Paiva, F., Caçador, I. and Canning-Clode, J. (2016) ‘Microplastics as vector for heavy metal contamination from the marine environment’, *Estuarine, Coastal and Shelf Science*, 178, pp. 189–195. doi: 10.1016/j.ecss.2015.12.003.

Brouček, J. (2014) ‘Effect of noise on performance, stress, and behaviour of animals’, *Slovak Journal of Animal Science*, 47(2), pp. 111–123. Available at: http://www.cvzv.sk/slju/14_2/8_Broucek.pdf.

Bruintjes, R., Purser, J., Everley, K. A., Mangan, S., Simpson, S. D. and Radford, A. N. (2016) ‘Rapid recovery following short-term acoustic disturbance in two fish species’, *Royal Society Open Science*, 3(1). doi: 10.1098/rsos.150686.

Brumm, H. (2004) ‘The impact of environmental noise on song amplitude in a territorial bird’, *Journal of Animal Ecology*, 73(3), pp. 434–440. doi: 10.1111/j.0021-8790.2004.00814.x.

Brumm, H. and Todt, D. (2002) ‘Noise-dependent song amplitude regulation in a territorial songbird’, *Animal Behaviour*, 63(5), pp. 891–897. doi: 10.1006/anbe.2001.1968.

Buxton, R. ., McKenna, M. F., Mennitt, D., Fristrup, K., Crooks, K., Angeloni, L. and Wittemyer, G. (2017) ‘Noise pollution is pervasive in U.S. protected areas’, *Science*, 533(May), pp. 437–490. doi: 10.1163/9789004313507_013.

Van Cauwenberghe, L., Vanreusel, A., Mees, J. and Janssen, C. R. (2013) ‘Microplastic pollution in deep-sea sediments’, *Environmental Pollution*, 182, pp. 495–499. doi: 10.1016/j.envpol.2013.08.013.

Chan, A. A. Y. H., Giraldo-Perez, P., Smith, S. and Blumstein, D. T. (2010) ‘Anthropogenic noise affects risk assessment and attention: The distracted prey hypothesis’, *Biology Letters*, 6(4), pp. 458–461. doi: 10.1098/rsbl.2009.1081.

Christensen, C., Kern, J. M., Bennitt, E. and Radford, A. N. (2016) ‘Rival group scent induces changes in dwarf mongoose immediate behavior and subsequent movement’, *Behavioral Ecology*, 27(6), pp. 1627–1634 doi: 10.1093/beheco/arw092.

Clark, C. W., Ellison, W. T., Southall, B. L., Hatch, L., Van Parijs, S. M., Frankel, A. and Ponirakis, D. (2009) ‘Acoustic masking in marine ecosystems: Intuitions, analysis, and implication’, *Marine Ecology Progress Series*, 395, pp. 201–222. doi: 10.3354/meps08402.

Clark, W. W. (1991) ‘Recent studies of temporary threshold shift (TTS) and permanent threshold shift (PTS) in animals’, *The Journal of the Acoustical Society of America*, 90(1), pp. 155–163. doi: 10.1121/1.401309.

Clergeau, P., Croci, S., Jokimäki, J., Kaisanlahti-Jokimäki, M. L. and Dinetti, M. (2006) ‘Avifauna homogenisation by urbanisation: Analysis at different European latitudes’, *Biological Conservation*, 127(3), pp. 336–344. doi: 10.1016/j.biocon.2005.06.035.

Clutton-Brock, T. H., O’Riain, M. J., Brotherton, P. N. M., Gaynor, D., Kansky, R., Griffin, A. S. and Manser, M. (1999) ‘Selfish sentinels in cooperative mammals’, *Science*, 284(5420), pp. 1640–1644. doi: 10.1126/science.284.5420.1640.

Cole, M., Lindeque, P., Halsband, C. and Galloway, T. S. (2011) 'Microplastics as contaminants in the marine environment: A review', *Marine Pollution Bulletin*, 62(12), pp. 2588–2597. doi: 10.1016/j.marpolbul.2011.09.025.

Collier, K., Radford, A. N., Townsend, S. W. and Manser, M. B. (2017) 'Wild dwarf mongooses produce general alert and predator-specific alarm calls', *Behavioral Ecology*, 28(5), pp. 1293–1301. doi: 10.1093/beheco/arx091.

Creel, S., Creel, N., Wildt, D. E. and Monfort, S. L. (1992) 'Behavioural and endocrine mechanisms of reproductive suppression in Serengeti dwarf mongooses', *Animal Behaviour*, 43(2), pp. 231–245. doi: 10.1016/S0003-3472(05)80219-2.

Creel, S., Dantzer, B., Goymann, W. and Rubenstein, D. R. (2013) 'The ecology of stress: Effects of the social environment', *Functional Ecology*, 27(1), pp. 66–80. doi: 10.1111/j.1365-2435.2012.02029.x.

Creel, S., Monfort, S. L., Creel, N. M., Wildt, D. E. and Waser, P. M. (1995) 'Pregnancy, oestrogens and future reproductive success in Serengeti dwarf mongooses', *Animal Behaviour*, 50(4), pp. 1132–1135. doi: 10.1016/0003-3472(95)80113-8.

Creel, S. and Waser, P. M. (1994) 'Inclusive fitness and reproductive strategies in dwarf mongooses', *Behavioral Ecology*, 5(3), pp. 339–348. doi: 10.1093/beheco/5.3.339.

Creel, S., Winnie, J. A., Christianson, D. and Liley, S. (2008) 'Time and space in general models of antipredator response: Tests with wolves and elk', *Animal Behaviour*, 76(4), pp. 1139–1146. doi: 10.1016/j.anbehav.2008.07.006.

Crino, O. L., Breuner, C. W., Blickley, J. L., Johnson, E. E. and Patricelli, G. L. (2013) 'Effects of experimentally elevated traffic noise on nestling white-crowned sparrow stress physiology, immune function and life history', *Journal of Experimental Biology*, 216(11), pp. 2055–2062. doi: 10.1242/jeb.081109.

Crutzen, P. J. (2002) ‘Geology of mankind’, *Nature,* 415(6867), pp. 23–23. doi: 10.1038/415023a.

Davies, S., Haddad, N. and Ouyang, J. Q. (2017) ‘Stressful city sounds: Glucocorticoid responses to experimental traffic noise are environmentally dependent’, *Biology Letters,* 13(10). doi: 10.1098/rsbl.2017.0276.

