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how anthropogenic noise and climate impact dwarf mongoose (Helogale parvula) behaviour

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A changing world: how anthropogenic noise and climate impact dwarf mongoose (*Helogale parvula*) behaviour

Photo by author

Lucy Westover

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 Life Sciences.

School of Biological Sciences, June 2023

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Summary of Thesis

Anthropogenic noise and climate change are both significant threats to the world’s ecosystems and species, causing a range of negative physiological and behavioural impacts. Research exploring the impacts of anthropogenic noise has focused on this threat in isolation, despite it often occurring in conjunction with other stressors. In this thesis, I first report the results of a field-based playback experiment used to explore the combined effects of an elevated predation threat and road noise on vigilance and foraging behaviour in dwarf mongooses (*Helogale parvula*). Whilst we found that both the threat of predation and road noise led to an equivalent increase in vigilance behaviour and a subsequent decrease in foraging behaviour, we did not find an additional effect when individuals were exposed to the combination of these stressors. Whilst there has been much research exploring the causes of climate change and how species will be affected by different climatic conditions, we know relatively little about its potential effects on animal behaviour. The second part of my thesis therefore reports on the use of long-term data to investigate the effect of rainfall and temperature on agonistic and sentinel behaviour. Our results showed that there was less agonistic behaviour when there was less rainfall in the non-breeding season, but no significant effect of rainfall in the breeding season. However, in both seasons there was significantly more sentinel behaviour seen in periods of lower rainfall. Temperature was not found to have a significant effect on agonistic or sentinel behaviour in either season. Results from both studies highlight the threats faced by wildlife from anthropogenic noise and a changing climate. They also demonstrate the need for further research in these areas on a range of species to give us a more comprehensive idea of how species will be impacted in an ever-changing world.

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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: 

Date: 14th June 2023
# Table of Contents

Summary of Thesis..................................................................................................................2

Acknowledgements................................................................................................................3

Author’s declaration.............................................................................................................4

Table of contents..................................................................................................................5

**Chapter 1: General Introduction**..................................................................................8

1.1 The Anthropocene...........................................................................................................9

1.2 Anthropogenic noise.......................................................................................................11

   1.2.1 What is anthropogenic noise and what causes it?.................................................11

   1.2.2 Impacts of noise on human health........................................................................12

   1.2.3 Physiological and developmental impacts of noise in non-human animals........13

   1.2.4 Behavioural impacts of noise in non-human animals...........................................13

   1.2.5 Combined stressor effects.......................................................................................16

1.3 Climate Change..............................................................................................................18

   1.3.1 What is climate change?.......................................................................................18

   1.3.2 IPCC climate scenarios.........................................................................................20

   1.3.3 Effects of climate change.......................................................................................21

1.4 Dwarf Mongooses.......................................................................................................25

   1.4.1 General biology and behaviour............................................................................25

   1.4.2 Study site and population.....................................................................................26

   1.4.3 Use of habituated populations in animal behaviour studies.................................27

1.5 Thesis aims and predictions..........................................................................................28

**Chapter 2: The combined effect of predation risk and anthropogenic noise on vigilance and foraging behaviour in dwarf mongooses**.................................................30
3.4.2 Effect of climate on sentinel behaviour........................................69

3.5 Discussion......................................................................................74

**Chapter 4: General Discussion**.........................................................78

4.1 Thesis findings..............................................................................79

4.2 Future studies..............................................................................81

4.3 Conclusion.....................................................................................83

**References**.....................................................................................84
Chapter 1: General Introduction

Photo by author
1.1 The Anthropocene

In 2000, it was proposed by Paul Crutzen that the Earth had left the Holocene and was entering a new (albeit unofficial) time-period known as the Anthropocene (Crutzen & Stoemer, 2000; Crutzen, 2002). In the Anthropocene, humans are considered the main driver for environmental change across the planet (Rockström et al., 2009). This new geological era began in the mid-20th century at the start of the Great Acceleration (Steffen et al., 2015; Waters et al., 2016). The Great Acceleration is the clear increase in both human population size and a range of different activities, such as the economy and consumption of resources including water, energy and fertiliser. Whilst there was some increase in these human activities as a result of the Industrial Revolution, this becomes more significant from 1950 (Steffen, 2021; Figure 1.1).

Figure 1.1 The trends in a range of human activities from 1750 to 2010. Adapted from Steffen et al. (2015).
Since entering the Anthropocene, we have seen multiple catastrophic environmental issues arise, including climate change, loss of biodiversity, and depleted and degraded natural resources (UNEP, 2019; IPCC, 2021; Becker, 2023). The main drivers of this environmental change include urbanisation, land use change, economic expansion and the development of new technologies, all of which are driven by an increasing human population (UNEP, 2019; Becker, 2023). A growing population can impact the environment through, for example, the overconsumption of natural resources and rapid urbanisation (OECD, 2016; UNEP, 2019). It is predicted that the global population will reach 9.8 billion in 2050 and 11.2 billion in 2100, meaning that we might continue to see an increase in overconsumption and urbanisation (UN, 2017). However, it is important to note that this increased rate of population growth is mostly seen in poorer countries who typically have lower environmental footprints and so we should avoid the blanket assumption that an increasing population leads to increased overconsumption (UNEP, 2019). Land use change is driving ecosystem degradation, which is threatening biodiversity, resilience to climate change, biomass productivity as well as leading to degradation of soil and water (Foley et al., 2005; EEA, 2022). It has been estimated that since 1960, land use change has affected 32% of global land area; much of this land use change is being driven by agriculture which has accounted for 65% of land use change from 1961 to 2011 (Alexander et al., 2015; Winkler et al., 2021). Economic expansion also drives degradation of habitats and ecosystems, and results in the depletion of natural resources as a growing economy encourages material growth. However, improved economic development and growth can also help us to reach our global sustainability goals (Everett et al., 2010; UNEP, 2019). Contrastingly, urbanisation directly causes degradation and fragmentation of habitats, generates noise and light pollution, leads to greater pressure on natural resources and can influence species interactions (UNEP, 2019; Theodorou, 2022). It is predicted that by 2050, 68% of the world’s population will live in urban areas and this urbanisation is believed to be a prominent threat to both ecosystems and biodiversity. Whilst urban areas can incorporate green spaces to help support a range of species, they permanently alter the habitat that is available to species and affect the connectedness between different habitats (UN, 2018; Simkin et al., 2022). Technological advancements can cause both positive and negative environmental change; we will need advances in technology to help make us more sustainable but
development of these technologies can have unintended consequences that can drive further environmental damage (UNEP, 2019).

Human drivers of environmental change are having severe consequences for all ecosystems and the species that inhabit them. Many scientists believe we are now heading into the sixth mass extinction; this is the only mass extinction event in history that has been driven by human activity, all those previously were caused by natural phenomena (Cowie et al., 2022). Extinction rates are estimated to be up to hundreds of times higher than in the last 10 million years, and it is currently thought that one million species are already facing extinction (IPBES, 2019). There are five widely recognised drivers of current biodiversity loss: climate change, habitat change, exploitation, the introduction of alien species and pollution (Pereira et al., 2012; Bowler et al., 2020). Anthropogenic noise is a significant and well-recognised pollutant threatening biodiversity, with the World Health Organisation describing it as one of the most dangerous pollutants for species in both aquatic and terrestrial environments (WHO, 2011; Kunc & Schmidt, 2019). Climate change also poses significant threats to species in all ecosystems due to the severity and wide-spread nature of the resulting impacts. There is thus a pressing need for us to understand fully the consequences of these environmental changes to ensure that we can effectively mitigate and remove the threat where possible.

1.2 Anthropogenic noise

1.2.1 What is anthropogenic noise and what causes it?

Whilst both biotic and abiotic noise is a natural part of the environment, there has been a rise in the amount of man-made (anthropogenic) noise in both terrestrial and marine environments (Francis & Barber, 2013; Shannon et al., 2016a). Biotic sounds are those made by animals, such as bird song, whilst abiotic sounds are those made by the physical environment, including the sound of crashing waves and wind through the trees (To et al., 2021). Contrastingly, anthropogenic noise results from human activities such as urban development, transportation, resource extraction, military operations and recreational events (Barber et al., 2009; Peng et al., 2015; Shannon et al., 2016a). Whilst there has been more research into the impacts of noise in the terrestrial environment, there is growing
evidence showing these impacts in the marine environment as well, highlighting the far-reaching influence of this pollutant (Peng et al., 2015; Duarte et al., 2021). Transportation is a notable source of anthropogenic noise found in both terrestrial and marine environments. Noise from roads is of particular significance, not only because of the prevalence of roads, but because there is ever more traffic present; in the UK, traffic levels are estimated to grow by as much as 54% by 2060 (Blickley & Patricelli, 2010; Department for Transport, 2022). Improving our understanding of the effects of this pollutant is important, partly because all the sources mentioned above are likely to increase and because, as we transition into a more sustainable society, there is likely to be an increase in noise sources that previously have not been as prevalent, for example noise from wind turbines (Jerem & Mathews, 2020; Teff-Seker et al., 2022).

1.2.2 Impacts of noise on human health

Noise pollution has long been known to cause many health issues in humans (WHO, 2011; EEA, 2020). Noise can annoy, disturb sleep, and cause stress, cognitive impairment, endocrine imbalance and cardiovascular issues (Babisch, 2011; WHO, 2011). These short- and long-term health impacts likely affect tens of millions of people worldwide (Levak et al., 2008). The short-term changes are mostly related to a person’s psychological state, for example how stressed they are, as well as some physical effects including higher blood pressure and heart rate. Some of the longer-term effects include loss of hearing and illnesses that result from stress following chronic exposure to noise pollution (Levak et al., 2008). Children are likely more vulnerable than adults to excessive noise as the former are exposed at a time when they are growing and experiencing the greatest cognitive development (Stansfeld & Clark, 2015). Road noise can lead to low birth weight (Gehring et al., 2014; Stansfeld & Clark, 2015), whilst the consequences of noise pollution on child cognition are particularly worrying due to the effects on comprehension, memory and test performance (Hygge et al., 2002; Stansfeld & Clark, 2015). Clearly, noise pollution has detrimental effects on human health; in Europe, long-term exposure to noise is estimated to cause 12,000 deaths per year (EEA, 2020). But these detrimental effects of noise are not limited to just humans (Francis & Barber, 2013; Shannon et al., 2016a; Dutilleux, 2017).
1.2.3 Physiological and developmental impacts of noise on non-human animals

Whilst the effects of anthropogenic noise on non-human animals have not been as well studied as in humans, the research to date shows clearly that noise can have both physiological and developmental impacts on a range of taxa (Francis & Barber, 2013; Shannon et al., 2016a; Dutilleux, 2017). Noise can cause changes in the endocrine system, metabolism, reproduction, growth, cardiovascular health, DNA and genes, among others (Kight & Swaddle, 2011). For example, noise exposure caused permanent damage to the sensory hair cells of the statocysts in cephalopods; these help the animal to balance and position themselves (Andre et al., 2011). Scallop larvae (Pecten novazelandiae) suffered delays in development and were much more likely to have body abnormalities when exposed to seismic activity (de Soto et al., 2013). Many studies have also shown that noise pollution can lead to increased cortisol levels (meaning individuals are more stressed), as seen in greater sage-grouse (Centrocercus urophasianus) (Blickley et al., 2012), White’s treefrogs (Litoria caerulea) (Kaiser et al., 2015), larval zebrafish (Danio rerio) (Lara & Vasconcelos, 2021) and lined seahorses (Hippocampus erectus) (Anderson et al., 2011). However, in mountain white-crowned sparrows (Zonotrichia leucophrys oriantha), traffic noise exposure led to reduced stress hormones and improved condition (Crino et al., 2013). These differing results highlight the importance of testing the effects of anthropogenic noise on a range of species. Perhaps even more concerningly, anthropogenic noise has been found to affect gene expression in some species. When Asian particoloured bats (Vespertilio sinensis) were exposed to noise, 169 genes were differentially expressed compared to the groups that were not exposed to this noise. These genes were responsible for fundamental cellular processes, metabolism, and both immune and stress responses (Song et al., 2020). Not only can noise impact all the body systems previously mentioned but these processes and systems can also influence each other, meaning that the effects of noise are probably more complex than has been illustrated so far (Kight & Swaddle, 2011).

1.2.4 Behavioural impacts of noise in non-human animals

Anthropogenic noise can lead to a range of behavioural changes at both the individual and species level, which can then have knock-on effects for populations and communities (Kok et
Noise can affect behaviour in four different ways: it can mask signals or cues in the acoustic environment (Barber et al., 2010), it can distract individuals (Chan et al., 2010), it can be perceived as a threat (Frid & Dill, 2002) or it can act as a stressor (Shannon et al., 2016b; Kleist et al., 2018; Eastcott et al., 2020).

The masking of acoustic information can either be complete, where none of the signal or cue is detected, or it can be partial, where the signal can be detected by the receiver but it is difficult to understand the content (Clark et al., 2009; Radford et al., 2014). Masking can, for example, reduce the ability to detect acoustic predator cues and cause changes in vocal signalling (e.g., amplitude, duration and frequency of songs and calls) in an attempt to ensure that acoustic information is still conveyed successfully (Antze & Koper, 2018; Erbe et al., 2022). Several bird species have been shown to alter their songs to try and improve signal transmission and detection in noisy environments. For instance, red-winged blackbirds (Agelaius phoeniceus) modified their song structure when exposed to noise; whilst this may have allowed the signal to be detected better, female receivers may be unable to recognise these songs or be less attracted to the modified songs meaning knock-on reproductive consequences (Hanna et al., 2011). Masking of animal communication has also led to negative effects on reproductive success in great tits (Parus major): individuals laid smaller clutches in areas with greater noise pollution, most likely due to noise overlapping with their song (Halfwerk et al., 2010). Masking can also result in declines in occupancy and abundance of species, including in songbirds (Bayne et al., 2008; Antze & Koper 2018).

The distracted prey hypothesis, as proposed by Chan et al. (2010), states that any stimulus perceivable to the animal has the capability of distracting it. This will cause the individual to reallocate its attention, meaning it will not respond appropriately to a threat. Anthropogenic noise has been shown to distract Caribbean hermit crabs (Coenobita clypeatus) such that they allowed a simulated predator to get closer to them than in control treatments (Chan et al., 2010). Distraction can also partially explain why dwarf mongooses (Helogale parvula) did not respond as expected to predator cues: when exposed to anthropogenic noise, individuals took longer to approach predatory faeces and interacted less with these olfactory cues (Morris-Drake et al., 2016). Noise pollution reduced foraging efficiency in three-spined sticklebacks (Gasterosteus aculeatus), likely because of individuals
shifting their attention away from the feeding task (Purser & Radford, 2011). There was a decrease in efficiency of spiny chromis (*Acanthochromis polyacanthus*) parental care because males exposed to motorboat noise were distracted and chased other fish instead (Nedelec *et al.*, 2017). European hermit crabs (*Pagurus bernhardus*) exposed to anthropogenic noise chose an optimal shell less frequently, which can lead to reduced fitness, and it has been hypothesised that this is due to individuals being distracted (Tidau & Briffa, 2019).

There is some evidence to suggest that individuals change their behaviour when exposed to anthropogenic noise in the same way that they would if they were exposed to predation threat; this phenomenon is known as the risk-disturbance hypothesis (Frid & Dill, 2002). These changes include increasing anti-predator behaviours; for instance, spending more time being vigilant (and, consequently, less time foraging) or being more likely to flee to cover (Berger-Tal *et al.*, 2019). Pronghorn antelope (*Antilocapra americana*) increased their rates of vigilance and foraged less when exposed to road traffic (Gavin & Komers, 2007). The risk-disturbance hypothesis has also been shown in a number of cetacean species: sperm whales (*Physeter macrocephalus*), long-finned pilot whales (*Globicephala melas*), humpback whales (*Megaptera novaeangliae*) and Northern bottlenose whales (*Hyperoodon ampullatus*) all reduced the amount they were foraging when exposed to both anthropogenic noise and sounds of a predator, implying similar levels of perceived risk (Miller *et al.*, 2022). However, some studies have found no support for the risk-disturbance hypothesis, and some have shown conflicting results on the same species. For example, elk (*Cervus elaphus*) and pronghorn did not perceive traffic noise as a form of predation risk, possibly because the study individuals were habituated to this particular human disturbance (Brown *et al.*, 2012). There was also little evidence seen for the risk-disturbance hypothesis in one study of pygmy marmosets (*Cebuella niveiventris*) (Hawkins & Papworth, 2022), but these results contradict those seen in previous research on the same species (Sheehan & Papworth, 2019). Whilst research has shown that some species will change their behaviour when exposed to anthropogenic disturbances in the same way that they would to a predator, other research has shown that some species (notably herbivores) might instead use highly disturbed areas. By doing this, it helps these species to avoid predators that may be sensitive to this disturbance, a phenomenon known as the predator shelter effect.
One study showed that both pronghorn and elk exhibited increased levels of feeding and decreased levels of vigilance behaviour in the more disturbed area; the opposite effects to what we would expect to see under the risk-disturbance hypothesis (Shannon et al., 2014a). Prey species in the Barandabhar corridor forest have also been shown to increase their occupation of sites significantly when humans are present compared to when humans are absent from these areas and it is suggested that this helps them to avoid predators (Lamichhane et al., 2023).

