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Fear of the Human "Super-Predator" In African Mammals

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Abstract

Humans' exploitive killing of virtually every mammal species globally may result in a perception of humans as feared, ultra-lethal predators. In Africa, mammals are central to the continent's tourism industry; however, it is largely unknown whether African mammals fear the presence of tourists. Firstly, I aimed to review how the presence of humans on the landscape affects African mammal behaviour. Of 31 studies, most authors reported that humans alter mammal behaviour in a manner that may negatively impact survival. To test if a fear of humans can pervade communities, I simulated the presence of humans, hunting, lions, and birds using an Automated Behavioural Response system. I recorded fleeing responses of 26 South African mammal species and found that the community fled most to human voices, especially when heard where hunting occurs. My results demonstrate that human presence induces a greater community-wide fear response than the presence of their natural predator.

Keywords

Human disturbance, human "super-predator", hunting, ecotourism, fear, antipredator behaviour, fleeing, vigilance, African mammals, manipulation, auditory playbacks, camera traps.

Summary for Lay Audience

Humans are experienced and skilled hunters that, when combined with advancements in technology, are capable of killing most types of mammals from large elephants to small mice. Yet, researchers do not fully understand the mechanism of how or why hunters, or humans in general, change the behaviour of these animals. Namely, do these animals fear us? This question is particularly important in Africa, as some African governments rely heavily on the income from wildlife-based tourism. After searching through all available scientific papers, I found 31 articles where researchers studied how humans can change the behaviour of mammals in Africa. Most articles reported that humans not only change the behaviour of African wildlife but do so in a way that may reduce their chances of survival. To test if humans can change the behaviour of multiple safari animals with hunting and tourism activities, I manipulated fear in 26 mammal species (such as elephants, giraffes, and zebra) with sounds of gunshots, dog barks, human voices, and snarls of their main predator – the lion, and then videotaped how often they ran away. To determine how fearful these mammals were to these sounds, I compared their behaviours to how often they ran away from a fifth sound of a harmless bird call. Out of all five sounds, mammals ran away from human voices the most, telling us that humans induce more fear than lions, dogs, or gunshots. Also, these mammals ran more to human voices in an area where hunting is legal than an area where hunting is illegal, which tells us that mammals change their behaviour depending on how often hunting occurs. Overall, I show that humans can induce fear in entire communities of mammals.

Co-Authorship Statement

Dr. Michael Clinchy (Western University, Canada) will be the second co-author on the manuscript that will be published from Chapter 3 of this thesis. Mike provided a great deal of input into the experimental design, conducted the data collection in the field (alongside Liana), managed the initial descriptive data for videos, and provided valuable advice on the statistical analyses and presentation of my results. Dr. Craig Packer (University of Minnesota, USA) will be the third co-author on the manuscript that will be published from Chapter 3 of this thesis. Craig provided valuable input into the experimental design and protocol for conducting fieldwork in South Africa. Dr. Mike Peel (Agricultural Research Council, South Africa) will be the fourth co-author on the manuscript that will be published from Chapter 3 of this thesis. Mike provided critical information of the study sites and species, allowing field data collection of wildlife behaviour in the Klaserie and Thornybush private reserves of South Africa to be feasible. Dr. Liana Zanette (Western University, Canada) will be the fifth co-author on the manuscript that will be published from Chapter 3 of this thesis. Liana provided a great deal of input into the experimental design, conducted the data collection in the field (alongside Mike) and statistical analyses, and continuously provided valuable advice on all aspects of my research project throughout my degree. Additionally, Dr. Liana Zanette (Western University, Canada) will be the second co-author on the manuscript that will be published from Chapter 2 of this thesis. Liana provided guidance in the beginning steps of designing the meta-analysis and provided feedback on the writing and data analysis of this chapter.