Davies, T. W., Duffy, J. P., Bennie, J. and Gaston, K. J. (2014) ‘The nature, extent, and ecological implications of marine light pollution’, *Frontiers in Ecology and the Environment*, 12(6), pp. 347–355. doi: 10.1890/130281.

Dimitriadis, C., Fournari – Konstantinidou, I., Sourbès, L., Koutsoubas, D. and Mazaris, A. D. (2018) ‘Reduction of sea turtle population recruitment caused by nightlight: Evidence from the Mediterranean region’, *Ocean and Coastal Management*, 153(July), pp. 108–115. doi: 10.1016/j.ocecoaman.2017.12.013.

Doney, S. C., Fabry, V. J., Feely, R. A. and Kleypas, J. A. (2009) ‘Ocean acidification: the other CO2 problem’, *Annual Review of Marine Science,* 1, pp. 169–92. doi: 10.1146/annurev.marine.010908.163834.

Dooling, R. J. and Popper, A. N. (2016a) ‘Some lessons from the effects of highway noise on birds’, *Proceedings of Meetings on Acoustics,* 27(1), doi: 10.1121/2.0000244.

Dooling, R. J. and Popper, A. N. (2016b) *Technical Guidance for Assessment and Mitigation of the Effects of Traffic Noise and Road Construction Noise on Birds*. Sacramento. Available at: http://www.dot.ca.gov/hq/env/noise/pub/caltransBirdReport_6_15_2016.pdf.

Dooling, R. and Popper, A. (2007) ‘The effects of highway noise on birds’, The California Department of Transportation Division of Environmental Analysis, Sacramento, CA, pp.1-74. Available at: http://www.researchgate.net/publication/228381219_The_effects_of_highway_noise_on_birds/file/32bfe510fac89d682a.pdf.

Dunlop, R. A. (2016) ‘The effect of vessel noise on humpback whale, *Megaptera novaeangliae*, communication behaviour’, *Animal Behaviour*, 111, pp. 13–21. doi: 10.1016/j.anbehav.2015.10.002.

Dutilleux, G. (2017) ‘Anthropogenic sound and terrestrial ecosystems : A review of recent evidence’, *Icben 2017*, pp. 1–9.

Eriksson, C., Pershagen, G. and Nilsson, M. (2018) ‘Biological mechanisms related to cardiovascular and metabolic effects by environmental noise’, *World Health Organisation Regional Office for Europe*, p. 19.

Evans, J. C., Dall, S. R. X. and Kight, C. R. (2018) ‘Effects of ambient noise on zebra finch vigilance and foraging efficiency’, *PLoS ONE*, 13(12), pp. 17–22. doi: 10.1371/journal.pone.0209471.

Ficken, M. S. (1990) ‘Acoustic characteristics of alarm calls associated with predation risk in Chickadees’, *Animal Behaviour*, 39(2), pp. 401–403. doi: 10.1016/S0003-3472(05)80889-9.

Finneran, J. J. (2015) ‘Noise-induced hearing loss in marine mammals: A review of temporary threshold shift studies from 1996 to 2015’, *The Journal of the Acoustical Society of America*, 138(3), pp. 1702–1726. doi: 10.1121/1.4927418.

Forman, R. T. T. and Alexander, L. E. (2002) ‘Roads and Their Major Ecological Effects’, *Annual Review of Ecology and Systematics*, 29(1), pp. 207–231. doi: 10.1146/annurev.ecolsys.29.1.207.

Fortin, D., Boyce, M. S., Merrill, E. H. and Fryxell, J. M. (2004) ‘Foraging Costs of Vigilance in Large Mammalian Herbivores in large mammalian herbivores costs of vigilance Foraging’, *Oikos*, 107(March), pp. 172–180.

Francis, C. D., Kleist, N. J., Ortega, C. P. and Cruz, A. (2012) ‘Noise pollution alters ecological services: Enhanced pollination and disrupted seed dispersal’, *Proceedings of the*

Royal Society B: Biological Sciences, 279(1739), pp. 2727–2735. doi: 10.1098/rspb.2012.0230.

Francis, C. D. (2015) 'Vocal traits and diet explain avian sensitivities to anthropogenic noise', *Global Change Biology,* 21(5), pp. 1809–1820. doi: 10.1111/gcb.12862.

Francis, C. D. and Barber, J. R. (2013) 'A framework for understanding noise impacts on wildlife: An urgent conservation priority', *Frontiers in Ecology and the Environment,* 11(6), pp. 305–313. doi: 10.1890/120183.

Francis, C. D., Ortega, C. P. and Cruz, A. (2009) 'Noise Pollution Changes Avian Communities and Species Interactions', *Current Biology,* 19(16), pp. 1415–1419. doi: 10.1016/j.cub.2009.06.052.

Francis, C. D., Ortega, C. P. and Cruz, A. (2011a) 'Noise pollution filters bird communities based on vocal frequency', *PLoS ONE,* 6(11). doi: 10.1371/journal.pone.0027052.

Francis, C. D., Ortega, C. P. and Cruz, A. (2011b) 'Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers', *Proceedings of the Royal Society B: Biological Sciences,* 278(1714), pp. 2025–2031. doi: 10.1098/rspb.2010.1847.

Frid, A. and Dill, L. (2002) 'Human-caused disturbance stimuli as a form of predation risk', *Ecology and Society,* 6(1), p.11. doi: 10.5751/ES-00404-060111.

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E. and Brashares, J. S. (2019) 'Landscapes of Fear: Spatial Patterns of Risk Perception and Response', *Trends in Ecology and Evolution,* 34(4), pp. 355–368. doi: 10.1016/j.tree.2019.01.004.

Van Geffen, K. G., Groot, A. T., Van Grunsven, R. H. A., Donners, M., Berendse, F. and Veenendaal, E. M. (2015) 'Artificial night lighting disrupts sex pheromone in a noctuid moth', *Ecological Entomology,* 40(4), pp. 401–408. doi: 10.1111/een.12202.

Gill, S. A., Job, J. R., Myers, K., Naghshineh, K. and Vonhof, M. J. (2015) ‘Toward a broader characterization of anthropogenic noise and its effects on wildlife’, *Behavioral Ecology,* 26(2), pp. 328–333. doi: 10.1093/beheco/aru219.

Grade, A. M. and Sieving, K. E. (2016) ‘When the birds go unheard: Highway noise disrupts information transfer between bird species’, *Biology Letters,* 12(4), pp. 7–10. doi: 10.1098/rsbl.2016.0113.