Noise has also been suggested to act as a stressor and this can have implications for animal behaviour as stress influences, for instance, feeding, movement and anti-predator behaviours (Erbe et al., 2022). In Ambon damselfish (*Pomacentrus amboinensis*), individuals exposed to boat noise responded less often and less quickly to attacks from predators, which may have been the result of increased stress (Simpson et al., 2016). In greater sage-grouse, exposure to anthropogenic noise led to increased stress levels which is thought to cause avoidance of noisy areas by some individuals but longer-term issues for those that choose to remain (Blickley & Patricelli, 2012; Blickley et al., 2012).

### 1.2.5 Combined stressor effects

Anthropogenic noise is rarely experienced alone by wildlife; animals simultaneously encounter a range of other natural and man-made stressors. Natural stressors include the weather, competition from conspecifics and heterospecifics, and predation risk (Munns, 2006). As the human population continues to grow, and our activities (e.g., urban development and resource extraction) expand, species and ecosystems are coming under increasing anthropogenic pressure (Crain et al., 2008; Dominoni et al., 2020) as a consequence of, for instance, deforestation, climate change, land-use change, light pollution and habitat fragmentation (McLaughlin et al., 2013; Erbe et al., 2022; Katabaro et al., 2022). We know a lot about the effects that these stressors individually have on a range of species, but far less work has investigated the potential cumulative effects (Breitburg et al., 1999; Crain et al., 2008; Willems et al, 2021). It is difficult to predict multi-stressor effects as they can act in at least three different ways (Darling et al., 2010): antagonistically (the combined impact of the multiple stressors is less than the individual impacts), additively (the combined
stressors are the sum of the stressors individually) or synergistically (combined stressor effects are greater than the sum of the individual stressor effects) (Crain et al., 2008; Darling et al., 2010; Hale et al., 2016; Dominoni et al., 2020; Willems et al., 2021). Of particular conservation concern are synergistic effects, which could be exacerbating stressors that on their own already cause negative effects (Crain et al., 2008). Synergistic effects may lead to a sudden decline in biodiversity (Folke et al., 2004; Darling et al., 2010). Conceptual models have been created and experiments conducted to gain a better understanding of how different species will react to multiple stressors (Vinebrooke et al., 2004). These combined stressors have been shown to affect, for instance, behaviour, body condition, offspring development and abundance (Dominoni et al., 2020; Ferraro et al., 2020; Willems et al., 2021; Wilson et al., 2021).

Of the studies that have explored multi-stressor effects, many have focused on anthropogenic stressors that co-occur in urban environments; in particular, the effects of light and noise pollution (Dominoni et al., 2020). For example, compared to when they were exposed to the pollutants individually, the combination of noise and light pollution impaired development in nestling western bluebirds (Sialia mexicana), likely reducing fledgling survival (Ferraro et al., 2020). Light and noise pollution also had a synergistic effect on bird abundance, with the declines exacerbated compared to when there was exposure to the stressors individually (Wilson et al., 2021). Interactions between parasitic frog-biting midges (Corethrella spp.) and their hosts, the tungara frog (Engystomops pustulosus), were affected by the combined stressors of noise and light pollution (McMahon et al., 2017). However, these stressors have not always been found to have a greater negative effect when combined. When pinyon mice (Peromyscus truei) were exposed to noise pollution, there was a negative effect on body condition whilst light pollution reduced trap success, but there was no additive or synergistic effect seen when the stressors were combined (Willems et al., 2021). Climate change-induced coral bleaching and fishing were both found to reduce coral cover on Kenyan reefs (fishing by 51% and coral bleaching by 74%), but the combination of these two stressors did not have a synergistic effect (Darling et al., 2010).

Whilst species are often exposed to co-occurring anthropogenic stressors, there are also natural stressors that could have an influence. Mendez et al. (2019) explored the effects of trampling (anthropogenic stressor) and wave disturbance (natural stressor) on mussel
beds (*Brachidontes* spp.), finding an antagonistic effect as trampled plots on the wave-exposed sites had less mussel cover loss than the trampled plots on the wave-protected sites. Chipmunks (*Tamias striatus*) and mice (*Peromyscus leucopus*) also showed antagonistic responses when exposed to predation risk and simultaneous road noise. Predation risk alone resulted in a reduced food intake, but individuals increased their food intake again when this threat was in conjunction with road noise (Giordano *et al.*, 2022). Contrastingly, when common lesser escuerzo (*Odontophrynus americanus*) were exposed to road noise and conspecific chorus noise in combination, individuals altered their calls more than when exposed to the stressors individually (Grenat *et al.*, 2019).

Anthropogenic noise and climate change are intrinsically linked; many of the activities that are causing a changing climate, including transportation and resource extraction, are also sources of anthropogenic noise (UNEP, 2022). For example, warming temperatures (caused by climate change) are leading to melting sea ice, making more environments accessible to human activities and therefore causing increased levels of anthropogenic noise (UNEP, 2022). Climate change also has the potential to influence how far noise pollution can spread. One way in which this is occurring is through ocean acidification which is being caused by increases in atmospheric carbon dioxide (Godbold & Calosi, 2013). In these increasingly acidic environments, low-frequency sounds can travel further; anthropogenic noise sources, such as shipping and seismic surveys, often generate low-frequency sounds (Partan, 2017).

The wide range of stressors and differing results seen to date highlights the importance of conducting more studies exploring the combined effects of stressors in a range of species. This is particularly important in cases where there is thought to be an additive or synergistic effect.

### 1.3 Climate Change

#### 1.3.1 What is climate change?

Climate change is defined by the Intergovernmental Panel on Climate Change (IPCC) as the significant changes in weather patterns that last for decades; this definition encompasses
climate change resulting both naturally and change caused by humans (IPCC, 2007). Current climate change, whilst largely being driven by anthropogenic causes, is influenced by natural factors as well (IPCC, 2013; Fakana, 2020).

Volcanic eruptions are one of the natural causes of climate change; these eruptions release large amounts of ash and sulphur (aerosol particles) into the stratosphere. The release of these particles shades solar radiation and thus leads to a cooling effect, which typically lasts a few years (Fakana, 2020; The Royal Society, 2020). For instance, the eruption of Mount Pinatubo in 1991 is thought to have caused a cooling effect of up to 0.5°C lasting up to three years (Hansen et al., 1992; Jain, 1993). Climate change can also be caused by alterations in the Earth’s orbit which result in natural cycles of warming and cooling periods known as the “Milankovitch cycles” (Jain, 1993; Fakana, 2020). The amount of solar output received by the Earth also influences the climate. More radiation being emitted from the sun causes increasing temperatures directly but it is also thought to have indirect effects by changing cloud formation processes (Fakana, 2020). Whilst these natural factors do influence the Earth’s climate, changes that have been observed for the last few decades cannot be explained by them, and instead scientists believe that the major driver of current climate change is human activity (The Royal Society, 2020).

Since the Industrial Revolution, humans have added greenhouse gases (mostly carbon dioxide, methane and nitrous oxide) to the atmosphere at an unprecedented scale. In that period, carbon dioxide concentrations have increased by over 40%, nitrous oxide by 20% and methane by 150% (Trenberth, 2018; The Royal Society, 2020). There is a plethora of ways in which humans are influencing the Earth’s climate, particularly through the burning of fossil fuels and deforestation (Trenberth, 2018). Forests act as carbon sinks, meaning that they absorb carbon dioxide from the atmosphere, helping to regulate the air and surface temperatures. Deforestation leads to loss of this critical carbon sink which, in turn, results in temperature increases (Fakana, 2020). Approximately three-quarters of the Earth’s land has seen human-induced alterations in usage in the last thousand years, which are likely responsible for 12–20% of greenhouse gas emissions (Watson & Schalatek, 2019; Winkler et al., 2021). These land-use changes primarily result from a growing human population, increasing consumption, more intense agriculture, overconsumption of natural resources and a greater demand for energy (Roy et al., 2022). The burning of fossil fuels (coal, oil and
gas) is also a major contributor to climate change, with it estimated to account for more than 75% of global greenhouse gas emissions and almost 90% of carbon dioxide emissions (United Nations, n.d). Greenhouse gases are also emitted through other human activities, including raising livestock, filling landfills and the use of refrigerants and fertilisers (The Royal Society, 2020). Humans are also contributing to climate change by emitting other pollutants (primarily from agricultural and industrial processes) that produce aerosols which in turn cool the Earth by reflecting sunlight back into space (Fakana, 2020; The Royal Society, 2020).

1.3.2 IPCC climate scenarios

Humans are clearly having a dramatic influence on the climate and it is crucial for us to try and reduce these impacts. The IPCC has reported five different climate-change scenarios depending on the actions that we take over the next few years (IPCC, 2021; Figure 1.2).

![Figure 1.2](image)

**Figure 1.2** The amount and rate of global surface temperature change depending on the amount of greenhouse gases emitted. The five possible scenarios for future climate change are based on how quickly humans reduce emissions, as well as socioeconomic factors that previous models failed to consider. The black line represents historical simulations and the shading for all lines represents uncertainty ranges. Adapted from IPCC Sixth Assessment Report (2021).
The most optimistic scenario (SSP1-1.9) presented by the IPCC would mean a 1.5°C warming by 2050 if we cut global emissions to net zero by 2050. In this scenario, there would be sustainable development that is the focus of global policies, reduced inequalities and low consumption of resources. This is the only scenario that would be in line with the Paris Agreement, a legally binding international treaty that states that we must keep to 1.5°C of warming (Climate Neutral Group, 2021; IPCC, 2021; UNFCCC, n.d.). However, even in this most optimistic scenario, the temperature increases are still higher than in recent decades (IPCC, 2021). In the SSP1-2.6 scenario, rapidly reducing emissions (but with net-zero emissions only reached after 2050) would keep warming to 1.8°C. The SSP2-4.5 scenario is known as the “middle of the road”; in this case, emissions remain at the levels they are now before reducing in the middle of the century but we do not reach net-zero by 2100. Under this scenario, temperatures are predicted to reach 2.7°C by 2100. The final two scenarios, SSP3-7.0 and SSP5-8.5, must be avoided. With SSP3-7.0, we will see warming of 3.6°C by 2100 due to carbon dioxide emissions doubling from their current levels by 2100. In this scenario, socioeconomic conditions will worsen globally, and countries will become increasingly more competitive and isolationist. In the final scenario (SSP5-8.5), we will see catastrophic effects to the planet, fuelled by a constant growth in fossil fuel use and overconsumption. Carbon dioxide emissions will double from what they are now by 2050 and temperatures will reach 4.4°C by 2100 (Climate Neutral Group, 2021; IPCC, 2021).

### 1.3.3 Effects of climate change

Anthropogenic climate change is already affecting weather patterns in every part of the planet but how bad future effects are depends on which climate scenario we follow (IPCC, 2021). Some changes already seen include increasing severity in heatwaves, droughts, wildfires, cyclones and precipitation (Ayanlade et al., 2020; IPCC, 2021). Whilst climate-change effects will be apparent at all temperature-increase scenarios, there is a stark difference between those seen with even a 1.5°C versus 2°C of warming. Under 1.5°C of warming, approximately 14% of the world’s population will experience severe heatwaves at least once every 5 years, but at 2°C this jumps to 37%. Droughts, floods and runoff will be less common under 1.5°C compared with 2°C. Flooding will impact up to 69 million people if temperatures increase by 1.5°C but this number increases to 79 million under 2°C; the rate
of sea level rise should also be slower under 1.5°C and so should give more people time to adapt. There will also be significantly more species of vertebrates, plants and insects lost at 2°C (IPCC, 2018). The effects of climate change will not be felt equally across Earth; the magnitude and rate of changes will be different both between countries and regions, but also within countries (EPA, 2017). The world’s poorest people will be some of the most vulnerable to climate change, and these changes to the climate will exacerbate the poverty and inequality already being seen. Women as well as young and elderly people are also particularly susceptible to the effects of climate change (IPCC, 2014; EPA, 2017).

Climate change is already having significant effects on human health which are predicted to worsen in the future. In the 2000s, it was estimated that anthropogenically caused climate change was causing the deaths of 150,000 people annually, and this is expected to rise to 250,000 between 2030 and 2050 (Patz et al., 2005; WHO, 2021). Heatwaves are one of the causes of these deaths; in Europe, between 22,000 and 45,000 people died in 2003 because of a heatwave where average temperatures were 3.5°C higher than usual (Kosatsky, 2003; Patz et al., 2005). These heatwaves can also lead to an increase in cardiovascular diseases (Kim et al., 2014). Climate change can impact health by negatively affecting the quality and quantity of crop yields, leading to greater food insecurity and malnutrition; food insecurity will cause inflation in food prices that will exacerbate these issues. In 2020, two billion people were food insecure and this number is likely to increase with climate change (Fanzo & Downs, 2021; FAO et al., 2021). Malnutrition caused by climate change can also lead to more infectious diseases and the changing environment may facilitate pathogen spread and persistence (Patz et al., 2005; Mora et al., 2022), something that is of particular concern for children (Fanzo & Downs, 2021; Agostoni et al., 2023). For example, Ross River virus in Australia was found to be influenced by the climate, specifically rainfall and maximum temperature (Tong et al., 2004; Patz et al., 2005). There is also evidence that climate change can negatively affect air pollution, leading to increases in respiratory diseases (Kim et al., 2014). Climate change also has knock-on consequences for mental health: increases in extreme weather conditions likely increase disorders such as anxiety, PTSD and depression (Page & Howard, 2010; Kim et al., 2014).

Not only does climate change influence humans but it also has consequences for ecosystems worldwide; these will vary in their sensitivity and response to climate change.
(Malhi et al., 2020). One way that climate change impacts ecosystems is by affecting primary productivity. Global primary productivity in terrestrial environments has increased over the last century due to increasing atmospheric carbon dioxide and increased nutrient additions from human activities. However, regional trends in primary productivity might differ to these global ones as production can be limited by air pollution, a lack of nutrients and water deficits (Lipton et al., 2018; Weiskopf et al., 2020). In marine environments, climate change can also affect primary productivity and these effects vary regionally. Climate change is causing ocean temperatures to rise, which can increase stratification and thus limit primary production. However, in other parts of the world, ocean primary productivity is increasing due to a lack of ice cover increasing sunlight availability (IPCC, 2013; Wasmund et al., 2019; Weiskopf et al., 2020). Climate change will also impact ecosystems by aiding the spread of invasive species, which are a major driver of biodiversity loss. For instance, increasing temperatures could allow invasive species to move into areas that previously would have been too cold for them. Ocean warming that leads to sea ice melt is, in turn, creating new shipping routes; invasive species can attach to these ships and get introduced this way. Climate change also has the potential to alter competitive interactions, making native species in those ecosystems either more or less susceptible to invasive species (Lipton et al., 2018; Finch et al., 2021). Climate-induced shifts in species distributions can alter interspecific interactions, including those between predators and prey and between plants and pollinators, and food-web structures. Increasing temperatures are changing what species are present in the community which is in turn likely to lead to increased competition, reduced resilience for the community and local extinctions (Lipton et al., 2018; Weiskopf et al., 2020).