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Chapter 1

1 General Introduction

1.1 Hunting of Wildlife

The overkilling of wildlife to extinction is an ongoing environmental crisis that putatively dates back to when humans migrated out of Africa during the late Pleistocene and targeted the megafauna of newly colonized areas (Mosimann & Martin 1975; Lyons et al 2004). Overexploitation is responsible for triggering the International Union for Conservation of Nature’s (IUCN) red listing for 14% of threatened mammals (Rosser & Mainka 2002), with 301 terrestrial mammal species currently threatened with extinction due to bushmeat hunting (Ripple et al 2016). Following habitat loss, overkill is the second most common threat to mammal species worldwide (Rosser & Mainka 2002), with regions in Southeast Asia and Africa hosting the most species threatened by hunting (Ripple et al 2016). In addition to directly affecting targeted species, the extinction or endangerment of top predators can have cascading effects in lower trophic levels, resulting in increased foraging in prey (Suraci et al 2016), decreased vigilance to predation risk in prey (Laundre et al 2001), and decreased abundance of vegetation (Ripple & Beschta 2003). It has also been proposed that the extinction of large vertebrates may also negatively contribute to climate change, as the termination of seed dispersal by large mammals would reduce globally important carbon sinks provided by tropical forests (Brodie & Gibbs 2009). Thus, it is crucial to understand how unsustainable hunting affects wildlife as the demand for mammal products continues to escalate (Rosser & Mainka 2002).

1.2 Effects of Human Presence and Hunting on Wildlife Behaviour

Due to human's overexploitation of wildlife for millennia, Darimont and colleagues (2015) have proposed that humans now fit an ecological role in the environment as a "super-predator", by which we exceed the killing rates and success of killing of the world's top non-human predators. As an ultra-lethal predator, humans can not only affect wildlife through direct killing, but also indirectly as humans have been shown to modify natural landscapes of fear (Ciuti et al 2012; Suraci et al 2019). Human-induced alterations of mammal behaviour have been observed across temporal and spatial scales, most likely driven by the perception of humans as a predator (Frid & Dill 2002). During hunting seasons, game animals will increase vigilance (Benhaiem et al 2008) or avoid areas where hunting occurs (Kilgo et al 1998; Lone et al 2015). Experimentally, persecuted European badgers (*Meles meles*) have been demonstrated to delay leaving their burrows to forage when nearby human presence is perceived (Clinchy et al 2016). Similarly, cougars (*Puma concolor*) have been shown to abandon their cache in response to the sound of a human voice (Smith et al 2017) as well as completely avoid landscapes when humans are perceived to be present (Suraci et al 2019). When comparing the behaviours of hunted and non-hunted populations within a mammal species, significant differences have been demonstrated in prey selection (Novack et al 2005), nocturnality (Zanon-Martinez et al 2016), and fleeing behaviours (Caro 1999) between individuals from each population. Furthermore, an experiment on elephants (*Loxodonta africana*) demonstrated that the effects of hunting can induce long-term changes to wildlife behaviour, as elephants that experienced separation from family members due to culling operations failed to distinguish important social cues from conspecifics (Shannon et al 2013).

Mammals also exhibit behavioural changes in response to human activity despite not being directly targeted or hunted by humans (Dertien et al 2021). Globally, mammals reduce their movement patterns in areas of high human footprint (Tucker et al 2018) as well as adjust their activity patterns throughout the day, becoming more nocturnal to avoid the diurnal presence of humans (Gaynor et al 2018). Recreational activities of hiking and biking can alter movement patterns and behaviours in various mammals such as ungulates (Taylor & Knight 2003; Stankowich 2008), bears (Smith et al 2012; Ordiz et al 2013, 2019), and cougars (Morrison et al 2014). In addition, tourism activities that allow humans to view wildlife at close proximity can also affect wildlife behaviour; for example, the presence of nearby tourists can induce an energetic trade off in gorillas (*Gorilla gorilla*) and lions (*Panthera leo*) whereby gorillas spend less time feeding and lions spend less time grooming to spend more time vigilant (Hayward & Hayward 2009; Klailova et al 2010). Furthermore, human presence can have cascading effects down the food web, as driving away top predators from areas of high human density increases foraging behaviour in prey species that are not targeted by humans (Muhly et al 2011; Suraci et al 2019). Therefore, in addition to the direct effects of killing wildlife, the indirect behavioural effects of a pervasive fear of humans in mammal communities must be investigated to comprehensively understand how humans affect wildlife.

1.3 Quantifying Fear Behaviours

Fear behaviours can be quantified through the observation of either an increase or presence of behaviours that aid in detecting, assessing, or escaping predation threats (such as fleeing, vigilance, and alarm calls) or a decrease or absence of other maintenance behaviours required for growth and reproduction (foraging, mating, movement, communication) (Murphy 1978; Lima & Dill 1990). Of these behaviours, the three most studied when investigating fear in wildlife are fleeing, vigilance, and foraging (Laundre et al 2010).