Güneralp, B. and Seto, K. C. (2013) ‘Futures of global urban expansion: Uncertainties and implications for biodiversity conservation’, *Environmental Research Letters,* 8(1), pp. 014025 doi: 10.1088/1748-9326/8/1/014025.

Guralnick, R. P., Kleist, N. J., Lowry, C. A., Cruz, A. and Francis, C. D. (2018) ‘Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community’, *Proceedings of the National Academy of Sciences,* 115(4), pp. E648–E657. doi: 10.1073/pnas.1709200115.

Halfwerk, W., Holleman, L. J. M., Lessells, C. M. and Slabbekoorn, H. (2011) ‘Negative impact of traffic noise on avian reproductive success’, *Journal of Applied Ecology,* 48(1), pp. 210–219. doi: 10.1111/j.1365-2664.2010.01914.x.

Hammer M.S., Swinburn T.K. and Neitzel R.L. (2014) ‘Environmental Noise Pollution in the United States: Developing an Effective Public Health Response’, *Environmental Health Perspectives,* 122(2), pp. 115–119.

Hildebrand, J. A. (2009) ‘Anthropogenic and natural sources of ambient noise in the ocean’, *Marine Ecology Progress Series,* 395, pp. 5–20. doi: 10.3354/meps08353.

Hiscocks, K. and M. R. Perrin (1991) ‘Den selection and use by dwarf mongooses and banded mongooses in South Africa’, *South African Journal of Wildlife Research,* 21(4), pp. 119–122.

Hoffmann, M., Roberts, R. L. and Kern, J. (2014) ‘Tree climbing and denning by Common Dwarf Mongoose *Helogale parvula*’, *Small Carnivore Conservation*, 50, pp. 66–67.

Hölker, F., Wolter, C., Perkin, E. K. and Tockner, K. (2010) ‘Light pollution as a biodiversity threat’, *Trends in Ecology and Evolution*, 25(12), pp. 681–682. doi: 10.1016/j.tree.2010.09.007.

Hollén, L. I. and Radford, A. N. (2009) ‘The development of alarm call behaviour in mammals and birds’, *Animal Behaviour*, 78(4), pp. 791–800. doi: 10.1016/j.anbehav.2009.07.021.

Holmes, L. A., Turner, A. and Thompson, R. C. (2012) ‘Adsorption of trace metals to plastic resin pellets in the marine environment’, *Environmental Pollution*, 160(1), pp. 42–48. doi: 10.1016/j.envpol.2011.08.052.

Holt, M. M., Noren, D. P., Veirs, V., Emmons, C. K. and Veirs, S. (2009) ‘ Speaking up: Killer whales (Orcinus orca) increase their call amplitude in response to vessel noise ’, *The Journal of the Acoustical Society of America*, 125(1), pp. EL27-EL32. doi: 10.1121/1.3040028.

Hothorn T., Hornik K., van de Wiel M.A., Zeileis A. (2006) 'A Lego system for conditional inference', *The American Statistician*, 60(3), 257–263. doi: 10.1198/000313006X118430.

Hu, Y. and Cardoso, G. C. (2010) ‘Which birds adjust the frequency of vocalizations in urban noise?’, *Animal Behaviour*, 79(4), pp. 863–867. doi: 10.1016/j.anbehav.2009.12.036.

Huang, P., Sieving, K. E. and Mary, C. M. S. (2012) ‘Heterospecific information about predation risk influences exploratory behavior’, *Behavioral Ecology*, 23(3), pp. 463–472. doi: 10.1093/beheco/arr212.

Hughes, A. C. (2017) ‘Understanding the drivers of Southeast Asian biodiversity loss’, *Ecosphere*, 8(1), e01624. doi: 10.1002/ecs2.1624.

Ito, R., Ikeuchi, I. and Mori, A. (2014) ‘A Day Gecko Darkens its Body Color in Response to Avian Alarm Calls’, *Current Herpetology,* 32(1), pp. 26–33. doi: 10.5358/hsj.32.26.

Jankowski, M. D., Franson, J. C., Möstl, E., Porter, W. P. and Hofmeister, E. K. (2010) ‘Testing independent and interactive effects of corticosterone and synergized resmethrin on the immune response to West Nile virus in chickens’, *Toxicology,* 269(1), pp. 81–88. doi: 10.1016/j.tox.2010.01.010.

Jennions, M. D. and Macdonald, D. W. (1993) ‘Cooperative breeding in Mammals’, *Trends in Ecology and Evolution*, 9(3), pp. 89–93.

de Jong, K., Amorim, M. C. P., Fonseca, P. J., Fox, C. J. and Heubel, K. U. (2018) ‘Noise can affect acoustic communication and subsequent spawning success in fish’, *Environmental Pollution*, 237, pp. 814–823. doi: 10.1016/j.envpol.2017.11.003.

Kastelein, R. A., Hoek, L., Gransier, R., Rambags, M. and Claeys, N. (2014) ‘Effect of level, duration, and inter-pulse interval of 1–2 kHz sonar signal exposures on harbor porpoise hearing’, *The Journal of the Acoustical Society of America,* 136(1), pp. 412–422. doi: 10.1121/1.4883596.

Kastelein, R. A., Gransier, R., Schop, J. and Hoek, L. (2015) ‘ Effects of exposure to intermittent and continuous 6–7 kHz sonar sweeps on harbor porpoise (Phocoena phocoena) hearing ’, *The Journal of the Acoustical Society of America,* 137(4), pp. 1623–1633. doi: 10.1121/1.4916590.

Katti, M. and Warren, P. S. (2004) ‘Tits , noise and urban bioacoustics’, *Trends in Ecology and Evolution,* (April), pp. 2003–2005. doi: 10.1016/j.tree.2003.12.006.

Kern, J. M., Laker, P. R. and Radford, A. N. (2017) ‘Contextual variation in the alarm call responses of dwarf mongooses, Helogale parvula’, *Animal Behaviour*, 127, pp. 43–51. doi: 10.1016/j.anbehav.2017.03.002.

Kern, J. M. and Radford, A. N. (2013) ‘Call of duty? Variation in use of the watchman’s song by sentinel dwarf mongooses, Helogale parvula’, *Animal Behaviour,* 85(5), pp. 967–975. doi: 10.1016/j.anbehav.2013.02.020.

Kern, J. M. and Radford, A. N. (2014) ‘Sentinel dwarf mongooses, Helogale parvula, exhibit flexible decision making in relation to predation risk’, *Animal Behaviour,* 98, pp. 185–192. doi: 10.1016/j.anbehav.2014.10.012.