Climate change can impact individual species in multiple ways, including causing range shifts, changing the timing of life cycle events, making them vulnerable to disease and through extinctions (Sattar et al., 2021). Phenological changes include altered migration timings and changes in the onset of flowering (Nature Climate Change, 2018). Migrating species are particularly sensitive to climate change: changing habitats could mean that traditional stopover sites may no longer be appropriate; individuals may not have the energy reserves to be able to make it to another site. Changes in resource availability might also mean species do not gain enough energy to complete their migration or that the reproductive cycle no longer aligns with food availability, which will lead to higher offspring
mortality (Moore, 2011; Seebacher & Post, 2015; Kubelka et al., 2022). Species will adapt to climate change in different ways and this will lead to more asynchronies between species as well as between the ecosystems that they inhabit (EPA, 2017). In response to climate change, both terrestrial and aquatic species are shifting their ranges north to higher elevations. How far individuals will travel depends on how well they can cope with the changing climate; ectotherms are likely to need to shift their range further than endotherms as they are not able to adapt to increasing temperatures physiologically (Ramalho et al., 2023). These range shifts are thought to be important for ensuring a species will survive but there is concern that this movement of species into new areas will cause issues for native species in the same way that invasive species do. However, some analysis has shown that these species are less likely to cause issues to native populations if they are shifting to nearby habitats (Nature Climate Change, 2020; Wallingford et al., 2020). There is a lot of uncertainty about how species will be impacted by diseases, particularly if the ranges of pathogens also start to change (Buttke et al., 2021). However, it is thought that climate change will likely encourage the spread of diseases and pests by increases in temperature and variable weather (Cohen et al., 2020).

As we have seen previously, climate change will have a significant effect on weather patterns and there is growing evidence to show that these changes will alter animal behaviour. The transmission of sound is affected by the weather conditions, in particular temperature, humidity and wind (Partan, 2017). Bats alter their echolocation calls depending on their environment, with individuals producing calls of lower frequency in areas where there was high sound absorption and during the rainy season (Snell-Rood, 2012). These alterations to bat call patterns suggest that climate changes might affect auditory communication between species (Snell-Rood, 2012; Partan, 2017). In aquatic environments, sound transmission can also be affected by ocean acidification, which is caused by increases in atmospheric carbon dioxide (Godbold & Calosi, 2013). In these increasingly acidic environments, anthropogenic noise will be able to travel further and will help to create noisier environments affecting the behaviour of many species (Miller et al., 2000; Partan, 2017; Penar et al., 2020).

Climate change and, in particular, increases in temperature are leading to a range of lethal and sublethal impacts on wildlife (du Plessis et al., 2012; Edwards et al., 2015). High
temperatures can cause mass die-off events. For example, 3500 wild flying-foxes (*Pteropus* spp.) died in 2002 when temperatures exceeded 42°C and, since 1994, more than 30,000 flying-foxes have reportedly died due to 19 similar extreme temperature events (Welbergen *et al.*, 2007). Sublethal effects of a changing climate include impacts on body condition, behaviour and reproductive success (du Plessis *et al.*, 2012; Edwards *et al.*, 2015). For instance, drought conditions led to meerkats (*Suricata suricatta*) decreasing cooperative sentinel behaviour in favour of foraging, to assure their individual fitness (Rauber *et al.*, 2019). Both pied babblers (*Turdoides bicolor*) and Western Australian magpies (*Cracticus tibicen dorsalis*) reduce the amount of foraging they do in hot temperatures leading to a loss in body condition (du Plessis *et al.*, 2012; Edwards *et al.*, 2015). Climate change also impacts reproductive and parental behaviours in a range of species. Some pied babbler individuals provision young significantly less on hot days and this leads to a reduction in offspring development (Wiley & Ridley, 2016). Indo-specific bottlenose dolphins (*Tursiops aduncus*) had significantly reduced female reproductive rates following a heatwave which is most likely explained by a decline in food availability (Wild *et al.*, 2019).

### 1.4 Dwarf Mongooses

#### 1.4.1 General biology and behaviour

Dwarf mongooses are the smallest mongoose species, and the smallest of Africa’s carnivores. Individuals weigh, on average, less than 300 g and measure ca. 50 cm in length (Rasa, 1976, 1987; Kern & Radford, 2013). They are part of the family Herpestidae, are found in woodland and savanna habitats (Creel & Waser, 1994), and are widely distributed from Ethiopia down to South Africa and across to Angola (Sharpe *et al.*, 2015). Dwarf mongooses can most commonly be found where there are termite mounds, rock outcrops or trees which can be used as their sleeping burrows (Sharpe *et al.*, 2015). They live in family groups of 12 individuals, on average, but there can be up to 30 individuals (Hendrichs, 1972; Rasa, 1976). Each group defends a territory, moving around that space and foraging together. Individuals will primarily feed on arthropods, but are also known to consume eggs, small mammals, snakes and lizards (Rasa, 1976; Sharpe *et al.*, 2015).
Dwarfmongooses forageprimarily by digging, which they cannot do whilst also being vigilant for theirmany aerial and terrestrial predators (Kern & Radford, 2014). They have therefore evolved sentinel behaviour where individuals act as a raised guard to look out for danger, allowing groupmates to focus on foraging (Kern & Radford, 2014). Alarm calls are produced to warn group members about any threats; they produce 11 distinct types of alarm call (although only five of these are commonly used) which include information about, for example, whether the threat is a terrestrial or aerial predator (Collier et al., 2017). Sentinels act flexibly, being influenced by both direct and indirect indicators of predation threat, as well as social factors (Kern & Radford, 2014). When acting as a sentinel, individuals often produce a “Watchman’s song” (a low amplitude call) that informs others of their position and current risk level, as well as providing information about their identity (Kern & Radford, 2013; Kern et al., 2016; Kern & Radford, 2018). Dwarf mongooses also eavesdrop on the alarm calls of heterospecifics, including tree squirrels (Paraxerus cepapi) and fork-tailed drongos (Dicrurus adsimilis) (Morris-Drake et al., 2017; Arbon et al., 2020).

Dwarf mongooses are cooperative breeders with groups consisting of a dominant breeding pair (who are usually the oldest individuals) and subordinate helpers of both sexes, who are either related to the breeding pair or individuals that have immigrated from another group (Rasa, 1977; Rood, 1990). Breeding is monopolised by the breeding pair, but it is possible for subordinate females to become pregnant; in another study population, subordinate females accounted for 12% of pregnancies seen (Creel & Waser, 1994). All adult group members take part in a range of cooperative activities, including allogrooming, sentinel behaviour and helping to raise the young by acting as babysitters and feeding, guarding and grooming them (Rasa, 1977; Rood, 1978; Creel & Waser, 1994; Kern & Radford, 2014). Individuals reward those who exhibited sentinel behaviour with grooming (Kern & Radford, 2018). However, group members also exhibit agonistic behaviour towards one another, either to reinforce their dominance status or to displace another individual from a foraging patch (Rasa, 1977; Morris-Drake et al., 2021).

1.4.2 Study site and population

The data for the two studies described in this thesis were collected on Sorabi Rock Lodge Reserve, located in Limpopo Province, South Africa (24°11’S,30°46’E). Sorabi is a 4 km² private game reserve that is part of southern Africa’s Savanna Biome. The reserve
experiences two distinct seasons: cold, dry winters (May–August) and hot, wet summers (September–April) (Kern & Radford, 2013). Temperature and rainfall data are collected on the reserve; for the time-period of our climate study, temperatures reached a minimum of 6°C in the winter and a minimum of 7°C in the summer. During this same period, temperatures reached a maximum of 37°C in the winter and a maximum of 43°C in the summer. There are a range of terrestrial and aerial predators of dwarf mongooses present throughout the year, including African rock pythons (*Python sebae*), honey badgers (*Mellivora capensis*), African wildcats, (*Felis lybica*), African fish-eagles (*Haliaeetus vocifer*) and brown snake-eagles (*Circaetus cinereus*) (Kern & Radford, 2014). The reserve also has the main R530 road running alongside it, meaning that the dwarf mongooses are exposed to road noise daily.

Data have been collected from a wild population of dwarf mongooses for the Dwarf Mongoose Research Project (DMRP) since it was established in 2011. Study individuals have been habituated to close (<5 m) human presence to allow close monitoring of their behaviour and life-history, as well as the running of experiments. Individuals are identified either from unique blonde hair-dye markings (Wella, Weybridge, UK) applied to different parts of their fur using an elongated paintbrush, or from natural features including scars (Kern & Radford, 2013). Being able to identify and be in close proximity to individuals means that we have a good understanding of the structure of each group; we know who the dominant and subordinate individuals are, as well as the age and sex of each group member. Adults were defined as individuals older than one year. For our anthropogenic-noise study, we used six groups (mean±SD group size = 11.7±5.2, range = 6–20) during July–September 2021. For the climate study, we used data from 11 groups between 2013 and 2020.

1.4.3 Use of habituated populations in animal behaviour studies

Habituation is described as the decrease in a response as a result of repeated exposure to a stimulus (Stein, 1966; Williamson & Feistner, 2011). By habituating our population of dwarf mongooses to close human presence, their natural behaviour and life-histories can be recorded, and field experiments run, in ecologically relevant scenarios. Whilst laboratory studies can help to decipher what mechanisms influence behaviour, experiments run in the
field provide ecological validity (Hoppitt et al., 2012). This can be particularly important when studying group-living animals where individuals frequently influence each other, something that would be less likely to occur in laboratory settings (Samuni et al., 2014). For example, captive groups of meerkats do not exhibit their natural social dynamics seen in the wild, highlighting how habituation to human observers is an important tool to understand animal behaviour (Hoppitt et al., 2012; Samuni et al., 2014).

There has been some debate and criticism of habituating animals to human presence, particularly relating to the habituation of non-human primates (Williamson & Feistner, 2011; Samuni et al., 2014; Green & Gabriel, 2020). Some of these concerns include risk of disease transmission (Homsy, 1999), stress (Woodford et al., 2002) and changing ranging patterns (Ando et al., 2008). These concerns, however, are not ones that we feel influence or alter behaviour in our population of dwarf mongooses. One reason for this is that when the DMRP was first established, preliminary observational sessions showed that individuals in our habituated groups exhibited the same behaviours as those in wild groups. For example, vigilance behaviour is exhibited in the same way in both habituated and wild groups, as both experience predation risk despite the former being exposed to human presence. Whilst there might be some absolute differences in behaviour between habituated and wild groups, in our work we are interested in the relative differences in behaviour between experimental treatments or different natural scenarios with all data collected from habituated groups. Furthermore, we are using this population as a study system to explore cooperative behaviours as well as how these behaviours are influenced by anthropogenic disturbances; something that is unlikely to be affected by habituation (Candea, 2013).

1.5 Thesis aims and predictions

The aim of this thesis is to provide an insight into how anthropogenic disturbances affect dwarf mongoose behaviour. The work particularly focused on how anthropogenic noise affects vigilance and foraging behaviour, and how agonistic and sentinel behaviour are impacted by climatic conditions (specifically temperature and rainfall). These are important avenues of research as whilst much is known about the different effects of anthropogenic
noise, very few studies have investigated noise in conjunction with other stressors, which could potentially be more ecologically relevant (Breitburg et al., 1999; Crain et al., 2008; Willems et al., 2021). Determining how climatic conditions affect behaviour is important because, despite climate change being an ever-increasing threat, little work has assessed the impacts on animal behaviour.

Multi-stressor effects on foraging and vigilance behaviour were investigated by running a field-based playback experiment on the habituated, wild population of dwarf mongooses (Chapter 2). To assess whether there is any combined effect when individuals are exposed to both an elevated predation risk and anthropogenic noise, individuals were first played either an alarm call (signalling there is a threat present) or close calls (calls individuals make whilst foraging, and thus a control), followed by playback of either road noise or ambient sound (as a control). The prediction was that there would be an initial increase in vigilance and a subsequent decrease in foraging behaviour following the alarm-call playback compared with the control close-call playback. When stressors were combined, it was predicted that there would be either an additive or synergistic effect, meaning there would be a great amount of vigilance and a decrease in foraging behaviour when exposed to both stressors, compared to being exposed to the stressors individually.

To assess the impacts of temperature and rainfall on agonistic and sentinel behaviour long-term data from the same population of dwarf mongooses were used (Chapter 3). Both behaviours were analysed at the season level with sentinel behaviour also being analysed at the daily level. It was predicted that in periods of hotter temperatures and low rainfall there would be an increase in agonistic interactions but, in contrast, there would be less sentinel behaviour in these same conditions.
Chapter 2: The combined effect of predation risk and anthropogenic noise on vigilance and foraging behaviour in dwarf mongooses

Photo by author
2.1 Abstract

Anthropogenic noise is a well-recognised and pervasive threat in the world’s ecosystems, with numerous studies demonstrating negative physiological, developmental and behavioural impacts on a range of taxa. However, research has tended to focus on the threat of anthropogenic noise in isolation; many species often experience this pollutant in conjunction with other stressors such as predation risk, with the combination potentially having a greater impact. Here, we used a field-based playback experiment to investigate the combined effects of elevated predation threat and road noise on the vigilance and foraging behaviour of dwarf mongooses (*Helogale parvula*). As expected, both playback of an alarm call and playback of road noise independently led to significantly more vigilance compared to playback of close calls and ambient sound, respectively. The two stressors had an equivalent effect on the total amount of vigilance shown and, in both cases, there was a trade-off with foraging: less of that behaviour was exhibited in response to alarm-call playback and to road-noise playback than the control playbacks; these similar changes in behaviour following both stressors lends support to the risk-disturbance hypothesis. The combination of the two stressors did not, however, generate a significantly different amount of vigilance or foraging compared to road noise alone. Thus, our experiment adds to the evidence that anthropogenic noise can have a negative impact but there was no indication of an additive or synergistic effect when combined with the natural stressor of elevated predation risk. Our findings help to highlight the complex and differing responses that different species have to combined stressors. If we are to understand the true full impacts of anthropogenic disturbances on species and communities, we must improve our understanding of their combined effects as all ecosystems are faced with multiple stressors arising from human activities.

2.2 Introduction

Anthropogenic (man-made) noise is a pervasive pollutant in the world’s terrestrial and marine ecosystems that has been increasing over recent decades (Shannon et al., 2016a). The increase in anthropogenic noise is primarily due to population growth, urbanisation, transportation and natural resource extraction, which are all projected to increase further in the future (Shannon et al., 2016a; Jerem & Mathews, 2021). For instance, road traffic almost
tripled in the US between 1970 and 2007, meaning that road-related noise also increased dramatically in that timeframe (Barber et al., 2010; Giordano et al., 2022). The effects of anthropogenic noise on humans have been researched extensively for decades, with clear evidence that there can be negative health consequences, including cardiovascular issues, and cognitive impairment (Kryter, 1994; EEA, 2020). In the last 20 years, there has also been a growing amount of research investigating the impacts of noise pollution on wildlife and ecosystems. Numerous studies have already found major consequences of noise for the physiology, development, behaviour and, ultimately, fitness of a wide range of non-human animal taxa (Francis & Barber, 2013; Shannon et al., 2016a; Dutilleux, 2017).

Anthropogenic noise can cause behavioural changes in four ways: it can mask acoustic signals or cues (Barber et al., 2010), it can distract individuals (Chan et al., 2010), it can act as a stressor (Kleist et al., 2018) and it can be perceived as a threat (Frid & Dill, 2002; Shannon et al., 2016b; Eastcott et al., 2020). The masking of important signals can cause changes to the way in which both the sender and the receiver behave (Halfwerk & Slabbekoorn, 2009; McMullen et al., 2014), and masking can also obscure important acoustic cues from both prey and predators (Simpson et al., 2014). For instance, superb fairy-wrens (Malurus cyaneus) and dwarf mongooses (Helogale parvula) respond less to the alarm calls of conspecifics and heterospecifics when experiencing additional noise (Morris-Drake et al., 2017; Zhou et al., 2019), and various bird species change the acoustic parameters of their songs to overcome masking (Slabbekoorn & Boer-Visser, 2006; Roca et al., 2016).