When an animal flees away from a potential threat, the behaviour indicates that the animal detected the threat and determined that the benefit of avoiding the threat outweighed the cost of abandoning the resources present in the area (Ydenberg & Dill 1986). The simplest method of interpreting fleeing behaviour is by recording the presence or absence of the behaviour when an animal is exposed to a predation threat (Stankowich & Blumstein 2005). When an individual flees in response to a given stimulus, the behaviour suggests that the individual perceives the stimulus as threatening and is fearful (Murphy 1978; Lima & Dill 1990). Flight initiation distance (FID), also known as flush distance (Stankowich & Blumstein 2005), is another commonly used measure of fleeing behaviour that indicates the distance between an approaching threat and the subject when the subject flees (Hediger 1934). A greater distance between the threat and the subject indicates a greater perceived level of threat and a greater fear response. However, a potentially confounding factor that must be considered when using this method is that FID can be influenced by the distance to cover of the subject, whereby nearby refuge is perceived by the subject as a quick escape

(Dill & Houtman 1989). Lastly, fear can be measured by the distance that an individual fled after being exposed to a predation threat, known as escape distance or displacement distance, whereby a longer distance indicates a greater fear response as more energy is required to flee a further distance (Taylor & Knight 2003; Reimers et al 2006). However, similar to FID, distance to cover must be considered (Dill & Houtman 1989; Reimers et al 2006).

Reactive vigilance behaviour indicates that the animal has stopped displaying a maintenance behaviour and is attempting to locate the source of a potential threat (Lima 1987). Vigilance is often described as an upright position of the head with slight rotation of the head, most likely indicating that the animal is scanning its environment for the source of the threat, sometimes referred to as scanning behaviour (Lazurus 1979; Hart & Lendrem 1984). The most common measures of vigilance include recording the presence or absence of the behaviour (similar to fleeing), the time spent being vigilant (known as scanning rate; Hart & Lendrem 1984), and alarm-initiation distance (AD or agitation distance) as the distance between an approaching threat and the subject when the subject first initiates a vigilance response (Dandenong 1979). Several factors may influence vigilance behaviour, including immediate vegetation cover, group size, position in herd, and time of day, as these factors may impair one or more sensory modalities of an individual (Roberts 1996; Matson et al 2005). Thus, if the vision of the subject is impaired and the detection or assessment of a threat is unattainable, the animal may perform more vigilance behaviours as the subject is more vulnerable to predation (Metcalfe 1984).

When fleeing and vigilance behaviours cannot be observed, a useful measure of fear is “giving up density” (GUD) which describes the trade off that an individual makes between exhibiting foraging and fear behaviours (Brown 1988). A specified quantity of food is provided for subjects and then the subject is exposed to a predation threat. The quantity of food left over is measured. GUD can indicate how much time an individual spent foraging, but more importantly determines how much time the individual did not spend foraging and instead spent displaying fleeing or vigilance behaviour. Therefore, fearful individuals eat less and leave behind more food resources (Brown 1988).

1.4 Measuring Fear using the Automated Behavioural Response System (ABR)

Studying wildlife behaviour in nature is challenging, as both the environment and the experimenter can act as confounding factors in the study’s design and influence the behaviour of an animal subject. Caravaggi and colleagues (2017) reviewed how camera traps have become a popular tool for studying wildlife behaviour as the videos captured provide a naturalistic perspective of how animals behave without the presence of nearby humans. Camera traps can also record video throughout the night and provide data for large carnivores and other nocturnal species, providing an up close view of more elusive species during times when it may have been too dangerous to directly observe wildlife. However, without a manipulation (or predator) present to alter the wildlife’s behaviour, the use of camera traps is limited to observational studies and correlational results.

Another commonly used tool that allows for experimentation and manipulation of animal behaviour are speaker systems that emit auditory playbacks (McGregor 2000).