Kern, J. M. and Radford, A. N. (2016) ‘Anthropogenic noise disrupts use of vocal information about predation risk’, *Environmental Pollution,* 218, pp. 988–995. doi: 10.1016/j.envpol.2016.08.049.

Kern, J. M., Sumner, S. and Radford, A. N. (2016) ‘Sentinel dominance status influences forager use of social information’, *Behavioral Ecology,* 27(4), pp. 1053–1060. doi: 10.1093/beheco/arv240.

Kight, C. R. and Swaddle, J. P. (2011) ‘How and why environmental noise impacts animals: An integrative, mechanistic review’, *Ecology Letters,* 14(10), pp. 1052–1061. doi: 10.1111/j.1461-0248.2011.01664.x.

Kight, C. R. and Swaddle, J. P. (2015) ‘Eastern bluebirds alter their song in response to anthropogenic changes in the acoustic environment’, *Integrative and Comparative Biology,* 55(3), pp. 418–431. doi: 10.1093/icb/icv070.

Klett-Mingo, J. I., Pavón, I. and Gil, D. (2016) ‘Great tits, Parus major, increase vigilance time and reduce feeding effort during peaks of aircraft noise’, *Animal Behaviour,* 115, pp. 29–34. doi: 10.1016/j.anbehav.2016.02.021.

Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M. and Fontaine, C. (2017) ‘Artificial light at night as a new threat to pollination’, *Nature,* 548(7666), pp. 206–209. doi: 10.1038/nature23288.

Laiolo, P. (2010) ‘The emerging significance of bioacoustics in animal species conservation’, *Biological Conservation*, 143(7), pp. 1635–1645. doi: 10.1016/j.biocon.2010.03.025.

Lewis, S. L. and Maslin, M. A. (2015) ‘Defining the Anthropocene’, *Nature,* 519(7542), pp. 171–180. doi: 10.1038/nature14258.

Lima, S.L. and Bednekoff, P. A. (1999a) ‘Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis’, *The American Naturalist,* 153(6), p. 649. doi: 10.2307/2463621.

Lima, S. L. and Bednekoff, P. A. (1999b) ‘Back to the basics of anti-predatory vigilance: the group-size effect’, *Animal Behaviour,* 49(1), pp. 11–20. Available at: http://www.sciencedirect.com/science/article/pii/0003347295801499.

Lima, S. L. and Dill, L. M. (1990) ‘Behavioral decisions made under the risk of predation: A review and prospectus’, *Canadian Journal of Zoology,* 68(4), pp. 619–640. doi: 10.1139/z90-092.

Lucass, C., Eens, M. and Müller, W. (2016) ‘When ambient noise impairs parent-offspring communication’, *Environmental Pollution,* 212, pp. 592–597. doi: 10.1016/j.envpol.2016.03.015.

Luo, J., Siemers, B. M. and Koselj, K. (2015) ‘How anthropogenic noise affects foraging’, *Global Change Biology,* 21(9), pp. 3278–3289. doi: 10.1111/gcb.12997.

Luther, D. A. and Derryberry, E. P. (2012) ‘Birdsongs keep pace with city life: Changes in song over time in an urban songbird affects communication’, *Animal Behaviour,* 83(4), pp. 1059–1066. doi: 10.1016/j.anbehav.2012.01.034.

Macgregor, C. J., Pocock, M. J. O., Fox, R. and Evans, D. M. (2019) ‘Effects of street lighting technologies on the success and quality of pollination in a nocturnally pollinated plant’, *Ecosphere,* 10(1), e02550. doi: 10.1002/ecs2.2550.

Magrath, R. D., Haff, T. M., Fallow, P. M. and Radford, A. N. (2015) 'Eavesdropping on heterospecific alarm calls: From mechanisms to consequences', *Biological Reviews*, 90(2), pp. 560–586. doi: 10.1111/brv.12122.

Marten, K. and Marler, P. (1977) 'Sound transmission and its significance for animal vocalization - I. Temperate habitats', *Behavioral Ecology and Sociobiology*, 2(3), pp. 271–290. doi: 10.1007/BF00299740.

Masini, C. V., Day, H. E. W. and Campeau, S. (2008) 'Long-term habituation to repeated loud noise is impaired by relatively short interstressor intervals in rats', *Behavioural Neuroscience*, 122(1), pp. 210–223. doi: 10.1158/0008-5472.CAN-10-4002.BONE.

McClure, C. J. W., Ware, H. E., Carlisle, J., Kaltenecker, G. and Barber, J. R. (2013) 'An experimental investigation into the effects of traffic noise on distributions of birds: Avoiding the phantom road', *Proceedings of the Royal Society B: Biological Sciences*, 280(1773). doi: 10.1098/rspb.2013.2290.

McClure, C. J. W., Ware, H. E., Carlisle, J. D. and Barber, J. R. (2016) 'Noise from a phantom road experiment alters the age structure of a community of migrating birds', *Animal Conservation*, 20(2), pp. 164–172. doi: 10.1111/acv.12302.

Mcdonald, R. I., Forman, R. T. T., Kareiva, P., Neugarten, R., Salzer, D. and Fisher, J. (2009) 'Urban effects, distance, and protected areas in an urbanizing world', *Landscape and Urban Planning*, 93(1), pp. 63–75. doi: 10.1016/j.landurbplan.2009.06.002.

McMullen, H., Schmidt, R. and Kunc, H. P. (2014) 'Anthropogenic noise affects vocal interactions', *Behavioural Processes*, 103, pp. 125–128. doi: 10.1016/j.beproc.2013.12.001.

Meillère, A., Brischoux, F., Ribout, C. and Angelier, F. (2015) 'Traffic noise exposure affects telomere length in nestling house sparrows', *Biology Letters*, 11(9). doi: 10.1098/rsbl.2015.0559.

Meillère, A., Brischoux, F. and Angelier, F. (2015) 'Impact of chronic noise exposure on antipredator behavior: An experiment in breeding house sparrows', *Behavioral Ecology*, 26(2), pp. 569–577. doi: 10.1093/beheco/aru232.

Monclús, R., Anderson, A. M. and Blumstein, D. T. (2015) 'Do Yellow-Bellied Marmots Perceive Enhanced Predation Risk When they are Farther from safety? An experimental study', *Ethology*, 121(9), pp. 831–839. doi: 10.1111/eth.12397.

Moore, C. J. (2008) 'Synthetic polymers in the marine environment: A rapidly increasing, long-term threat', *Environmental Research*, 108(2), pp. 131–139. doi: 10.1016/j.envres.2008.07.025.