The remaining three mechanisms can affect behaviours beyond just those related to acoustic information. Distraction by noise has been demonstrated in Caribbean hermit crabs (Coenobita clypeatus), which allowed a predator to get closer to them before they hid (Chan et al., 2010). By contrast, some studies have shown that noise does not distract individuals. For example, when blue-tailed skinks (Emoia impar) were exposed to white-noise playback their flight initiation distance was not reduced showing that the increased levels of noise did not cause distraction (Kelligrew et al., 2021). Furthermore, barn swallows (Hirundo rustica) were more responsive to the threat of a predator when exposed to noise, allowing them to avoid the predation threat quicker and therefore didn’t support this distraction hypothesis (Matyjasiak et al., 2023). Noise-induced stress can lead to physiological and developmental
changes: for instance, bird hatchling success can be reduced due to the disrupting of glucocorticoid signalling caused by noise (Kleist et al., 2018); and noise pollution has also been shown to have a negative impact on key stages of zebrafish (Danio rerio) development (Lara & Vasconcelos, 2021). The perception of noise as a threat can cause behavioural changes, including increases in vigilance and reductions in foraging, that are qualitatively similar to those seen in response to predation threats (Berger-Tal et al., 2019); this is known as the risk-disturbance hypothesis (Frid & Dill, 2002). Whilst many studies have now documented behavioural effects of anthropogenic noise, the majority have examined the impact of noise in isolation despite it often occurring in conjunction with other stressors. It has long been suggested that a greater understanding of the combined effects of multiple stressors is needed to understand fully the true effects of human disturbance on animals (Breitburg et al., 1999; Crain et al., 2008; Shannon et al., 2016a).

Multiple stressors can potentially act additively (the combined effect is the sum of the individual stressor effects), antagonistically (less than the sum of the individual stressor effects) or synergistically (greater than the sum of the individual stressor effects) (Crain et al., 2008; Dominoni et al., 2020; Willems et al., 2021). Relevant research has mostly focused on combinations of anthropogenic stressors; in particular, noise and light pollution (Buxton et al., 2020; Dominoni et al., 2020; Ferraro et al., 2020; Willems et al., 2021). For example, Caribbean hermit crabs exposed to both noise and light pollution allowed a predator to move even closer compared to when there was just exposure to road noise, indicating an additive effect (Chan et al., 2010; Buxton et al., 2020). Wilson et al. (2021) found a synergistic effect on bird abundance when artificial light exposure was combined with noise pollution: species that decreased in abundance due to noise exposure showed even greater declines with the introduction of light pollution. However, animals face not only multiple anthropogenic stressors, but also experience natural stressors like predation risk. In a study of common lesser escuerzos (Odontophrynus americanus), for example, the combination of road noise and conspecific chorus noise had a greater effect on individual’s calls, causing them to increase the dominant frequency more, compared to when the two stressors were presented individually (Grenat et al., 2019). Contrastingly, chipmunks (Tamias striatus) and mice (Peromyscus leucopus) reduced their food intake significantly when exposed to predation risk but simultaneous exposure to road noise seemed to eliminate this effect, with
individuals increasing their food intake again (Giordano et al., 2022). Some research has shown that anthropogenic disturbances can cause a more extreme response than the threat of predation. For instance, European mink (Mustela lutreola) remained hidden when presented with faecal odours of a predator, and the same response, albeit more exaggerated, was seen when individuals were exposed to anthropogenic noise (Ortiz-Jimenez et al., 2021). More experimental tests investigating the impacts of anthropogenic noise combined with other natural stressors (such as predation risk), as well as direct comparisons of the response of animals to the two different threats, are needed to understand fully the impacts of this global pollutant.

We used a field-based playback experiment to investigate the combined effect of predation threat and road noise on vigilance and foraging behaviour in a wild population of dwarf mongooses. Dwarf mongooses are diurnal, cooperative breeders which live in groups of up to 30 individuals (Rasa, 1977; Kern & Radford, 2016). Foraging individuals spend most of the time digging with their head down, so are unable to be vigilant simultaneously. Consequently, group members act as a sentinel to scan for danger and to warn foragers of any potential threats (Rasa, 1989; Kern & Radford, 2016). Anthropogenic noise has already been shown to have a range of effects on the behaviour of dwarf mongooses: they are less responsive to surveillance calls made by sentinels, individuals respond less appropriately to the presence of olfactory predator cues, and they are less likely to flee when they hear a heterospecific alarm call (Kern & Radford, 2016; Morris-Drake et al., 2016, 2017).

In our experiment, individuals first received playback of either close calls (given whilst foraging) or an alarm call (given to warn of danger), followed by playback of either ambient sound or road noise. We expected an initial increase in vigilance and decrease in foraging following the alarm-call playback compared to close-call playback, as there is a perceived increase in predation risk. If the combination of predation threat and anthropogenic noise had an additive or synergistic effect, we expected there to be a further increase in vigilance and decrease in foraging in response to road-noise playback that followed alarm-call playback. Contrastingly, if these stressors were to act antagonistically, we would expect to see less vigilance behaviour and more foraging behaviour following both playbacks than if the effects were either additive or synergistic. Finally, we directly compared the vigilance behaviour exhibited when individuals were exposed to predation threat vs road...
noise. The risk-disturbance hypothesis predicts that the two stressors would cause an equivalent increase in time being vigilant.

2.3 Methods

2.3.1 Study site and population

Data for this study were collected between July and September 2021 on Sorabi Rock Lodge Reserve, Limpopo Province, South Africa (24°11’S,30°46’E), where the Dwarf Mongoose Research Project (DMRP) has been based since 2011. Sorabi is a private game reserve and is part of southern Africa’s Savanna Biome; more details on the study site can be found in Kern & Radford (2013). The reserve has the main R530 road running alongside it, making road noise a relevant pollutant that the dwarf mongooses experience daily.

Dwarf mongoose groups consist of a dominant breeding pair and subordinate helpers of both sexes; they are cooperative breeders, with the subordinates helping the dominant pair to raise their young (Rood, 1990). Subordinates can be related family members or individuals that have immigrated to that group from elsewhere (Rasa, 1977; Kern & Radford, 2013). Throughout the day, group members move around their territory together, foraging for insects and small vertebrates; foragers emit low-amplitude ‘close’ calls continuously (Kern & Radford, 2014). Whilst the group is foraging, individuals perform sentinel behaviour—acting as a raised guard to scan for danger (Kern & Radford, 2014)—as foragers are unable to dig for food and be vigilant simultaneously. The individual acting as a sentinel warns groupmates of potential predation threats by producing specific alarm calls that indicate whether there is an aerial or terrestrial predator (Kern & Radford, 2013; Collier et al., 2017).

In this study, six groups of wild dwarf mongooses were used (mean±SD group size = 11.7±5.2, range = 6–20). All study individuals have been habituated to close (<5 m) human presence which has allowed long-term data on their life history to be gathered. Individuals within groups are identified using blonde hair-dye markings (Wella, Weybridge, UK), which are applied to different areas of their fur using an elongated paintbrush, or through natural identifying features like scars (Kern & Radford, 2013). Dominant and subordinate adults
(individuals older than one year) were used in the experiment. Dominant individuals are identified through observations of agonistic and scent-marking behaviour (Rasa, 1977; Kern & Radford, 2014).

2.3.2 Playback experiment

The aim of the experiment was to investigate the combined effects of predation threat and road noise on the vigilance and foraging behaviour of dwarf mongooses. To do this, a 2x2 experimental design was used in which each focal individual (N = 17 individuals in six groups) received four different playback treatments: alarm call followed by road noise, alarm call followed by ambient sound, close calls followed by road noise and close calls followed by ambient sound.

2.3.2.1 Sound recordings and playback generation

Sound recordings were made of ambient sound, road noise, close calls and aerial alarm calls in calm weather conditions with no wind or rain. The calls and ambient sound were recorded for this study on a Marantz PMD661 solid-state recorder (Marantz, Kanagawa, Japan) using a Sennheiser MKE600 shotgun microphone (Sennheiser, Wedemark, Germany) with a Rycote Softie windshield (Rycote Microphone Windshields, Stroud, Gloucestershire, UK). Road-noise recordings created for Kern & Radford (2016) were used; these were made with a Marantz PMD660 182 solid-state recorder and a Sennheiser ME66 shotgun microphone with a Rycote Softie windshield. Ambient-sound recordings were made in the centre of each group’s territory at least 50 m from any mongoose or human activity. They were collected around midday to ensure conditions were relevant to both morning and afternoon experimental sessions. The microphone was positioned to face away from the main R530 road and was 10 cm from the ground, as this is the head height of a dwarf mongoose. Road-noise recordings were made 10 m from the R530 road, with the microphone facing the passing traffic. Matched close calls and aerial alarm calls were recorded from the same subordinate group members. Close calls were collected from foragers with the microphone positioned within 1
m of the focal individual to ensure only that mongoose’s calls were recorded. Alarm calls were collected when an individual alerted the group to the presence of an aerial predator.

All tracks were created and edited in Audacity (version 3.0.2). A unique 5-min ambient-sound track was made for each focal individual within each group. All vocalisations from heterospecifics and conspecifics, as well as any man-made noise, were removed from a recording to make a track. Unique road-noise tracks were created for each focal individual; the same road-noise tracks from Kern & Radford (2016) were used but were extended to be 5-min. These tracks contained the mean number and type of vehicles observed during traffic counts on the R530 (Kern & Radford, 2016; Eastcott et al., 2020). Only vehicle noise was included in these road-noise tracks; no other anthropogenic noise (such as airplanes) was included. Both close-call and alarm-call tracks were 44 s in duration and comprised four calls, each separated by 12 s of ambient sound from the territory of the individual whose calls were used in the track; ambient sound was also played for 2 s at the beginning and end of the tracks. The close-call tracks consisted of four close calls whilst the alarm-call tracks consisted of three close calls followed by one aerial alarm call (Figure 2.1). The close-call and alarm-call tracks were each 44 s and included multiple close calls in them to imitate a foraging groupmate. Individuals would not usually be exposed to an alarm call without previously having heard the individual producing close calls whilst foraging. The tracks were made to be 44 s so that they were long enough to imitate a foraging individual, but not so long that the trial would likely have to be abandoned. Each focal individual was played close-calls and alarm-calls of the same groupmate, but different focal individuals in the same group received playbacks from different groupmates. All focal individuals received unique road-noise and ambient-sound playbacks to minimise the chances of habituation to the tracks. A HandyMAN TEK 1345 sound meter (Metrel UK Ltd, Epsom, Surrey, UK) was used to ensure that the sound levels were standardised across all playback tracks of the same type. Playbacks were at natural amplitudes in line with Kern & Radford (2016) and Morris-Drake et al. (2017): ambient-sound peak amplitude = 40 dB SPLA at 10 m, road-noise peak amplitude = 65 dB SPLA at 10 m, alarm-call peak amplitude = 55 dB SPLA at 1.5 m and close-call peak amplitude = 45 dB SPLA at 1.5 m.
Figure 2.1 Spectrograms of each playback track type that a focal individual received: a) close calls (four of this call type), b) alarm calls (three close calls and then a single aerial alarm call), c) ambient sound, and d) road noise. Spectrograms were created in Raven Lite (version 2.0.4).
2.3.2.2 Experimental protocol

All four trials to a focal individual were carried out within 5 days, all either in the morning (07:30–12:00) or afternoon (12:30–17:00), with a maximum of two trials per day; at least 30 min was left between trials on the same day. Treatment order was counterbalanced between focal individuals. Trials were only carried out in calm weather conditions (no wind or rain) and in areas of medium habitat density. Prior to the start of a trial, more than 50% of the group (including the focal individual) had to be foraging and the focal individual had to be amongst other group members (i.e., not on the periphery of the group). Trials were not started if there had been a latrine event in the last 30 min or a conspecific or heterospecific alarm call in the last 10 min. Trials were abandoned for 24 h: if the focal individual moved out of sight for longer than 15 s, moved more than 5 m from the loudspeaker, or became a sentinel or groomed for more than 10 s; if there was an alarm call (either conspecific or heterospecific); or if the group started to latrine. In total, 12 trials were repeated for these reasons.

Following the close-call or alarm-call playback, there was a one-minute observation period during which there was no playback. The focal individual was then played either a road-noise or ambient-sound track, during which there was a second one-minute observation period. We chose this one-minute observation period as we determined this to be long enough to observe any behaviour resulting from either the close or alarm call but not so long that there was a risk of the trial needing to be abandoned. Previous work on the DMRP had an observation period of two minutes which we thought was too long for this experiment. Individuals were then exposed to one minute of either ambient sound or road noise to match the length of time of the previous observation period. The two stressors (playback of an alarm-call or playback of road-noise) were not played simultaneously to focal individuals to avoid masking of the tracks. As individuals were exposed to both stressors through a single sensory modality (unlike other stressors such as light and noise) we decided that to ascertain the impacts of these stressors effectively, they should be played separately to individuals. All tracks were played through a loudspeaker (Rokono B10, Boundless Technology Limited, Devon, UK) which was connected to an MP3 player (Kubik Evo, Kubik Digital Electronics). The loudspeaker was positioned on the ground 2–5 m from the focal individual, hidden from view. All foraging and vigilance behaviour was recorded continuously.
into a Dictaphone (Sony ICD-PX370) during both the one-minute observation period between tracks in a trial and during the ambient-sound or road-noise playback. Focal individuals were defined as foraging when they had their head down looking for food, they were digging or were eating a prey item, and defined as vigilant when they had their head up and were scanning the area. When the focal individual was grooming, moving or acting as a sentinel, this was also recorded into the Dictaphone.

2.3.3 Data analysis

Data analysis was split into three parts. Part 1 examined the impact of alarm calls on vigilance and foraging behaviour. Part 2 examined the impact of road noise following an alarm call for both vigilance and foraging behaviours. Part 3 examined whether there was a difference in vigilance behaviour following an alarm-call playback or a road-noise playback. For all trials, the total time spent vigilant and the total time spent foraging were first calculated for relevant periods. To determine what drove the overall difference in each of these behaviours, the number of vigilance and foraging bouts and the mean duration of these bouts were also calculated. To assess the effect of alarm calls (Part 1), these response variables were calculated from the one-minute period following alarm-call or close-call playback. To assess the additional effect of road noise (Part 2), the response variables were calculated for the first minute of either the ambient-sound or road-noise playback. To compare the effect of alarm calls with road noise (Part 3), response variables were calculated from the one-minute period following an alarm-call playback and the first minute of a road-noise playback. For alarm calls, we took the mean values of the two alarm-call trials; for road noise, we used the trial where close calls were followed by road noise to avoid any combined-stressor effects.

All statistical analysis was carried out using R version 4.2.1 (R Core Team, 2022), with results considered significant at $p < 0.05$. The matched design of the experiment and the use of more than one focal individual per group meant that there was repeated sampling of individuals and groups, and so mixed models were used. All response variables were plotted to check whether the data were normally distributed. Where the response variables fitted the assumptions of parametric testing, linear mixed models (LMMs) were used. Where the
assumptions of parametric testing were not met with the raw data, generalised linear mixed models (GLMMs) were used or the data were log or square-root transformed before modelling with LMMs. The lme4 package was used for all LMMs and GLMMs (Bates et al., 2015).

For Part 1, call type (close call, alarm call), trial order (first, second, third, fourth) and their interaction were included as fixed effects. For Part 2, treatment (close call then ambient sound, close call then road noise, alarm call then ambient sound, alarm call then road noise), trial order (first, second, third, fourth) and their interaction were included as fixed effects. For Part 3, threat (road noise, alarm call) was included as a fixed effect; as trial order was not found to be generally important in the models previously run, and mean values were used for the alarm-call response, trial order was not included as a fixed effect. Individual ID nested in group ID were included as random terms in all models. For each response variable, the maximal model (with all terms retained) is reported. Post-hoc comparisons with the Benjamini-Hochberg procedure were made using the emmeans package to allow comparisons between treatments (Benjamini & Hochberg, 1995; Lenth, 2022).

2.4 Results

2.4.1 Part 1: Responses to an alarm call

Hearing an alarm call affected both vigilance and foraging behaviour of dwarf mongooses. Following an alarm-call playback compared to a close-call playback, individuals spent significantly more time vigilant (LMM: $f = 73.313$, $df = 1$, $p < 0.001$; Table 2.1a; Figure 2.2a). As a consequence, there was significantly less time spent foraging in the aftermath of an alarm-call playback than a close-call playback ($f = 35.021$, $df = 1$, $p < 0.001$; Table 2.1b; Figure 2.2b).
Table 2.1 Output of linear mixed models investigating a) total square-root transformed vigilance duration and b) total log-transformed foraging duration of focal individuals in response to alarm-call and close-call playbacks. The maximal model is shown with significant terms in bold. Effect ± standard error is shown for the fixed effects and variance ± standard deviation is shown for the random terms (italicised). The reference level for call type is alarm call. N = 17 individuals in six groups.