Speakers are programmed to play a certain sequence of auditory playbacks by the experimenter to elicit behavioural responses to wildlife that are within the speaker's acoustic range (McGregor 2000). In 2014, Hettena and colleagues reviewed 180 different experiments that have been conducted using playbacks as a tool to assess behavioural responses to predators in all types of species from toads to elephants. Despite addressing the main caveat of using camera traps and allowing data to be collected on the cause and effect of wildlife behaviour, an experimenter must still be present in the field to not only operate the speaker system but to also detect appropriate subjects and directly observe and record their behaviours (Suraci et al 2017). Therefore, the conclusions reached by playback experiments may be influenced by the presence of humans, which would be particularly problematic when studying the effects of human disturbance as animals may be attracted (Nowak et al 2014) or averted (Suraci et al 2017) by the presence of a human experimenter.

The Automated Behavioural Response (ABR) system combines the benefits of camera traps and speaker systems while simultaneously eliminating the drawbacks of both tools (all material reviewed from Suraci et al 2017 unless stated otherwise). The ABR operates with a motion sensor, such that when an animal moves within range, the ABR begins recording video of the animal. The principal difference that makes the ABR unique is that after a few seconds have passed, a sound is emitted from the ABR's attached speaker system and manipulates the behaviour of the animal. Thus, the ABR can capture video of behaviours from before and after the playback, allowing experimenters to observe wildlife and collect behavioural data without the influence of their presence, at any time of the day or night. Previous studies have successfully used the ABR to experimentally test a fear of human presence in mammal species such as badgers (Clinchy et al 2016), bobcats (*Lynx rufus*) (Suraci et al 2019), and cougars (Smith et al 2017; Suraci et al 2019).

1.5 Research Objectives

My research aimed to investigate how simulated human presence and hunting affects the behaviour of African mammals. My objective for Chapter 2 was to collect, assess, and review current literature to summarize our current knowledge of how human disturbance affects mammal behaviour in Africa. I predicted that all forms of human disturbance negatively impact African mammals. My objective for Chapter 3 was to experimentally test a fear of human presence and hunting in a South African mammal community and compare their behavioural responses between predator types (human presence, hunting sounds, non-human predator) and between areas of high- and low-intensity hunting. I hypothesized that human-induced behavioural effects in mammals are pervasive and can impact entire communities. I predicted that human presence and hunting would be perceived by a mammal community as predation threats and elicit a greater occurrence of fleeing and vigilance behaviours. In my final chapter, I discussed the significance of my research by reviewing the potential consequences of a pervasive fear of humans in wildlife and how my research can better inform wildlife management.

1.6 Study Species in South Africa

In Chapter 2, I focused my literature search to broadly encompass any free-living mammal species endemic to Africa; whereas for my experiment in Chapter 3, my study subjects consisted of any mammal species that triggered the ABRs in the Greater Kruger National Park (GKNP). My experimental set up manipulated and recorded video of a total of 30 South African mammal species in GKNP (Appendix A), ranging from small-sized mongooses to mega-sized elephants. This mammal community offers a unique and optimal opportunity to study behaviour, as the GKNP offers an intact yet complex multi-predator, multi-prey system with all five large carnivore species present: hyenas (*Crocuta crocuta*), lions, leopards (*Panthera pardus*), wild dogs (*Lycaon pictus*), and cheetahs (*Acinonyx jubatus*) (Maputla et al 2015). Large carnivores typically prey on antelopes, such as impalas (*Aepyceros melampus*) and gazelles; however, lions will also hunt larger species such as buffalo (*Syncerus caffer*), wildebeest, giraffes (*Giraffa camelopardalis*), and the offspring of elephants and rhinoceroses (Hayward & Kerley 2005, 2008). Rigoudy and colleagues (in review) have experimentally demonstrated that lions are the most feared non-human predator in this community, most likely due to their large size, strength, and hunting strategy. Activity patterns greatly range across species, with carnivores being typically nocturnal, herbivores typically diurnal, while hippopotamuses (*Hippopotamus amphibius*), buffalo, and elephants vary in their activities between night and daytime (Kingdon 2013a, p. 187; Kingdon 2013b, p. 72 & 130; Owen-Smith 2015). The majority of subjects were adults, as my colleagues Dr. Zanette and Dr. Clinchy collected field data in the dry season (May to September) to avoid excess vegetation blocking the view of the cameras. Seasonal breeding and births typically occur during the rainy season (October to April) when vegetation and water resources are abundant, with the exception of a few continuous breeders in the community including elephants, rhinoceroses, and giraffes (Fairall 1968).