Morelli, F., Beim, M., Jerzak, L., Jones, D. and Tryjanowski, P. (2014) 'Can roads, railways and related structures have positive effects on birds? - A review', *Transportation Research Part D: Transport and Environment*, 30, pp. 21–31. doi: 10.1016/j.trd.2014.05.006.

Morley, E. L., Jones, G. and Radford, A. N. (2014) 'The importance of invertebrates when considering the impacts of anthropogenic noise', *Proceedings of the Royal Society B: Biological Sciences*, 281(1776), pp. 2013–2683. doi: 10.1098/rspb.2013.2683.

Morris-Drake, A., Bracken, A. M., Kern, J. M. and Radford, A. N. (2017) 'Anthropogenic noise alters dwarf mongoose responses to heterospecific alarm calls', *Environmental Pollution*, 223, pp. 476–483. doi: 10.1016/j.envpol.2017.01.049.

Morris-Drake, A., Christensen, C., Kern, J. M. and Radford, A. N. (2019) 'Experimental field evidence that out-group threats influence within-group behavior', *Behavioral Ecology*, pp. 1–11, arz095, doi: 10.1093/beheco/arz095.

Morris-Drake, A., Kern, J. M. and Radford, A. N. (2016) 'Cross-modal impacts of anthropogenic noise on information use', *Current Biology*, 26(20), pp. R911–R912. doi: 10.1016/j.cub.2016.08.064.

Mourelatou, A. (2018) *Environmental indicator report 2018: In support to the monitoring of the Seventh Environment Action Programme*, European Environment Agency.

Nedelec, S. L., Mills, S. C., Lecchini, D., Nedelec, B., Simpson, S. D. and Radford, A. N. (2016) ‘Repeated exposure to noise increases tolerance in a coral reef fish’, *Environmental Pollution*, 216(September), pp. 428–436. doi: 10.1016/j.envpol.2016.05.058.

Nemeth, E., Kempenaers, B., Matessi, G. and Brumm, H. (2012) ‘Rock sparrow song reflects male age and reproductive success’, *PLoS ONE*, 7(8), e43259. doi: 10.1371/journal.pone.0043259.

Nemeth, E. and Brumm, H. (2009) ‘Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization?’, *Animal Behaviour*, 78(3), pp. 637–641. doi: 10.1016/j.anbehav.2009.06.016.

Neo, Y. Y., Seitz, J., Kastelein, R. A., Winter, H. V., ten Cate, C. and Slabbekoorn, H. (2014) ‘Temporal structure of sound affects behavioural recovery from noise impact in European seabass’, *Biological Conservation*, 178, pp. 65–73. doi: 10.1016/j.biocon.2014.07.012.

Neo, Y. Y., Hubert, J., Bolle, L. J., Winter, H. V. and Slabbekoorn, H. (2018) ‘European seabass respond more strongly to noise exposure at night and habituate over repeated trials of sound exposure’, *Environmental Pollution*, 239, pp. 367–374. doi: 10.1016/j.envpol.2018.04.018.

Nichols, T. A., Anderson, T. W. and Širović, A. (2015) ‘Intermittent noise induces physiological stress in a coastal marine fish’, *PLoS ONE*, 10(9), pp. 1–13. doi: 10.1371/journal.pone.0139157.

Nowacek, D. P., Thorne, L. H., Johnston, D. W. and Tyack, P. L. (2007) ‘Responses of cetaceans to anthropogenic noise’, *Mammal Review*, 37(2), pp. 81–115. doi: 10.1902/jop.2016.150698.

Otten, W., Kanitz, E., Puppe, B., Tuchscherer, M., Brüssow, K. P., Nürnberg, G. and Stabenow, B. (2004) 'Acute and long term effects of chronic intermittent noise stress on hypothalamic-pituitary-adrenocortical and sympatho-adrenomedullary axis in pigs', *Animal Science*, 78(2), pp. 271–283. doi: 10.1017/s1357729800054060.

Owens, J. L., Stec, C. L. and O'Hatnick, A. (2012) 'The effects of extended exposure to traffic noise on parid social and risk-taking behavior', *Behavioural Processes*, 91(1), pp. 61–69. doi: 10.1016/j.beproc.2012.05.010.

Pangle, W. M. and Holekamp, K. E. (2010) 'Functions of vigilance behaviour in a social carnivore, the spotted hyaena, Crocuta crocuta', *Animal Behaviour*, 80(2), pp. 257–267. doi: 10.1016/j.anbehav.2010.04.026.

Parks, S. E., Johnson, M., Nowacek, D. and Tyack, P. L. (2011) 'Individual right whales call louder in increased environmental noise', *Biology Letters*, 7(1), pp. 1–3. doi: 10.1098/rsbl.2010.0451.

Parks, S. E., Holden, W. M., Reinert, L. K., Walsh, K. A., Langkilde, T., Swierk, L., Rollins-Smith, L. A. and Tennessen, J. B. (2018) 'Frogs adapt to physiologically costly anthropogenic noise', *Proceedings of the Royal Society B: Biological Sciences*, 285(1891), p. 20182194. doi: 10.1098/rspb.2018.2194.

Partan, S. R. (2017) 'Multimodal shifts in noise: switching channels to communicate through rapid environmental change', *Animal Behaviour*, 124, pp. 325–337. doi: 10.1016/j.anbehav.2016.08.003.

Passchier-Vermeer, W. and Passchier, W. F. (2000) 'Noise exposure and public health', *Environmental Health Perspectives*, 108(SUPPL. 1), pp. 123–131.

Peng, C., Zhao, X. and Liu, G. (2015) 'Noise in the sea and its impacts on marine organisms', *International Journal of Environmental Research and Public Health*, 12(10), pp. 12304–12323. doi: 10.3390/ijerph121012304.

Petrelli, A. R., Levenhagen, M. J., Wardle, R., Barber, J. R. and Francis, C. D. (2017) 'First to Flush: The Effects of Ambient Noise on Songbird Flight Initiation Distances and Implications for Human Experiences with Nature', *Frontiers in Ecology and Evolution,* 5(67). doi: 10.3389/fevo.2017.00067.

Pimm, S. L., Russell, G. J., Gittleman, J. L. and Brooks, T. M. (1995) 'The Future of Biodiversity', *Science,* 269, pp. 347–350.