<table>
<thead>
<tr>
<th>Fixed Effect</th>
<th>Effect ± SE</th>
<th>df</th>
<th>f value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>a) Total vigilance duration</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>3.562 ± 0.430</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Call Type</td>
<td>-3.342 ± 0.583</td>
<td></td>
<td>73.313</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Trial Order</td>
<td></td>
<td>3</td>
<td>0.026</td>
<td>0.994</td>
</tr>
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<td>Call Type: Trial Order</td>
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<td>3</td>
<td>1.223</td>
<td>0.310</td>
</tr>
<tr>
<td>Individual ID in Group ID</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group</td>
<td>0.029 ± 0.172</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| **b) Total foraging duration**|             |    |         |       |
| (Intercept)                   | 3.777 ± 0.054 |    |         |       |
| Call Type                     | 0.300 ± 0.073 |    | 35.021  | <0.001|
| Trial Order                   |             | 3  | 0.488   | 0.692 |
| Call Type: Trial Order        |             | 3  | 1.337   | 0.271 |
| Individual ID in Group ID     | 0.000       |    |         |       |
| Group                         | <0.001 ± 0.025 |    |         |       |
Figure 2.2 The effect of close-call and alarm-call playbacks on a) total vigilance duration and b) total foraging duration. Shown in the boxplots are the median and interquartile range; raw data points (dots) from the same focal individual are connected by dashed lines. There can be multiple data points of the same value and so the number of visible points is less than the sample size. N = 17 individuals in six groups.

The treatment difference in the total time an individual spent vigilant was driven by differences in both the number of vigilance bouts and the mean duration of those bouts. There were significantly more occurrences of vigilance behaviour following the alarm-call playback compared with the close-call one (LMM: $f = 72.837, df = 1, p < 0.001$; Table 2.2a;
Moreover, the mean duration of vigilance bouts was significantly greater after hearing playback of an alarm call compared to that of close calls ($f = 63.993$, $df = 1$, $p < 0.001$; Table 2.2b; Figure 2.3b). The overall lesser time spent foraging following alarm-call playback compared to close-call playback was despite more foraging bouts occurring after the former ($f = 4.485$, $df = 1$, $p = 0.040$; Table 2.3a; Figure 2.3c); it was the mean duration of foraging bouts that was significantly lower following alarm-call playback than close-call playback ($f = 15.406$, $df = 1$, $p < 0.001$; Table 2.3b; Figure 2.3d).

Table 2.2 Output of the linear mixed models investigating a) number of vigilance occurrences and b) mean log-transformed vigilance duration of focal individuals in response to alarm-call and close-call playbacks. The maximal model is shown with significant terms shown in bold. Effect ± standard error is shown for the fixed effects and variance ± standard deviation is shown for the random terms (italicised). The reference level for call type is alarm call. N = 17 individuals in six groups.

<table>
<thead>
<tr>
<th>Fixed Effect</th>
<th>Effect ± SE</th>
<th>df</th>
<th>f value</th>
<th>P</th>
</tr>
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<td><strong>a) Total vigilance occurrences</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>0.037 ± 0.004</td>
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<tr>
<td>Call Type</td>
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<td>72.837</td>
<td>&lt;0.001</td>
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<td>Trial Order</td>
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<td>1.506</td>
<td>0.223</td>
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<td>Call Type: Trial Order</td>
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<td>1.868</td>
<td>0.145</td>
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<td><strong>Individual ID in Group ID</strong></td>
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<td></td>
</tr>
<tr>
<td><strong>Group</strong></td>
<td>&lt;0.001 ± 0.005</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>b) Mean vigilance duration</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>1.978 ± 0.273</td>
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<tr>
<td>Call Type</td>
<td>-1.849 ± 0.375</td>
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<td>63.993</td>
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<td>Trial Order</td>
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<td>3</td>
<td>0.243</td>
<td>0.866</td>
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<td>Call Type: Trial Order</td>
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<td>0.498</td>
<td>0.685</td>
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<td><strong>Individual ID in Group ID</strong></td>
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<td></td>
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<tr>
<td><strong>Group</strong></td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2.3 Output of the linear mixed models investigating a) number of foraging occurrences and b) mean log-transformed foraging duration of focal individuals in response to alarm-call and close-call playbacks. The maximal model is shown with significant terms shown in bold. Effect ± standard error is shown for the fixed effects and variance ± standard deviation is shown for the random terms (italicised). The reference level for call type is alarm call. N = 17 individuals in six groups.

<table>
<thead>
<tr>
<th>Fixed Effect</th>
<th>Effect ± SE</th>
<th>df</th>
<th>f value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>a) Total foraging occurrences</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>(Intercept)</td>
<td>0.034 ± 0.004</td>
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<tr>
<td>Call Type</td>
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<td>4.485</td>
<td><strong>0.040</strong></td>
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<td>Trial Order</td>
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<td>3</td>
<td>1.223</td>
<td>0.312</td>
</tr>
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<td>Call Type: Trial Order</td>
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<td>3</td>
<td>0.740</td>
<td>0.533</td>
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<tr>
<td>Individual ID in Group ID</td>
<td>&lt;0.001 ± 0.005</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group</td>
<td>&lt;0.001 ± 0.003</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>b) Mean foraging duration</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>3.131 ± 0.167</td>
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<tr>
<td>Call Type</td>
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<td>15.406</td>
<td><strong>&lt;0.001</strong></td>
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<td>Trial Order</td>
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<td>3</td>
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<td>Call Type: Trial Order</td>
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<td>3</td>
<td>0.923</td>
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<td>Individual ID in Group ID</td>
<td>0.032 ± 0.179</td>
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<td></td>
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</tr>
<tr>
<td>Group</td>
<td>0.020 ± 0.139</td>
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</table>
Figure 2.3 The effect of close-call and alarm-call playbacks on a) number of vigilance occurrences, b) mean vigilance duration c) number of foraging occurrences and d) mean foraging duration. Shown in the boxplots are the median and interquartile range; raw data points (dots) from the same focal individual are connected by dashed lines. There can be multiple data points of the same value and so the number of visible points is less than the sample size. N = 17 individuals in six groups.

2.4.2 Part 2: Responses to the combination of road noise and the threat of predation

Both the total time that an individual spent being vigilant (LMM: $f = 30.384$, $df = 3$, $p < 0.001$; Table 2.4a) and that spent foraging ($f = 13.812$, $df = 3$, $p < 0.001$; Table 2.4b) were significantly affected by playback treatment. Individuals spent more time being vigilant when played road noise compared to ambient sound, but there was no significant difference found between the two road-noise treatments; hearing an alarm call rather than close calls prior to
the road-noise playback did not lead to individuals spending more time being vigilant (Table 2.5; Figure 2.4a). Consequently, individuals spent less time foraging after hearing road-noise playback compared to ambient-sound playback, but there was no significant difference in foraging time between the two road-noise treatments (Table 2.5 Figure 2.4b).

Table 2.4 Output of linear mixed models when investigating a) total square-root transformed vigilance duration and b) total square-root transformed foraging duration of focal individuals in response to ambient-sound and road-noise playbacks following either an alarm-call or close-call playback. The maximal model is shown with significant terms shown in bold. Effect ± standard error is shown for the fixed effects and variance ± standard deviation is shown for the random terms (italicised). The reference level for treatment is Alarm–Ambient playbacks. N = 17 individuals in six groups.

<table>
<thead>
<tr>
<th>Fixed Effect</th>
<th>Effect ± SE</th>
<th>df</th>
<th>f value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Total vigilance duration</td>
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<td></td>
<td></td>
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<tr>
<td>(Intercept)</td>
<td>0.936 ± 0.679</td>
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<tr>
<td>Treatment</td>
<td>3</td>
<td>30.384</td>
<td>&lt;0.001</td>
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<tr>
<td>Alarm – Road</td>
<td>4.112 ± 1.070</td>
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<tr>
<td>Close – Ambient</td>
<td>-0.573 ± 0.982</td>
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<tr>
<td>Close – Road</td>
<td>2.527 ± 0.901</td>
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<tr>
<td>Trial Order</td>
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<td>0.699</td>
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<td>Treatment: Trial Order</td>
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<td>0.693</td>
<td>0.712</td>
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<td>Individual ID in Group ID</td>
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<tr>
<td>Group</td>
<td>0.229 ± 0.479</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>b) Total foraging duration</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>7.661 ± 0.463</td>
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<tr>
<td>Treatment</td>
<td>3</td>
<td>13.812</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Alarm – Road</td>
<td>-2.131 ± 0.718</td>
<td></td>
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<tr>
<td>Close – Ambient</td>
<td>0.013 ± 0.660</td>
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<tr>
<td>Close – Road</td>
<td>-1.246 ± 0.606</td>
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<td>Trial Order</td>
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<td>Treatment: Trial Order</td>
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<td>Individual ID in Group ID</td>
<td>0.031 ± 0.177</td>
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<td>Group</td>
<td>0.134 ± 0.367</td>
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</table>
Figure 2.4 The effect of the four different treatments on a) total vigilance duration and b) total foraging duration. Shown in the boxplots are the median and interquartile ranges; raw data points (dots) from the same focal individual are connected by dashed lines. There can be multiple data points of the same value and so the number of visible points is less than the sample size. N = 17 individuals in six groups. *** denotes $p = 0.001$ and **** denotes $p < 0.001$.

The treatment effect on total vigilance time was driven by significant differences in both the number of vigilance occurrences (LMM: $f = 22.621$, $df = 3$, $p < 0.001$; Table 2.6a) and their mean duration ($f = 14.727$, $df = 3$, $p < 0.001$; Table 2.6b). There were more occurrences of vigilance behaviour and bouts were, on average, longer when individuals were played back road noise compared to ambient sound, but no significant difference in either measure depending on whether alarm-call or close-call playback preceded the road noise (Table 2.5; Figure 2.5a,b). Similarly, the treatment effect on total foraging time was driven by significant differences in both the number of foraging occurrences ($f = 16.028$, $df =$
3, \( p < 0.001; \) Table 2.7a) and their mean duration (\( f = 23.632, df = 3, p < 0.001; \) Table 2.7b).

There were fewer occurrences of foraging behaviour and bouts were, on average, shorter when individuals were played back road noise compared to ambient sound, but no significant difference in either measure between the two road-noise treatments (Table 2.5; Figure 2.5c,d).

**Table 2.5** Benjamini Hochberg post hoc test output investigating the effects of the different treatments on the response variables shown. Significant terms are shown in bold. A = close call followed by ambient sound, B = alarm call followed by ambient sound, C = close call followed by road noise, and D = alarm call followed by road noise. \( N = 17 \) individuals in six groups.

<table>
<thead>
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<th>Post-hoc comparison</th>
<th>Total vigilance duration</th>
<th>Total foraging duration</th>
<th>Total vigilance occurrences</th>
<th>Total foraging occurrences</th>
<th>Mean vigilance duration</th>
<th>Mean foraging duration</th>
</tr>
</thead>
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<tr>
<td>A–B</td>
<td>0.620</td>
<td>0.939</td>
<td>0.459</td>
<td>0.546</td>
<td>0.778</td>
<td>0.818</td>
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<tr>
<td>A–C</td>
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<td>0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.001</td>
<td>&lt;0.001</td>
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<tr>
<td>A–D</td>
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<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
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<td>B–C</td>
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<td>0.001</td>
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<tr>
<td>B–D</td>
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<td>C–D</td>
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<td>0.987</td>
<td>0.546</td>
<td>0.590</td>
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Table 2.6 Output of linear mixed models when investigating a) number of vigilance occurrences and b) mean square-root transformed vigilance duration of focal individuals in response to ambient-sound and road-noise playbacks following either an alarm-call or close-call playback. The maximal model is shown with significant terms shown in bold. Effect ± standard error is shown for the fixed effects and variance ± standard deviation is shown for the random terms (italicised). The reference level for treatment is Alarm–Ambient playbacks. N = 17 individuals in six groups.

<table>
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<tr>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>0.011 ± 0.009</td>
<td></td>
<td>22.621</td>
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<tr>
<td>Treatment</td>
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<td></td>
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<tr>
<td>Alarm – Road</td>
<td>0.064 ± 0.014</td>
<td></td>
<td>14.727</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Close – Ambient</td>
<td>&lt;-0.001 ± 0.013</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Close – Road</td>
<td>0.029 ± 0.012</td>
<td></td>
<td>0.556</td>
<td>0.647</td>
</tr>
<tr>
<td>Trial Order</td>
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<td></td>
<td>0.547</td>
</tr>
<tr>
<td>Treatment: Trial Order</td>
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<tr>
<td>Group</td>
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b) Mean vigilance duration

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<td>0.556</td>
<td>0.647</td>
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<td>Close – Ambient</td>
<td>-0.539 ± 0.799</td>
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<tr>
<td>Close – Road</td>
<td>1.231 ± 0.737</td>
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<td>0.251</td>
<td>0.984</td>
</tr>
<tr>
<td>Trial Order</td>
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<td>0.647</td>
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<tr>
<td>Treatment: Trial Order</td>
<td></td>
<td>9</td>
<td>0.251</td>
<td>0.984</td>
</tr>
<tr>
<td>Individual ID in Group ID</td>
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<td></td>
<td></td>
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<tr>
<td>Group</td>
<td>0.097 ± 0.311</td>
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Table 2.7 Output of linear mixed models when investigating a) number of foraging occurrences and b) mean square-root transformed foraging duration of focal individuals in response to ambient-sound and road-noise playbacks following either an alarm-call or close-call playback. The maximal model is shown with significant terms shown in bold. Effect ± standard error is shown for the fixed effects and variance ± standard deviation is shown for the random terms (italicised). The reference level for treatment is Alarm–Ambient playbacks. N = 17 individuals in six groups.

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<th>f value</th>
<th>P</th>
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<td><strong>a) Total foraging occurrences</strong></td>
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<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>0.027 ± 0.009</td>
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<td>0.978</td>
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<td>Close – Ambient</td>
<td>0.047 ± 0.013</td>
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<td>23.632</td>
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<tr>
<td>Close – Road</td>
<td>3.960 ± 1.034</td>
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<td>8.320</td>
<td>0.114</td>
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<tr>
<td>Trial Order</td>
<td>-2.500 ± 0.950</td>
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<td>0.602</td>
</tr>
<tr>
<td>Treatment: Trial Order</td>
<td>6.536 ± 0.714</td>
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<td>2.206</td>
<td>0.037</td>
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<td>9</td>
<td>0.000</td>
<td>0.999</td>
</tr>
<tr>
<td>Group</td>
<td>&lt;0.001 ± 0.007</td>
<td>9</td>
<td>0.000</td>
<td>0.999</td>
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<th>f value</th>
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<tbody>
<tr>
<td><strong>b) Mean foraging duration</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>6.536 ± 0.714</td>
<td>3</td>
<td>23.632</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Treatment</td>
<td>-3.960 ± 1.126</td>
<td>3</td>
<td>8.320</td>
<td>0.114</td>
</tr>
<tr>
<td>Alarm – Road</td>
<td>0.114 ± 1.034</td>
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<td>0.625</td>
<td>0.602</td>
</tr>
<tr>
<td>Close – Ambient</td>
<td>-2.500 ± 0.950</td>
<td>3</td>
<td>0.768</td>
<td>0.646</td>
</tr>
<tr>
<td>Close – Road</td>
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<td>9</td>
<td>0.000</td>
<td>0.999</td>
</tr>
<tr>
<td>Trial Order</td>
<td>0.241 ± 0.491</td>
<td>9</td>
<td>0.000</td>
<td>0.999</td>
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Figure 2.5 The effect of the four different treatments on a) total vigilance occurrences, b) mean vigilance duration, c) total foraging occurrences and d) mean foraging duration. Shown in the boxplots are the median and interquartile ranges; raw data points (dots) from the same focal individual are connected by dashed lines. There can be multiple data points of the same value and so the number of visible points is less than the sample size. N = 17 individuals in six groups. *** denotes p = 0.001 and **** denotes p <0.001.

2.4.3 Part 3: Difference in vigilance response to alarm calls and road noise
There was some evidence for a difference in vigilance response to playback of road noise and alarm calls. Overall, there was no significant difference in the time that individuals spent being vigilant after hearing road noise compared to an alarm call (LMM: $f = 2.401$, $df = 1$, $p = 0.133$; Table 2.8a; Figure 2.6a). However, the number of vigilance occurrences was significantly influenced by playback type, with individuals showing more bouts of vigilance after hearing road noise compared to an alarm call (GLMM: $f = 22.259$, $p < 0.001$; Table 2.8b; Figure 2.6b). By contrast, the mean duration of vigilance bouts was slightly longer after hearing an alarm call compared with road noise but this was difference not statistically significant ($f = 0.630$, $p = 0.330$; Table 2.8c; Figure 2.6c).
Table 2.8 Output of the mixed models investigating the impact of road noise and alarm calls on the a) total vigilance duration (linear mixed model), b) number of vigilance occurrences and c) mean vigilance duration of the focal individual; gamma family, inverse link generalised linear mixed models were run for b) and c). The maximal model is shown with significant terms shown in bold. Effect ± standard error is shown for the fixed effects and variance ± standard deviation is shown for the random terms (italicised). The reference level for threat is alarm call. N = 17 individuals in six groups.

<table>
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<th>f value</th>
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<td><strong>a) Total vigilance duration</strong></td>
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<td></td>
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<td>(Intercept)</td>
<td>11.638 ± 2.759</td>
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<tr>
<td>Threat</td>
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<td>2.401</td>
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<tr>
<td>Group</td>
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<td><strong>b) Total vigilance occurrences</strong></td>
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<td></td>
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<tr>
<td>(Intercept)</td>
<td>0.974 ± 0.004</td>
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<td>22.259</td>
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<tr>
<td>Threat</td>
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<tr>
<td>Individual ID in Group ID</td>
<td>&lt;0.001 ± 0.009</td>
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<tr>
<td>Group</td>
<td>0.000 ± 0.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>c) Mean vigilance duration</strong></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>0.146 ± 0.024</td>
<td>1</td>
<td>0.630</td>
<td>0.330</td>
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<tr>
<td>Threat</td>
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<td></td>
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<td>Individual ID in Group ID</td>
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<td>Group</td>
<td>&lt;0.001 ± &lt;0.001</td>
<td></td>
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53
Figure 2.6 The effect of alarm-call and road-noise playbacks on a) total vigilance duration, b) number of vigilance occurrences and c) mean vigilance duration. Shown in the boxplots are the median and interquartile range; raw data points (dots) from the same focal individual are connected by dashed lines. There can be multiple data points of the same value and so the number of visible points is less than the sample size. N = 17 individuals in six groups.

2.5 Discussion

Vigilance and foraging behaviour in dwarf mongooses were significantly affected when exposed both to an alarm call and to road noise. Immediately following an alarm-call playback, individuals were more vigilant and spent less time foraging than following close-call playback. When exposed to road-noise playback, individuals also spent more time being vigilant and less time foraging compared to when they received ambient-sound playback. However, there was no significant difference found between the two road-noise treatments:
there was no combined effect when an individual was exposed to road noise in conjunction with the threat of a predator compared to when an individual was exposed to road noise alone. When comparing the effects of the two stressors, there was some evidence to suggest road noise and the predation threat have different influences on vigilance behaviour.

As predicted, alarm-call playback led to greater vigilance when compared with the playback of close calls. This increased vigilance response is consistent with other studies in dwarf mongooses (Collier et al., 2017), as well as Richardson's ground squirrels (Urocitellus richardsonii) (Wilson & Hare, 2006; Hare & Warkentin, 2012) and Western Australian magpies (Gymnorhina tibicen) (Silvestri et al., 2019) among many other species. Similarly, road-noise playback led to more vigilance behaviour compared to when the individuals were exposed to ambient-sound playback. This result is consistent with Eastcott et al. (2020), who found that dwarf mongooses increase their vigilance after hearing road-noise playbacks and that there is intrapopulation variation in responses depending on age and dominance. Increased vigilance in response to anthropogenic noise has also been demonstrated in other species such as California ground squirrels (Ostospermophilus beecheyi) (Rabin et al., 2006), prairie dogs (Cynomys ludovicianus) (Shannon et al., 2016b), chipmunks and mice (Giordano et al., 2022). These behavioural changes could be because road noise masks important acoustic cues (e.g., those generated by predators or heterospecific alarm calls) and signals (e.g., alarm calls) that indicate danger (Morris-Drake et al., 2017; Erbe et al., 2022), so the mongooses compensate visually with increased vigilance (Barber et al., 2010). Another possibility for the greater vigilance is that individuals are perceiving the road noise as a threat in the same way that they would predation and reacting with the same behavioural changes (Blair et al., 2016; Collins et al., 2022).

Our direct comparison of vigilance behaviour in response to alarm-call and road-noise playback found no significant difference in the overall time spent on that activity. However, there was some evidence that the two stressors affected vigilance behaviour differently in a more nuanced way: dwarf mongooses looked up more often when exposed to road noise compared to when there was an increased threat of predation; by contrast, vigilance bouts were, on average, shorter in response to road-noise playback although this difference with alarm-call playback was not statistically significant. The similar overall vigilance response to road-noise and alarm-call playbacks lends support to the risk-
disturbance hypothesis (Frid & Dill, 2002) whereby animals react in the same way that they do to natural predators when they are exposed to anthropogenic disturbance. To date, few studies have explored this directly and the studies that have been done have conflicting results. For example, work on pygmy marmosets (*Cebuella pygmaea*) found that whilst noise could change the behaviour of these animals, there was little evidence to support the risk-disturbance hypothesis (Hawkins & Papworth, 2022). However, Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*) responded to traffic noise in the same way they would in the presence of a predator by reducing the distance between nearest neighbours (Owens *et al*., 2012). Ortiz-Jimenez *et al.* (2021) have suggested that European mink (*Mustela lutreola*) might have an innate anti-predatory response that they use when exposed to an unknown threat source, again providing support for the risk-disturbance hypothesis (Frid & Dill, 2002). Future work should look to compare the impacts of predation risk and road noise both on an individual’s behaviour and physiologically, but also the fitness consequences, to help our understanding of the relative effects of these two stressors.

Whenever we observed an increase in vigilance, in response to either alarm calls or road noise, there was a concomitant reduction in foraging. This trade-off is seen in a range of species and contexts. For instance, yellow-bellied marmots (*Marmota flaviventris*) trade-off foraging for vigilance behaviour and, when exposed to alarm calls, they increase their vigilance behaviour and decrease the time spent foraging (Blumstein & Daniel, 2004). Eastern chipmunks (*Tamias striatus*) also increase their personal vigilance after hearing an alarm call, with individuals taking fewer seeds at a slower rate when foraging (Baack & Switzer, 2000). Prairie dogs showed a similar response of increasing vigilance behaviour and consequently a decrease in foraging behaviour after hearing road noise (Shannon *et al*., 2014b). Many species must balance the dual risks of predation and starvation (Lima & Dill, 1990; Hare & Warkentin, 2012), and trade-offs between foraging and vigilance have been shown to have knock on consequences for fitness: for example, great tits (*Parus major*) laid smaller clutches in noisier areas, potentially because individuals may have to spend more time scanning for predators and then have less energy to invest in reproduction (Quinn *et al*., 2006; Halfwerk *et al*., 2010). Future work with dwarf mongooses should look to quantify if there is a fitness consequence to trading off foraging for greater vigilance behaviour.
Contrary to what we predicted, there was no combined effect when individuals were exposed to the two stressors, predation risk and road noise, sequentially. A recent study in shore crabs (*Carcinus maenas*) similarly found no combined effect of predation threat and noise (Hubert *et al.*, 2023). The lack of a combined effect in our study might be because the effect of the alarm call was brief; there was a 1 min gap between the individual hearing the alarm call before they were exposed to the road noise. The lack of a vigilance difference between the two treatments finishing with ambient sound suggests that the greater vigilance resulting from the alarm call had finished by the time the second playback occurred. Other studies have exposed individuals to the threats simultaneously (Giordano *et al.*, 2022); as a result, a stronger combined response might then be predicted. Another possible reason why we found no combined effect was that the dwarf mongooses were only exposed to the stressors for very short periods compared to other studies. Dominoni *et al.* (2020), for example, played road noise continuously from 17:15 on day 1 until 08:15 on day 6 of their treatment week. Unlike our experiment, some studies have shown a combined effect when individuals are exposed to multiple stressors (Grenat *et al.*, 2019; Ferraro *et al.*, 2020; Wilson *et al.*, 2020; Giordano *et al.*, 2022); the differences in results highlight why further work is needed as all animals experience multiple stressors all the time. Moreover, most studies looking at the effects of combined stressors on animals have focused on light pollution and anthropogenic noise (Buxton *et al.*, 2020; Ferraro *et al.*, 2020; Dominoni *et al.*, 2020; Willems *et al.*, 2021); future work also needs to assess the impacts of other combined anthropogenic stressors, such as anthropogenic noise and habitat fragmentation, as well as looking at natural stressors in combination with anthropogenic stressors.

Our results show that both the threat of predation and road noise cause individuals to be more vigilant and, consequently, decrease the amount of time they spend foraging. This trade-off between vigilance and foraging when exposed to both stressors of predation threat and anthropogenic noise is in line with studies on a range of other species. Not only can anthropogenic noise impact individuals, but it can also result in community-level changes in abundance and distribution of some species (McClure *et al.*, 2013; Ware *et al.*, 2015). Future work should investigate community-level changes involving the dwarf mongooses, including further consideration into how communication with heterospecifics might be affected under combined stressors. This future work needs to consider fitness.
consequences directly to help understand the true impacts of anthropogenic disturbances on animals. Future research also needs to explore and test potential solutions to this problem, rather than solely pointing out the problematic effects of noise. Fully understanding the impacts that anthropogenic noise has on the development, physiology and behaviour of animals is crucial to help scientists and governments create legislation that effectively mitigates this pollutant and conserves the species impacted.
Chapter 3: Effects of rainfall and temperature on agonistic and sentinel behaviour in dwarf mongooses

Photo by author
3.1 Abstract

Climate change is a global threat, recognised as one of the most important issues that humans need to tackle due to the severity and scope of its impacts. There is a plethora of evidence showing the causes of climate change as well as predictions for how ecosystems and species will be affected under different temperature scenarios. However, relatively little research has assessed the effects of climatic conditions on animal behaviour. In this study, we used long-term data to investigate the effect of rainfall and temperature on agonistic and sentinel behaviour in a wild population of dwarf mongooses (*Helogale parvula*). Agonistic behaviour decreased when there was less rainfall in the non-breeding season but there was no significant effect of rainfall seen in the breeding season. Contrastingly, the amount of sentinel behaviour observed increased as the amount of rainfall decreased in both the breeding and non-breeding season. Temperature was found to have no significant effect on agonistic behaviour in either season, or on sentinel behaviour in the breeding season. In the non-breeding season, however, higher temperatures did lead to greater amounts of sentinel behaviour but this was not quite significant. Our study showed that climatic conditions do have the potential to affect behaviour, but further research is needed on a range of other species to see how widespread these effects are and to consider interspecific variation. This will help us to understand community and population level effects of this global threat.

3.2 Introduction

Climate change, meaning the long-term change in temperature and weather patterns, is one of the most pressing issues the world currently faces (United Nations, 2020; Fu & Waltman, 2022). Scientists are unanimous in their consensus that this change in climate is being driven by human activities, with 99% of the scientific literature coming to this conclusion (Lynas et al., 2021). Some of the human activities that are driving these climatic alterations include: land-use changes, combustion of fossil fuels and agricultural practices (The Royal Society, 2020). In every region across the globe, climate change is affecting the severity and frequency of extreme weather events, including droughts, floods, hurricanes and tornadoes, which has led to loss and damages to both nature and people (The Royal Society, 2020; IPCC, 2023). Ecosystems and the species that live within them are being severely affected by climate change. For instance, extreme heat events have led to mass mortalities across a
range of species including bats (Pruvot et al., 2019), African savanna elephants (Loxodonta africana) (Wang et al., 2021) and birds (McKechnie & Wolf, 2010). Species also face sublethal effects which include impacts on body condition, behaviour and reproductive success (du Plessis et al., 2012; Edwards et al., 2015). In southern African arid-zone birds, for instance, sublethal fitness consequences of high temperatures are thought to have a greater effect than lethal fitness consequences (Conradie et al., 2019).

Changes in temperature and rainfall in particular are driving sublethal impacts in wildlife, especially in arid and semi-arid environments (Bourne et al., 2020). Whilst high temperatures and periods without rainfall are normal features of arid environments, the frequency of such extreme weather conditions is increasing and the situation is predicted to worsen in the coming years (New et al., 2006; Bourne et al., 2020; The Royal Society, 2020). These climatic conditions can have a range of sublethal behavioural effects, with consequences for body condition and reproductive success. For example, droughts alter the trade-off between cooperative behaviours and foraging in meerkats (Suricata suricatta), with individuals reducing their contribution to sentinel behaviour in favour of foraging to maximise their own direct fitness (Rauber et al., 2019). When temperatures rise too high, pied babblers (Turdoides bicolor) trade-off foraging for thermoregulatory behaviours, resulting in too little mass gain (du Plessis et al., 2012). Similar foraging and thermoregulatory behaviour trade-offs have been seen in Western Australian magpies (Cracticus tibicens dorsalis) which reduce foraging in hot temperatures and thus suffer a loss in body condition (Edwards et al., 2015). These temperature-related negative effects on body condition can also affect parental care. In pied babblers, for instance, some individuals provisioned young significantly less on hot days and this led to reduced offspring development (Wiley & Ridley, 2016). Ultimately, high temperatures and drought conditions can lead to population declines: for instance, burrowing owls (Athene cunicularia) experienced a delay to breeding and reduced nesting success (Cruz-McDonnell & Wolf, 2016), whilst Sceloporus lizards alter their activity patterns with resultant declines in numbers and local extinctions (Sinervo et al., 2010). More studies on how climatic conditions affect wildlife behaviour are needed for us to gain a better understanding on how species will be impacted by current and future climate change.
For this preliminary study, we used long-term data to investigate the potential effects of climatic conditions (specifically rainfall and maximum temperature) on agonistic and sentinel behaviour in a wild population of dwarf mongooses (*Helogale parvula*). Dwarf mongooses are cooperative breeders living in groups with a dominant breeding pair and subordinate helpers (Rasa, 1977; Kern & Radford, 2016). Groupmates move around a shared territory collectively, foraging for insects and small vertebrates. As individuals forage by digging in the ground, they are unable to be vigilant simultaneously and so group members take turns to perform sentinel behaviour (raised guarding) where they look out for predators and warn groupmates of danger (Kern & Radford, 2014). As well as behaving cooperatively, dwarf mongooses also act agonistically towards each other – acting aggressively either to reinforce their dominance or to displace an individual from a foraging patch (Rasa, 1977; Morris-Drake *et al*., 2021). Previously, it has not been possible to study the effects of climate on this population of wild dwarf mongooses due to a lack of data. Now, however, there has been a 12-year study and so there are sufficient data available to answer these questions.

We chose to focus specifically on rainfall and maximum temperature as our climate parameters as we predicted they would have a greater effect on agonistic and sentinel behaviour (compared to other climatic variables) due to their effects on food availability. We predicted that in harsher conditions (i.e., hotter temperatures and periods of low rainfall), there would be an increase in agonistic interactions. We predicted an increase in agonistic interactions in hotter temperatures as increased levels of aggression in these more extreme conditions have already been demonstrated in a range of other species (Anderson *et al*., 2000; Kua *et al*., 2020; Fattorini *et al*., 2023). Our prediction that there would be more agonistic interactions in periods of low rainfall assumed that there would be less food availability which would lead to increased competition for resources; a trend that has been seen in several other species (Sneddon *et al*., 2006; Correia *et al*., 2014; Fattorini *et al*., 2023). Contrastingly, we predicted that with both increasing temperature and decreasing rainfall, there would be less sentinel behaviour. We believed that there would be less sentinel behaviour when temperatures were greater as individuals tend to be inactive for longer periods on hotter days and so would need to maximise time spent foraging rather than being on sentinel. Furthermore, we predicted that in periods of low rainfall we would see less sentinel behaviour as there might be lower food availability and so individuals would
choose to maximise foraging time rather than going on sentinel, as seen in meerkats (Rauber et al., 2019).

3.3 Methods

3.3.1 Study site and population

Data were collected on Sorabi Rock Lodge Reserve, Limpopo Province, South Africa (24°11’S, 30°46’E) as part of a long-term study of dwarf mongooses. The Dwarf Mongoose Research Project (DMRP) has been monitoring habituated wild groups since 2011. Sorabi is a private game reserve and is part of southern Africa’s Savanna Biome which experiences cold, dry winters (May–August; mean±SD maximum temperature = 25.9±1.1°C, range = 2–37°C; mean±SD total rainfall = 43±45 mm, range = 6–118 mm) and hot, wet summers (September–April; mean±SD maximum temperature = 30.6±1.2°C, range = 7–43°C; mean±SD total rainfall = 271±110 mm, range = 128–443 mm). Daily minimum and maximum temperature and rainfall are collected on the reserve from a weather station. More details on the study site can be found in Kern & Radford (2013).