Pohl, N. U., Leadbeater, E., Slabbekoorn, H., Klump, G. M. and Langemann, U. (2012) 'Great tits in urban noise benefit from high frequencies in song detection and discrimination', *Animal Behaviour,* 83(3), pp. 711–721. doi: 10.1016/j.anbehav.2011.12.019.

Polak, M., Wiacek, J., Kucharczyk, M. and Orzechowski, R. (2013) 'The effect of road traffic on a breeding community of woodland birds', *European Journal of Forest Research,* 132(5–6), pp. 931–941. doi: 10.1007/s10342-013-0732-z.

Poot, H., Ens, B. J., Vries, H. De, Donners, M. a H., Wernand, M. R. and M, J. (2008) 'Green Light for Nocturnally Migrating Birds Ecology and Society : Green Light for Nocturnally Migrating Birds', *Ecology and Society,* 13(2), pp. 1–7, article 47.

Popper, A. N. and Hastings, M. C. (2009) 'The effects of human-generated sound on fish.', *Integrative Zoology,* 4(1), pp. 43–52. doi: 10.1111/j.1749-4877.2008.00134.x.

Potvin, D. A. and MacDougall-Shackleton, S. A. (2015) 'Traffic noise affects embryo mortality and nestling growth rates in captive zebra finches', *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology,* 323(10), pp. 722–730. doi: 10.1002/jez.1965.

Potvin, D. A., Mulder, R. A. and Parris, K. M. (2014) 'Silvereyes decrease acoustic frequency but increase efficacy of alarm calls in urban noise', *Animal Behaviour,* 98, pp. 27–33. doi: 10.1016/j.anbehav.2014.09.026.

Potvin, D. A., Parris, K. M. and Mulder, R. A. (2011) ‘Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in silvereyes (Zosterops lateralis)’, *Proceedings of the Royal Society B: Biological Sciences*, 278(1717), pp. 2464–2469. doi: 10.1098/rspb.2010.2296.

Proppe, D. S., Sturdy, C. B. and St. Clair, C. C. (2013) ‘Anthropogenic noise decreases urban songbird diversity and may contribute to homogenization’, *Global Change Biology*, 19(4), pp. 1075–1084. doi: 10.1111/gcb.12098.

Purser, J., Bruintjes, R., Simpson, S. D. and Radford, A. N. (2016) ‘Condition-dependent physiological and behavioural responses to anthropogenic noise’, *Physiology and Behavior*, 155(January), pp. 157–161. doi: 10.1016/j.physbeh.2015.12.010.

Purser, J. and Radford, A. N. (2011) ‘Acoustic noise induces attention shifts and reduces foraging performance in three-spined sticklebacks (Gasterosteus aculeatus)’, *PLoS ONE*, 6(2), e17478. doi: 10.1371/journal.pone.0017478.

Quinn, J. L., Whittingham, M. J., Butler, S. J. and Will, C. (2006) ‘Noise, predation risk compensation and vigilance in the chaffinch *Fringilla coelebs*’, *Journal of Avian Biology*, 37(6), pp.601-608.

Rabin, L. A., Coss, R. G. and Owings, D. H. (2006) ‘The effects of wind turbines on antipredator behavior in California ground squirrels (*Spermophilus beecheyi*)’, *Biological Conservation*, 131(3), pp. 410–420. doi: 10.1016/j.biocon.2006.02.016.

Radford, A., Morley, E. and Jones, G. (2012) The effects of noise on biodiversity, Defra Report NO0235. *Department for Environment, Food, & Rural Affairs*, London.

Radford, A. N., Lèbre, L., Lecaillon, G., Nedelec, S. L. and Simpson, S. D. (2016) ‘Repeated exposure reduces the response to impulsive noise in European seabass’, *Global Change biology*, 22(10), pp. 3349–3360. doi: 10.1111/gcb.13352.

Radle, A. L. (2007) 'The Effect Of Noise On Wildlife: A Literature Review', *World Forum for Acoustic Ecology*, pp. 1–16.

Rasa, A. (1977) 'Ecology & Sociology of dwarf mongoose (*Helogale undulata rufula*)', *Ethology*, 43(4), pp.337-406

Rasa, A. (1986) 'Coordinated Vigilance in dwarf mongoose family groups: The "Watchman's Song" Hypothesis and the costs of guarding', *Ethology*, 71(4), pp.340-344

Rasa, O. A. (1983) 'Dwarf mongoose and hornbill mutualism in the Taru desert, Kenya', *Behavioral Ecology and Sociobiology*, 12(3), pp. 181–190. doi: 10.1007/BF00290770.

Rasa, O. A. E. (1987) 'Behaviour & Social Structure in relation to ecology', *Advances in the Study of Behaviour*, 17, pp. 121–163.

Rasa, O. A. E. (1987) 'Vigilance behaviour in dwarf mongooses: selfish or altruistic?', *South African Journal of Science*, 83(10), pp. 587–590.

Rasa, O. A. E. (1989) 'Behavioural Parameters of vigilance in the dwarf mongoose: social acquisition of a sex-biased role', *Behaviour*, 110(1), pp.125-145

Read, J., Jones, G. and Radford, A. N. (2014) 'Fitness costs as well as benefits are important when considering responses to anthropogenic noise', *Behavioral Ecology*, 25(1), pp. 4–7. doi: 10.1093/beheco/art102.

Robinson, B. G. and Merrill, E. H. (2013) 'Foraging-vigilance trade-offs in a partially migratory population: Comparing migrants and residents on a sympatric range', *Animal Behaviour*, 85(4), pp. 849–856. doi: 10.1016/j.anbehav.2013.02.004.

Rolland, R. M., Parks, S. E., Hunt, K. E., Castellote, M., Corkeron, P. J., Nowacek, D. P., Wasser, S. K. and Kraus, S. D. (2012) 'Evidence that ship noise increases stress in right whales', *Proceedings of the Royal Society B: Biological Sciences*, 279(1737), pp. 2363–2368. doi: 10.1098/rspb.2011.2429.

Rood, J. P. (1990) 'Group size, survival, reproduction, and routes to breeding in dwarf mongooses', *Animal Behaviour*, 39(3), pp. 566–572. doi: 10.1016/S0003-3472(05)80423-3.

Rosa, P. and Koper, N. (2018) 'Integrating multiple disciplines to understand effects of anthropogenic noise on animal communication':, *Ecosphere*, 9(2), e02127 doi: 10.1002/ecs2.2127.

Rytwinski, T. and Fahrig, L. (2013) 'Why are some animal populations unaffected or positively affected by roads?', *Oecologia*, 173(3), pp. 1143–1156. doi: 10.1007/s00442-013-2684-x.