Dwarf mongooses are cooperative breeders with groups consisting of a dominant breeding pair and subordinate helpers of both sexes (Rood, 1990). Groups can include both family members and unrelated individuals that have immigrated from elsewhere (Rasa, 1977; Kern & Radford, 2013). The study groups have been habituated to close (<5 m) human presence, with individuals identified from unique blonde hair-dye markings (Wella, Weybridge, UK) applied to different areas of their fur using an elongated paintbrush, or from natural features such as scars (Kern & Radford, 2013). Habituation and individual identification have allowed long-term life-history and behavioural data to be gathered.

3.3.2 Observational data collection and checking

The aim of this study was to investigate whether climatic conditions affect sentinel behaviour and agonistic interactions. We used behavioural data collected between 2013 and 2020 from 11 dwarf mongoose groups. Only data from this eight-year period were used for this study because prior to this there were limited behavioural data gathered; 2013 was the
first year in which we have regular agonistic and sentinel behaviour being recorded. During this period, field researchers monitored the population year-round, with each study group being seen regularly to maintain habituation and reapply dye marks. Researchers collect a range of data when following the group members from the morning sleeping burrow to the evening sleeping burrow. This data collection involves weighing individuals, recording group composition and various life-history events (e.g., pregnancies, births, immigration, emigration), as well as behavioural observations of grooming, sentinel and foraging activity, agonistic interactions between groupmates, latrine use, group movement and inter-group interactions. These data are inputted into the long-term database and routinely checked by both the field manager and data manager to ensure there are no mistakes, including removing any typos, duplicate entries and incorrect observations of individuals.

In this study, we focused on investigating the impacts of climate on agonistic interactions and sentinel behaviour as both these behaviours are conducted routinely by individuals and so, if affected by climate, could have a significant impact on their daily lives. We also wanted to compare the impacts on an antagonistic, negative behaviour (agonistic interactions) with those on a cooperative, positive behaviour (acting as a sentinel). Agonistic interactions are where individuals act aggressively towards their groupmates either to reinforce their rank or to displace a lower-ranking individual from a foraging patch (Rasa, 1977; Morris-Drake et al., 2021). Both types of agonistic interaction were recorded ad lib whenever an event was seen. Sentinel behaviour is where an individual acts as a raised guard, scanning for dangers and warning other group members of predation threats by giving alarm calls. Sentinel scans were conducted every 30 minutes, when it was recorded whether there was a sentinel present or not.

3.3.3 Data analysis

Initially, we analysed both sets of behavioural data (agonistic interactions and sentinel behaviour) at a season level. We did this because agonistic interactions are relatively rare and so daily rate data are heavily zero-inflated. Data were split into breeding and non-breeding seasons for each year; the breeding season was classed as the beginning of October until the end of February and the non-breeding season was from the beginning of
April to the end of August each year. For our study we chose to use standardised blocks of
time for the breeding and non-breeding seasons that are the same each year to make
analysis simpler. We defined the start of the breeding season as the month in which there is
usually the first sign of oestrus in the population and the end as the month when the final
litters in the population have usually emerged. All behavioural datasets were collated from
the same 11 dwarf mongoose groups. We used the total amount of rainfall and the mean
daily maximum temperature from each breeding and non-breeding season as our climate
parameters. For the agonistic interaction data, the daily rates of foraging displacements and
dominance aggression were calculated and then summed, with a mean value for total
agonistic interaction rate calculated for each group in each breeding and non-breeding
season. The proportion of sentinel scans where a sentinel was present was calculated for all
monitored days and then a mean of these daily proportions was calculated for each
breeding and non-breeding season. In both the agonistic interactions and sentinel behaviour
datasets there are different numbers of seasons used between analyses as some years were
excluded from analysis due to insufficient behavioural data being available.

We then further analysed the sentinel data at the daily level as these data were not
zero-inflated. For this analysis, we only used maximum temperature as our climate variable
because its effects are potentially apparent on a daily basis, whereas we predicted that the
effects of rainfall would mostly be present at a season level (through impacts on the amount
of vegetation and food). Furthermore, when there is heavy rain, dwarf mongooses can
remain inactive meaning there are no behavioural data to record.

All statistical analysis was carried out using R version 4.2.1 (R Core Team, 2022), with
results being considered as significant at p < 0.05. Due to the repeated sampling of
individuals and groups, mixed models were used. All response variables were plotted to
check whether the data were normally distributed. For all response variables we ran
generalised linear mixed models (GLMMs) using the lme4 package (Bates et al., 2015). Most
response variables were proportion data so we ran GLMMs with a beta distribution using
the glmmTMB and betareg packages (Grün et al., 2012; Brooks et al., 2017). To account for 0
and 1 inflated data in the daily sentinel dataset, data were transformed as recommended by
the betareg package (Smithson & Verkuilen, 2006). The two climate parameters used (total
rainfall and maximum temperature) were analysed in separate models as these were
strongly correlated ($R^2 = 0.633$, Spearman’s rank $= 0.879$, $p < 0.001$). For the seasonal analyses, climatic condition (either total rainfall or mean maximum temperature) and group size were included as fixed effects and group identity was included as a random term. For the daily sentinel models, maximum temperature and group size were included as fixed effects and group identity nested in year were included as random terms. For each response variable, the maximal model (with all terms retained) is reported.

3.4 Results

3.4.1 Effect of climate on agonistic interactions

The total amount of rainfall affected the rate of dwarf mongoose agonistic interactions in the non-breeding season but not the breeding season. In the breeding season, there was no significant influence of total rainfall on the agonistic interaction rate (GLMM: $\chi^2 = 0.057$, $df = 1$, $p = 0.811$; Table 3.1a; Figure 3.1a). By contrast, there was a positive relationship between amount of rainfall and the rate of agonistic interactions in non-breeding seasons ($f = 5.030$, $df = 1$, $p = 0.011$; Table 3.1b; Figure 3.1b).
Table 3.1 Output of the generalised linear mixed models (GLMMs) investigating the impact of total rainfall on the mean rate of agonistic interactions in a) the breeding season (GLMM: beta family, cloglog link) and b) the non-breeding season (GLMM: gamma family, inverse link). The maximal model is presented with significant terms shown in bold. Effect ± standard error is shown for the fixed effects and variance ± standard deviation is shown for the random terms (italicised). N = 7 breeding seasons and 8 non-breeding seasons from 11 groups.

<table>
<thead>
<tr>
<th>Fixed Effect</th>
<th>Effect ± SE</th>
<th>df</th>
<th>$\chi^2$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Breeding season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>-3.200 ± 0.543</td>
<td>1</td>
<td>0.057</td>
<td>0.811</td>
</tr>
<tr>
<td>Total Rainfall</td>
<td>&lt;0.001 ± 0.001</td>
<td>1</td>
<td>5.030</td>
<td>0.011</td>
</tr>
<tr>
<td>Group Size</td>
<td>0.054 ± 0.042</td>
<td>1</td>
<td>1.640</td>
<td>0.200</td>
</tr>
<tr>
<td>Group</td>
<td>&lt;0.001 ± &lt;0.001</td>
<td></td>
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<tr>
<td>b) Non-breeding season</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>9.773 ± 2.742</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Rainfall</td>
<td>-0.039 ± 0.015</td>
<td>1</td>
<td>5.030</td>
<td>0.011</td>
</tr>
<tr>
<td>Group Size</td>
<td>-0.108 ± 0.286</td>
<td>1</td>
<td>0.127</td>
<td>0.706</td>
</tr>
<tr>
<td>Group</td>
<td>2.932 ± 1.712</td>
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</tbody>
</table>
Figure 3.1 The effect of total rainfall on the mean rate of agonistic interactions in a) the breeding season (BS) and b) the non-breeding season (NONBS). The black lines show the fitted models, and the grey areas show the 95% confidence intervals. N = 6 breeding seasons and 8 non-breeding seasons from 11 groups.

Temperature was not found to have a significant effect on agonistic interactions in dwarf mongooses in either the breeding season (GLMM: $\chi^2 = 0.325, df = 1, p = 0.569$; Table 3.2a) or the non-breeding season ($f = 0.838, df = 1, p = 0.330$; Table 3.2b).
Table 3.2 Output of the generalised linear mixed models (GLMMs) investigating the impact of mean maximum temperature on the mean rate of agonistic interactions in a) the breeding season (GLMM: beta family, cloglog link) and b) the non-breeding season (GLMM: gamma family, inverse link). The maximal model is presented with significant terms shown in bold. Effect ± standard error is shown for the fixed effects and variance ± standard deviation is shown for the random terms (italicised). N = 7 breeding seasons and 8 non-breeding seasons from 11 groups.

<table>
<thead>
<tr>
<th>Fixed Effect</th>
<th>Effect ± SE</th>
<th>df</th>
<th>$\chi^2$ / f value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Breeding season</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>-4.824 ± 3.038</td>
<td>1</td>
<td>0.325</td>
<td>0.569</td>
</tr>
<tr>
<td>Maximum Temperature</td>
<td>0.058 ± 0.101</td>
<td>1</td>
<td>0.985</td>
<td>0.321</td>
</tr>
<tr>
<td>Group Size</td>
<td>0.044 ± 0.044</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group</td>
<td>&lt;0.001 ± &lt;0.001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>b) Non-breeding season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>21.537 ± 15.010</td>
<td>1</td>
<td>0.838</td>
<td>0.330</td>
</tr>
<tr>
<td>Maximum Temperature</td>
<td>-0.562 ± 0.577</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group Size</td>
<td>0.003 ± 0.319</td>
<td>1</td>
<td>0.000</td>
<td>0.992</td>
</tr>
<tr>
<td>Group</td>
<td>1.835 ± 1.355</td>
<td></td>
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</tbody>
</table>

3.4.2 Effect of climate on sentinel behaviour

The total amount of rainfall affected the proportion of sentinel behaviour seen in both the breeding and non-breeding season. In the breeding season, there was significantly more sentinel behaviour seen with lower levels of rainfall (GLMM: $\chi^2 = 28.886$, df = 1, $p < 0.001$; Table 3.3a; Figure 3.3a). This same increase in sentinel behaviour as the amount of rainfall decreases was also seen in the non-breeding season ($\chi^2 = 19.501$, df = 1, $p < 0.001$; Table 3.3b; Figure 3.3b).
Table 3.3 Output of the generalised linear mixed models (GLMMs) investigating the impact of total rainfall on the mean proportion of sentinel behaviour in a) the breeding season (GLMM: beta family, logit link) and b) the non-breeding season (GLMM: beta family, inverse link). The maximal model is presented with significant terms shown in bold. Effect ± standard error is shown for the fixed effects and variance ± standard deviation is shown for the random terms (italicised). N = 6 breeding seasons, and 7 non-breeding seasons from 11 groups.

<table>
<thead>
<tr>
<th>Fixed Effect</th>
<th>Effect ± SE</th>
<th>df</th>
<th>$\chi^2$</th>
<th>P</th>
</tr>
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<tbody>
<tr>
<td><strong>a) Breeding season</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>1.607 ± 0.337</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Rainfall</td>
<td>-0.010 ± 0.001</td>
<td>1</td>
<td>28.886</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Group Size</td>
<td>0.038 ± 0.028</td>
<td>1</td>
<td>1.806</td>
<td>0.179</td>
</tr>
<tr>
<td>Group</td>
<td>&lt;0.001 ± &lt;0.001</td>
<td></td>
<td></td>
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<tr>
<td><strong>b) Non-breeding season</strong></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>1.788 ± 0.133</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Rainfall</td>
<td>0.008 ± 0.002</td>
<td>1</td>
<td>19.501</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Group Size</td>
<td>-0.037 ± 0.166</td>
<td>1</td>
<td>5.043</td>
<td>0.025</td>
</tr>
<tr>
<td>Group</td>
<td>0.011 ± 0.105</td>
<td></td>
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</tbody>
</table>
Figure 3.3 The effect of total rainfall on mean proportion of sentinel behaviour in a) the breeding season (BS) and b) the non-breeding season (NONBS). The black lines show the fitted models, and the grey areas show the 95% confidence intervals. N = 6 breeding seasons, and 7 non-breeding seasons from 11 groups.

In the breeding season, there was no significant effect of temperature on the proportion of sentinel behaviour (GLMM: $\chi^2 = 1.828$, df = 1, $p = 0.176$; Table 3.4a; Figure 3.4a). However, in the non-breeding season, higher temperatures led to more sentinel behaviour but this is not quite statistically significant ($\chi^2 = 3.820$, df = 1, $p = 0.050$; Table 3.4b; Figure 3.4b).
Table 3.4 Output of the generalised linear mixed models (GLMMs) investigating the impact of maximum temperature on the mean proportion of sentinel behaviour in a) the breeding season (GLMM: beta family, logit link) and b) the non-breeding season (GLMM: beta family, cloglog link). The maximal model is presented with significant terms shown in bold. Effect ± standard error is shown for the fixed effects and variance ± standard deviation is shown for the random terms (italicised). N = 6 breeding seasons, and 7 non-breeding seasons from 11 groups.

<table>
<thead>
<tr>
<th>Fixed Effect</th>
<th>Effect ± SE</th>
<th>df</th>
<th>$\chi^2$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Breeding season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>3.588 ± 2.474</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum Temperature</td>
<td>-0.112 ± 0.083</td>
<td>1</td>
<td>1.828</td>
<td>0.176</td>
</tr>
<tr>
<td>Group Size</td>
<td>0.046 ± 0.037</td>
<td>1</td>
<td>1.562</td>
<td>0.211</td>
</tr>
<tr>
<td>Group</td>
<td>&lt;0.001 ± &lt;0.001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>b) Non-breeding season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>-2.293 ± 1.008</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum Temperature</td>
<td>0.076 ± 0.039</td>
<td>1</td>
<td>3.820</td>
<td>0.050</td>
</tr>
<tr>
<td>Group Size</td>
<td>0.019 ± 0.017</td>
<td>1</td>
<td>1.238</td>
<td>0.266</td>
</tr>
<tr>
<td>Group</td>
<td>&lt;0.001 ± &lt;0.001</td>
<td></td>
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</table>
Figure 3.4 The effect of mean maximum temperature on mean proportion of sentinel behaviour in a) the breeding season (BS) and b) the non-breeding season (NONBS). The black lines show the fitted models, and the grey areas show the 95% confidence intervals. N = 6 breeding seasons, and 7 non-breeding seasons from 11 groups.

There was no significant effect of temperature on daily sentinel behaviour seen in either the breeding or non-breeding season. In the breeding season, there was no significant influence of temperature on the proportion of daily sentinel behaviour seen (GLMM: $\chi^2 = 1.123$, df = 1, $p = 0.289$; Table 3.5a). This lack of significant effect was also apparent in the non-breeding season ($\chi^2 = 0.033$, df = 1, $p = 0.855$; Table 3.5b).
Table 3.5 Output of the generalised linear mixed models (GLMMs) investigating the impact of maximum temperature on the daily proportion of sentinel behaviour in a) the breeding season (GLMM: beta family, logit link) and b) the non-breeding season (GLMM: beta family, logit link). The maximal model is presented with significant terms shown in bold. Effect ± standard error is shown for the fixed effects and variance ± standard deviation is shown for the random terms (italicised). N = 8 breeding seasons, and 7 non-breeding seasons from 11 groups.

<table>
<thead>
<tr>
<th>Fixed Effect</th>
<th>Effect ± SE</th>
<th>df</th>
<th>( \chi^2 )</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>a) Breeding season</strong></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>-0.167 ± 0.359</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum Temperature</td>
<td>0.009 ± 0.008</td>
<td>1</td>
<td>1.123</td>
<td>0.289</td>
</tr>
<tr>
<td>Group Size</td>
<td>0.046 ± 0.011</td>
<td>1</td>
<td>18.349</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><strong>Group ID in Year</strong></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Year</td>
<td>0.068 ± 0.262</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>b) Non-breeding season</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>0.238 ± 0.362</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum temperature</td>
<td>0.002 ± 0.011</td>
<td>1</td>
<td>0.033</td>
<td>0.855</td>
</tr>
<tr>
<td>Group Size</td>
<td>0.015 ± 0.012</td>
<td>1</td>
<td>1.734</td>
<td>0.188</td>
</tr>
<tr>
<td><strong>Group ID in Year</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year</td>
<td>0.055 ± 0.235</td>
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</tbody>
</table>

3.5 Discussion

There is some evidence that agonistic and sentinel behaviour in dwarf mongooses is affected by climatic conditions, but this can be dependent on season. Rainfall did not influence agonistic interactions in the breeding season but did so in the non-breeding season: at that time of year, less total rainfall meant fewer agonistic interactions. By contrast, temperature did not have a significant effect on agonistic interactions in either season. At a season level, there was more sentinel behaviour when there was less rainfall in both the breeding and non-breeding season. However, temperature again did not significantly affect the amount of
sentinel behaviour seen in either season at both the season and daily level. Overall, rainfall had a greater influence on both agonistic and sentinel behaviour than temperature in our population of dwarf mongooses.