Sapolsky, R. M., Romero, L. M. and Munck, A. U. (2000) 'How Do Glucocorticoids Influence Stress Responses? Preparative Actions', *Endocrine Reviews*, 21(1), pp. 55–89.

Schaub, A., Ostwald, J. and Siemers, B. M. (2008) 'Foraging bats avoid noise', *Journal of Experimental Biology*, 212(18), pp. 3036–3036. doi: 10.1242/jeb.037283.

Schmidt, R., Morrison, A. and Kunc, H. P. (2014) 'Sexy voices - no choices: Male song in noise fails to attract females', *Animal Behaviour*, 94, pp. 55–59. doi: 10.1016/j.anbehav.2014.05.018.

Schneider, T. C. and Kappeler, P. M. (2014) 'Social systems and life-history characteristics of mongooses', *Biological Reviews*, 89(1), pp. 173–198. doi: 10.1111/brv.12050.

Schroeder, J., Nakagawa, S., Cleasby, I. R. and Burke, T. (2012) 'Passerine birds breeding under chronic noise experience reduced fitness', *PLoS ONE*, 7(7), e39200 doi: 10.1371/journal.pone.0039200.

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. and Wittemyer, G. (2016) ‘A synthesis of two decades of research documenting the effects of noise on wildlife’, *Biological Reviews*, 91(4), pp. 982–1005. doi: 10.1111/brv.12207.

Shannon, G., Crooks, K. R., Wittemyer, G., Fristrup, K. M. and Angeloni, L. M. (2016) ‘Road noise causes earlier predator detection and flight response in a free-ranging mammal’, *Behavioral Ecology*, 27(5), pp. 1370–1375. doi: 10.1093/beheco/arw058.

Sharpe, L., Kern, J. and Linh San, E. (2015) ‘Helogale parvula. The IUCN Red List of Threatened Species 2015’, 8235, p. e.T41609A45206516.

Sharpe, L. L., Hill, A. and Cherry, M. I. (2013) ‘Individual recognition in a wild cooperative mammal using contact calls’, *Animal Behaviour*, 86(5), pp. 893–900. doi: 10.1016/j.anbehav.2013.07.023.

Sharpe, L. L., Joustra, A. S. and Cherry, M. I. (2010) ‘The presence of an avian co-forager reduces vigilance in a cooperative mammal’, *Biology Letters*, 6(4), pp. 475–477. doi: 10.1098/rsbl.2009.1016.

Siemers, B. M. and Schaub, A. (2011) ‘Hunting at the highway: Traffic noise reduces foraging efficiency in acoustic predators’, *Proceedings of the Royal Society B: Biological Sciences*, 278(1712), pp. 1646–1652. doi: 10.1098/rspb.2010.2262.

Simpson, S. D., Radford, A. N., Nedelec, S. L., Ferrari, M. C. O., Chivers, D. P., McCormick, M. I. and Meekan, M. G. (2016) ‘Anthropogenic noise increases fish mortality by predation’, *Nature Communications*, 7(1), pp. 1–7. doi: 10.1038/ncomms10544.

Simpson, S. D., Purser, J. and Radford, A. N. (2015) ‘Anthropogenic noise compromises antipredator behaviour in European eels’, *Global Change Biology*, 21(2), pp. 586–593. doi: 10.1111/gcb.12685.

Sirot, E. (2010) ‘Should risk allocation strategies facilitate or hinder habituation to nonlethal disturbance in wildlife?’, *Animal Behaviour*, 80(4), pp. 737–743. doi: 10.1016/j.anbehav.2010.07.014.

Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C. and Popper, A. N. (2010) ‘A noisy spring: The impact of globally rising underwater sound levels on fish’, *Trends in Ecology and Evolution*, 25(7), pp. 419–427. doi: 10.1016/j.tree.2010.04.005.

Slabbekoorn, H. and den Boer-Visser, A. (2006) ‘Cities Change the Songs of Birds’, *Current Biology*, 16(23), pp. 2326–2331. doi: 10.1016/j.cub.2006.10.008.

Smith, M. E. (2004a) ‘Acoustical stress and hearing sensitivity in fishes: does the linear threshold shift hypothesis hold water?’, *Journal of Experimental Biology*, 207(20), pp. 3591–3602. doi: 10.1242/jeb.01188.

Smith, M. E. (2004b) ‘Noise-induced stress response and hearing loss in goldfish (Carassius auratus)’, *Journal of Experimental Biology*, 207(3), pp. 427–435. doi: 10.1242/jeb.00755.

Spiga, I., Aldred, N. and Caldwell, G. S. (2017) ‘Anthropogenic noise compromises the anti-predator behaviour of the European seabass, Dicentrarchus labrax (L.)’, *Marine Pollution Bulletin*, 122(1–2), pp. 297–305. doi: 10.1016/j.marpolbul.2017.06.067.

Steffen, W., Crutzen, P. J. and Mcneill, J. R. (2007) ‘The Anthropocene - Are Humans Now Overwhelming the Great Forces of Nature?’, *Ambio*, 36(8) pp. 614–621.

Swaddle, J. P. and Page, L. C. (2007) ‘High levels of environmental noise erode pair preferences in zebra finches: implications for noise pollution’, *Animal Behaviour*, 74(3), pp. 363–368. doi: 10.1016/j.anbehav.2007.01.004.

Templeton, C. N., Zollinger, S. A. and Brumm, H. (2016) ‘Traffic noise drowns out great tit alarm calls’, *Current Biology*, 26(22), pp. R1173–R1174. doi: 10.1016/j.cub.2016.09.058.

Thiel, M., Luna-Jorquera, G., Álvarez-Varas, R., Gallardo, C., Hinojosa, I. A., Luna, N., Miranda-Urbina, D., Morales, N., Ory, N., Pacheco, A. S., Portflitt-Toro, M. and Zavalaga, C. (2018) ‘Impacts of Marine Plastic Pollution From Continental Coasts to Subtropical Gyres—Fish, Seabirds, and Other Vertebrates in the SE Pacific’, *Frontiers in Marine Science*, 5(July), pp. 1–16. doi: 10.3389/fmars.2018.00238.

Thompson, R. C., Moore, C. J., Saal, F. S. V. and Swan, S. H. (2009) ‘Plastics, the environment and human health: Current consensus and future trends’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1526), pp. 2153–2166. doi: 10.1098/rstb.2009.0053.

Thornton, A., Samson, J. and Clutton-Brock, T. (2010) ‘Multi-generational persistence of traditions in neighbouring meerkat groups’, *Proceedings of the Royal Society B: Biological Sciences*, 277(1700), pp. 3623–3629. doi: 10.1098/rspb.2010.0611.

Tolentino, V. C. de M., Baesse, C. Q. and Melo, C. de (2018) ‘Dominant frequency of songs in tropical bird species is higher in sites with high noise pollution’, *Environmental Pollution*, 235, pp. 983–992. doi: 10.1016/j.envpol.2018.01.045.

Tuxbury, S. M. and Salmon, M. (2005) ‘Competitive interactions between artificial lighting and natural cues during seafinding by hatchling marine turtles’, *Biological Conservation*, 121(2), pp. 311–316. doi: 10.1016/j.biocon.2004.04.022.

Tyack, P. L. (2008) ‘Large-Scale Changes in the Marine Acoustic Environment’, *Journal of Mammalogy*, 89(3), pp. 549–558.

UNEP (2018) *SINGLE-USE PLASTICS: A roadmap for sustainability*.

United Nations (2017) *World Population Prospects: The 2017 Revision. Department of Economics and Social Affairs, Population Division*.

Vasconcelos, R. O., Amorim, M. C. P. and Ladich, F. (2007) ‘Effects of ship noise on the detectability of communication signals in the Lusitanian toadfish’, *Journal of Experimental Biology*, 210(12), pp. 2104–2112. doi: 10.1242/jeb.004317.

Vegter, A. C., Barletta, M., Beck, C., Borrero, J. *et al.* (2014) ‘Global research priorities to mitigate plastic pollution impacts on marine wildlife’, *Endangered Species Research*, 25(3), pp. 225–247. doi: 10.3354/esr00623.

Veron, G., Colyn, M., Dunham, A. E., Taylor, P. and Gaubert, P. (2004) ‘Molecular systematics and origin of sociality in mongooses (Herpestidae, Carnivora)’, *Molecular Phylogenetics and Evolution*, 30(3), pp. 582–598. doi: 10.1016/S1055-7903(03)00229-X.

Voellmy, I. K., Purser, J., Flynn, D., Kennedy, P., Simpson, S. D. and Radford, A. N. (2014) ‘Acoustic noise reduces foraging success in two sympatric fish species via different mechanisms’, *Animal Behaviour,* 89, pp. 191–198. doi: 10.1016/j.anbehav.2013.12.029.

Wale, M. A., Simpson, S. D. and Radford, A. N. (2013) ‘Noise negatively affects foraging and antipredator behaviour in shore crabs’, *Animal Behaviour*, 86(1), pp. 111–118. doi: 10.1016/j.anbehav.2013.05.001.

Walsh, E. P., Arnott, G. and Kunc, H. P. (2017) ‘Noise affects resource assessment in an invertebrate’, *Biology Letters*, 13(4), pp. 10–13. doi: 10.1098/rsbl.2017.0098.

Wang, J., Tan, Z., Peng, J., Qiu, Q. and Li, M. (2016) ‘The behaviors of microplastics in the marine environment’, *Marine Environmental Research*, 113, pp. 7–17. doi: 10.1016/j.marenvres.2015.10.014.

Ware, H. E., McClure, C. J. W., Carlisle, J. D. and Barber, J. R. (2015) ‘A phantom road experiment reveals traffic noise is an invisible source of habitat degradation’, *Proceedings of the National Academy of Sciences*, 112(39), pp. 12105–12109. doi: 10.1073/pnas.1504710112.

Warren, P. S., Katti, M., Ermann, M. and Brazel, A. (2006) ‘Urban bioacoustics: It’s not just noise’, *Animal Behaviour*, pp. 491–502. doi: 10.1016/j.anbehav.2005.07.014.

Weyers, P., Janke, W., Macht, M. and Weijers, H. G. (1994) ‘Social and non-social open field behaviour of rats under light and noise stimulation’, *Behavioural Processes*, 31(2–3), pp. 257–267. doi: 10.1016/0376-6357(94)90011-6.

WHO Regional Office for Europe (2011) *Burden of disease from environmental noise: quantification of healthy life years lost in Europe*. Geneva, Switzerland.

Williams, R., Wright, A. J., Ashe, E., Blight, L. K., Bruintjes, R., Canessa, R., Clark, C. W., Cullis-Suzuki, S., Dakin, D. T., Erbe, C., Hammond, P. S., Merchant, N. D., O’Hara, P. D., Purser, J., Radford, A. N., Simpson, S. D., Thomas, L. and Wale, M. A. (2015) ‘Impacts of anthropogenic noise on marine life: Publication patterns, new discoveries, and future directions in research and management’, *Ocean and Coastal Management*, 115, pp. 17–24. doi: 10.1016/j.ocecoaman.2015.05.021.

Woodall, L. C., Sanchez-Vidal, A., Canals, M., Paterson, G. L. J., Coppock, R., Sleight, V., Calafat, A., Rogers, A. D., Narayanaswamy, B. E. and Thompson, R. C. (2014) ‘The deep sea is a major sink for microplastic debris’, *Royal Society Open Science*, 1(4), pp. 140317–140317. doi: 10.1098/rsos.140317.

Wright, A., Soto, A. J., Aguilar Baldwin, N. and Linda, A. (2007) ‘Anthropogenic Noise as a Stressor in Animals: A Multidisciplinary Perspective’, *International Journal of Comparative Psychology*, 20(2), pp. 250-273. Available at: https://escholarship.org/uc/item/46m4q10x.

Wright, S. L., Thompson, R. C. and Galloway, T. S. (2013) ‘The physical impacts of microplastics on marine organisms: A review.’, *Environmental Pollution*, 178, pp. 483–92. doi: 10.1016/j.envpol.2013.02.031.

Wysocki, L. E., Dittami, J. P. and Ladich, F. (2006) 'Ship noise and cortisol secretion in European freshwater fishes', *Biological Conservation,* 128(4), pp. 501–508. doi: 10.1016/j.biocon.2005.10.020.

Zalasiewicz, J., Williams, M., Haywood, A. and Ellis, M. (2011) 'The anthropocene: A new epoch of geological time?', *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences,* 369(1938), pp. 835–841. doi: 10.1098/rsta.2010.0339.

Zhou, Y., Radford, A. N. and Magrath, R. D. (2019) 'Why does noise reduce response to alarm calls? Experimental assessment of masking, distraction and greater vigilance in wild birds', *Functional Ecology,* Online early. doi: 10.1111/1365-2435.13333.