Contrary to our predictions, rainfall in the breeding season did not affect agonistic interactions and the effect in the non-breeding season was the opposite to what we expected: a decreased rate of agonistic interactions when there was less rather than more rainfall. We expected to see more agonistic interactions in periods of low rainfall due to a reduction in food availability leading to more conflicts over resources (Fattorini et al., 2023), as seen in a range of species including titi monkeys (Callicebus coimbrai) (Correia et al., 2014), three-spined sticklebacks (Gasterosteus aculeatus) (Sneddon et al., 2006) and Apennine chamois (Rupicapra pyrenaica ornata) (Fattorini et al., 2023). As the majority of agonistic interactions in dwarf mongoose groups are foraging displacements, we would expect to see this increased competition over resources in times of drought (Sharpe et al., 2016; Morris-Drake et al., 2021). In the breeding season, there is much more rainfall and so we might not be seeing an effect of rainfall as there is a plentiful food supply throughout the season due to this high rainfall. Contrastingly, the non-breeding season is usually much drier and so when there is an increase in rainfall, this might cause a sudden increase in food availability leading to an increase in agonistic interactions. Individuals may also be using this sudden change in food availability as an opportunity to assert dominance, if they have had a chance to consume more food than other group members.

There was no significant effect of temperature on agonistic interactions in either the breeding or non-breeding season. This contradicts our prediction that there would be an increase in agonistic interactions as temperatures increased, which was based on findings in other species such as Apennine chamois (Fattorini et al., 2023), Appalachian stream salamanders (including: Desmognathus ocoee, D. monticola and D. quadramaculatus) (Bissell & Cecala, 2019) and the golden Julie cichlid (Julidochromis ornatus) (Kua et al., 2020), as well as humans (Anderson et al., 2000; Miles-Novelo & Anderson, 2019). However, in some species there can be a range of factors that influence the impact temperature has on agonistic behaviour (Fisher et al., 2021). For example, when exposed to high temperatures, higher-ranked cockroaches (Nauphoeta cinerea) decreased their levels of aggression whilst lower-ranked individuals increased the amount of aggression they were exhibiting (Spohn &
Moore, 1997). In sand field crickets (*Gryllus firmus*), time of day impacted how affected they were by high temperatures; they were less aggressive in fights at hotter temperatures but only in the morning (Nguyen & Stahlschmidt, 2019). It is still unknown what mechanisms link temperature and aggression, and there have been very few studies exploring this, particularly in mammals (Fisher *et al.*, 2021).

Our results show that as rainfall decreases, there is a significant increase in the amount of sentinel behaviour seen in both the breeding and non-breeding seasons. This contradicts our predictions where we expected there to be less sentinel behaviour seen in periods of lower rainfall. In meerkats, sentinel behaviour decreased in drought conditions, but there was no difference in the likelihood of an individual acting as sentinel in dry and wet conditions (Rauber *et al.*, 2019). Perhaps we did not see the predicted decrease in sentinel behaviour as individuals in our study were exposed to just dry conditions as opposed to a drought. There might also be less sentinel behaviour with increased rainfall in the breeding season because the latter causes a major increase in vegetation cover. Many threats to dwarf mongooses are from aerial predators and so individuals might feel safer in the high vegetation and choose to maximise the time they can spend foraging when food is plentiful, rather than choosing to act as a sentinel. The same effect may also be seen in the non-breeding season because a particularly wet preceding breeding season followed by a wetter non-breeding season may result in sustained high levels of vegetation. In meerkats, individuals forage closer together in wetter conditions which may also reduce the need for sentinel behaviour to occur (Toni *et al.*, 2020).

Higher temperatures led to more sentinel behaviour in the non-breeding season, which was the opposite to our prediction. On hotter days, individuals are inactive for longer periods of time and so individuals will need to maximise their foraging time at the expense of sentinel behaviour (Rauber *et al.*, 2019). Whilst there have not been any other studies (that we are aware of) exploring the impact of temperature on sentinel behaviour, some have examined other cooperative behaviours. Pied babbler adults provision young significantly less on hot days, but this was affected by rank: dominant individuals provisioned less, whilst the subordinate helpers continued to provision at the same rate (Wiley & Ridley, 2016). Contrastingly, meerkat adults were found to continue provisioning young at similar rates on hot days as on cooler ones (Van de Ven *et al.*, 2019). We found a nearly significant
trend for dwarf mongoose sentinel behaviour in the non-breeding season to increase as temperatures increased. This trend is driven by data from the 2019 non-breeding and breeding seasons, when the mean maximum temperatures (28.5°C and 32.5°C, respectively) were the hottest in the datasets analysed. These consecutively hot seasons could mean that there was even less vegetation cover than in usual non-breeding seasons, increasing predator risk and thus the need for sentinel activity. Our results also show that in this period, there was more within-group conflict, likely driven by a lack of resource availability due to decreased amounts of vegetation. This conflict over resources could also be leading to more between-group conflict; this type of conflict has been shown to increase the amount of sentinel behaviour occurring and could also be driving this increase in sentinel behaviour that we are seeing (Morris-Drake et al., 2021).

Our results show that both agonistic and sentinel behaviour in dwarf mongooses are affected by climatic conditions. Some of our results are in line with other studies which show changes in behaviour due to the climate, but these studies also show there is huge variation in how species respond to climatic extremes. Future work should look to investigate the impacts of climate on behaviour in a range of species to gauge a better idea of interspecific variation and the reasons for it. Changing behaviour is often one of the first strategies used by animals to cope in anthropogenically altered environments and understanding how these behaviours are affected by climate change is critical if we are to mitigate these effects in the future. By understanding these changes, we will also understand the limits that these behaviours have in protecting species from a changing environment and therefore helping us to ascertain how affected a species will be by current and future climate change (Wong & Candolin, 2015).
Chapter 4: General Discussion

Photo by author
4.1 Thesis findings

The overall aim of my study was to assess the effects of both anthropogenic noise and climatic conditions on the behaviour of dwarf mongooses (*Helogale parvula*). Specifically, I investigated how vigilance and foraging behaviour are influenced by the combination of an elevated predation threat and road noise, as well as how agonistic interactions and sentinel behaviour differ depending on temperature and rainfall. Many previous studies on a range of species have documented the behavioural impacts of anthropogenic noise, but far fewer have explored the effects of noise in conjunction with other stressors (Shannon et al., 2016a). This exploration of combined stressors is necessary if we are to understand fully the impacts that humans are having on wildlife (Breitburg et al., 1999; Crain et al., 2008; Shannon et al., 2016a). Understanding how animal behaviour will be affected by climate change has so far been relatively under researched; currently, it is unclear how many species will react and adapt to extreme climate conditions and how much intraspecific variation there will be in response to these conditions (Buchholz et al., 2019). However, work already conducted has shown that both temperature and rainfall can lead to a range of sublethal consequences, highlighting the importance of further research into this area (Edwards et al., 2015; Rauber et al., 2019; Bourne et al., 2020; Wang et al., 2021).

Our results showed that vigilance behaviour is significantly affected when dwarf mongooses are exposed to an elevated predation threat or to road noise. We found that the playback of an alarm call led to the expected greater vigilance, and that this difference in behaviour was similarly seen when individuals were exposed to road-noise playback. However, contrary to our predictions, there was no combined effect (i.e., even greater vigilance) when individuals were exposed to both these threats. Similarly, Hubert et al. (2023) showed that there was no combined effect of boat noise and predator presence on the valve gape behaviour of mussels (*Mytilus* spp.). This contradicts some studies that have reported a combined (i.e., additive, antagonistic or synergistic) effect when individuals have been exposed to multiple stressors (Chan et al., 2010; Grenat et al., 2019).

One reason for these variations in combined stressor effects may be because individuals are being exposed to the stressors for differing lengths of time. Playbacks in our experiment, for example, were relatively short compared to the duration that other species were exposed to their stressors (Dominoni et al., 2020; Hubert et al., 2023). Although, for lots of
species, they are unlikely to be exposed to stressors continuously and so this might only be relevant for a subset of species. In our dwarf mongoose population, individuals are not exposed to road noise and predation threat continuously, and so to expose them to continuous playback tracks might not give an accurate representation of how they will be impacted by these combined stressors. Another reason for the difference could be that we were not actually exploring the combined effects of these stressors and may have just been seeing the effects of individuals being exposed to road noise. Due to time constraints, it was not possible to run a pilot experiment examining how long the effects of the alarm-call playback would last. The lack of difference between the amount of vigilance behaviour exhibited between treatments suggests that the vigilance resulting from the alarm call had already worn off by the time individuals were exposed to the road-noise playback. One way to avoid this limitation would be to expose individuals to the threats simultaneously, as has occurred in other studies (Giordano et al., 2022).

Our study showed some evidence to suggest that climatic conditions influence both agonistic and sentinel behaviour in dwarf mongooses. We found that there were fewer agonistic interactions when there was less rainfall in the non-breeding season, but no significant effect of rainfall on these interactions in the breeding season. This contradicts other studies on three-spined sticklebacks (Gasterosteus aculeatus) (Sneddon et al., 2006), titi monkeys (Callicebus coimbrai) (Correia et al., 2014) and Apennine chamois (Rupicapra pyrenaica ornata) (Fattorini et al., 2023) which show an increase in agonistic interactions in periods of drought. Our results may be different to other studies because in dwarf mongooses, most agonistic behaviour is foraging related. As there is lots of rainfall in the breeding season, food availability will be higher and so there would be fewer agonistic interactions occurring. However, in the non-breeding season, where it is drier, individuals go from having not much food available to a large abundance in high rainfall; this sudden increase in food availability could lead to an increase in agonistic behaviour. In some other studies conducted, the agonistic interactions that have been assessed have been over dominance rank rather than foraging patches, as was seen in the three-spined sticklebacks, which may explain why our results were different to this study (Sneddon et al., 2006). However, the study on titi monkeys was assessing agonistic interactions relating to foraging (Correia et al., 2014). Our results may differ to this study because our study population has
not been exposed to drought conditions, just dry periods. Sentinel behaviour was significantly influenced by the amount of rainfall in both seasons: when there was less rainfall, there was more sentinel behaviour conducted. In another study conducted on meerkats (*Suricata suricatta*), they found that less sentinel behaviour was conducted during times of drought (Rauber et al., 2019). Again, we may not have seen these same effects as individuals in our study system have not been exposed to drought conditions.

Temperature was not found to have a significant effect on agonistic interactions in either the breeding or non-breeding season. Studies on golden Julie cichlids (*Julidochromis ornatus*) (Kua et al., 2020), Appalachian stream salamanders (Bissell & Cecala, 2019) and humans (Anderson et al., 2000; Miles-Novelo & Anderson, 2019) have previously found an increase in agonistic behaviour as temperatures increase. As with agonistic behaviour, we found no significant effect of temperature on sentinel behaviour in the breeding season. However, in the non-breeding season, higher temperatures did lead to more sentinel behaviour but this was not quite significant. This trend seen in the non-breeding season is being driven by sentinel behaviour seen in the 2019 breeding and non-breeding seasons where there were the hottest temperatures recorded on the reserve. During these particularly hot, consecutive seasons there may have been less vegetation cover than usual which might have increased the need for more sentinel behaviour that we otherwise would not have seen. One reason for some of these differences between our results and other studies may be that there was genuinely no effect to be seen, or another possibility is that our study population have not experienced these climate extremes that go above the critical threshold to affect their behaviour (Edwards et al., 2015; Rauber et al., 2019).

### 4.2 Future studies

Future work should look to understand whether there are any fitness consequences to individuals trading off foraging behaviour to be more vigilant; a trade-off that was seen in our anthropogenic-noise study when individuals were exposed to both predation threat and road noise. Other studies have shown that this trade-off can have knock-on fitness consequences including leading to a reduction in reproductive success (Ciuti et al., 2012; Wang et al., 2021; Worku et al., 2021). It would be beneficial to assess these trade-off costs
both as combined risks, but also to compare the impacts of predation risk and road noise separately to aid understanding of the two stressors.

In our study exploring the effects of climatic conditions on dwarf mongoose behaviour, some of the interpretations of our results were based on the amount of vegetation cover present. This was both in terms of the amount of cover there was but also using vegetation cover as a proxy for food availability. However, the amount of vegetation cover present is not something that is recorded in the Dwarf Mongoose Research Project database. Future work should consider using remote sensing and GIS technology to measure the amount of vegetation cover and how this changes through different seasons and as the climate changes (Allawai & Ahmed, 2020; Rousta et al., 2020; Zaitunah & Sahara, 2021). Body-mass measurements of individuals could also potentially be used as a proxy to assess whether changes in food availability cause changes in agonistic interactions and whether this is influenced by climatic conditions.

There is clearly a need for a better understanding of the effects of anthropogenic noise on wildlife, particularly as this stressor is projected to worsen in the future (Shannon et al., 2016a; Jerem & Mathews, 2021). Whilst much is known about how individual behaviour is affected by noise, more research is needed on how dyadic interactions within and between species are affected, as well as the consequences of noise for population sizes and community structure. This research is particularly needed for aquatic and nocturnal species and communities as less research has been conducted in these areas, and these are also environments where acoustic signals can be of particular importance (Kok et al., 2023). More studies undertaken on a range of species, assessing a range of different stressors, both anthropogenic and natural, are also necessary if we are to understand fully the impact humans are having on wildlife. For example, it would be helpful to look at combined stressors where they are occurring together, such as anthropogenic noise and habitat fragmentation (Shannon et al., 2016a). Finally, further exploration of mitigation strategies is crucial if we are to minimise, and ideally prevent, the harmful effects of noise. Steps have already been taken to research potential solutions (including low emission zones and reduced speed limits), but a greater understanding of these is crucial if we are to implement cost-effective strategies that do mitigate these impacts (Dablanc & Montenon, 2015; Licitra & Vogiatzis, 2019; Rice et al., 2022).
Assessing the impacts of environmental conditions on animal behaviour is crucial if we are to understand their ability to adapt and survive in the face of climate change. Our study joins the limited research that has been conducted assessing these effects of climatic conditions on behaviour and highlights the need for behavioural scientists to start investigating these impacts more (Buchholz et al., 2019). By understanding how species will change their behaviour to respond to changes in the climate, we can then further understand population-level effects (Gunn et al., 2021). Another avenue for further research would be to see if extreme weather events have effects on the survival rates of young and thus reproductive success (McKechnie & Wolf, 2010; Cruz-McDonnell & Wolf, 2016; Woodroffe et al., 2017). Skews in sex ratios have been highlighted as a potential effect of climate change and more research into both these demographic effects can also aid understanding of how climate can affect communities and ecosystems more widely (Wong & Candolin, 2015; Bourne et al., 2018). Understanding the effects different climate extremes have on animal behaviour and physiology will also allow us to understand further the constraints that these traits have to protect species from these changing climates (Wong & Candolin, 2015; Buchholz et al., 2019).

4.3 Conclusion

Both anthropogenic noise and climate change are human-driven threats that are of growing concern to species all over the world (Shannon et al., 2016a; United Nations, 2020). Our work has highlighted the impact of these threats on behaviour in dwarf mongooses through field-based playback experiments and long-term analysis from the Dwarf Mongoose Research Project. Specifically, we have shown that both road noise and the threat of predation lead to an increase in vigilance behaviour at a cost to foraging, but that these effects are not worsened when these threats are combined. Agonistic and sentinel behaviour was also found to be influenced by changes in the climate with less agonistic behaviour being seen when there was less rainfall in the non-breeding season and more sentinel behaviour observed as there is a decrease in the amount of rainfall. We recommend further research is conducted in both these areas as these topics are relatively under-researched and could help us to understand the true impact humans are having on wildlife.
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