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Chapter 2

2 Effects of Human Disturbance on African Mammal Behaviour: A Literature Review and Meta-Analysis.

2.1 Introduction

As a consequence of humans' exploitive killing of wildlife (Darimont et al 2015), many wildlife species respond to human presence and activities in the same manner as they would towards their natural predators, indicating that wildlife likely perceive and fear humans as a predation threat (Frid & Dill 2002). The strength of an antipredator behaviour is often positively associated with the prey's perception of the threat level of a predator (Lima & Dill 1990). Thus, as humans kill at rates of up to 9 times more than non-human predators (Darimont et al 2015), it is hypothesized that humans are perceived by wildlife as an ultra-threatening "super-predator". Humans have elicited fear responses of large carnivores with few if any previously known predators (Stillfried 2015) and greater fear responses than large carnivores in lower trophic levels (Ciuti et al 2012; Frizzelle, Chapter 3). Over the past two decades, multiple meta-analyses have highlighted and reviewed the behavioural changes observed in mammals in response to human disturbance, such as increased fleeing behaviours (Stankowich 2008), increased nocturnality (Gaynor et al 2018), decreased movement patterns (Tucker et al 2018), decreased foraging (Zanette & Clinchy 2020), and altered social behaviours (Verdade 1996). However, some forms of human disturbance are more feared by mammals than others, as indicated by the strength of behavioural responses (Murphy & Romanuk 2012; Tablado & Jenni 2017; Nickel et al

2020). In mammals, human presence may elicit stronger behavioural effects than other forms of disturbance – for example, ungulates are more vigilant towards humans on foot than they are to vehicles or road noise (Stankowich 2008). Mesocarnivores also avoid humans, especially in developed areas (Nickel et al 2020). Moreover, interactions of multiple human disturbances may influence mammal behaviour, as observed in studies where hunted populations prompt stronger fleeing behaviours in response to perceived human presence than non-hunted populations (Caro 1999; Tarakini et al 2014; Stankowich 2008; Frizzelle, Chapter 3).

In Africa, a prominent source of human disturbance is the international tourism industry, whereby millions of North American and Europeans annually visit African countries to view, photograph, and hunt native wildlife (Lindsey et al 2007; WTTC 2019). In 2019, the wildlife tourism sector generated $70.6 billion and supplied 8.8 million jobs, overall contributing to 3% of Africa's annual gross domestic product (GDP) (WTTC 2019; IMF 2021). In comparison, North America's wildlife tourism sector generated $37.6 billion and supplied less than half a million jobs, contributing 0.002% to the continent's GDP (WTTC 2019; IMF 2021). The COVID-19 pandemic highlighted the importance of the international tourism industry to the economies of African countries, with South Africa projected as the third most affected nation in the world due to lost tourism revenue amidst travel restrictions (UN 2021). In addition to South Africa's 8.1% loss in GDP and 11.8% loss in employment of tourism-related labour (UN 2021), Africa suffered disproportionately more than other regions as tourism revenue dropped 49.2% and 7.2 million jobs were lost between 2019 and 2020 (WTTC 2021).

The majority of ecological studies on wildlife are, nonetheless, conducted in North America or Europe (Martin et al 2012; Nuñez et al 2019; Montgomery et al 2020; Christie et al 2020). For example, a recent meta-analysis that explored how human kill rates influence behavioural or physiological changes in mammals reported that almost half of their collection of 187 studies focused solely on Canadian or American species (Montgomery et al 2020), compared to 33 studies that focused on African species. Most ecological literature that has investigated the consequences of Africa's tourism industry have focused on how the diversity (Di Minin et al 2013), conservation (Lindsey et al 2005), and population dynamics (Kruger 2005) of mammal species are affected. Yet, these studies do not address how fear behaviour is altered in response to tourism and other human disturbances on mammals, dismissing the behavioural responses of mammals that are often the driving mechanism for population-level movement, reproduction, and survival (Brown et al 1999; Zanette & Clinchy 2020).

The goal of my review and meta-analysis was to collect, analyze, and summarize what is currently known in the literature about how human disturbance affects fear behaviour of free-living African mammals. I aimed to compare and contrast this collection of results by calculating the averaged magnitude and direction of human-induced behavioural effects reported for each behaviour or disturbance type (Salo et al 2010; Zanette & Clinchy 2020). In my paper, I address three principal questions, which are: 1) Does human disturbance have an overall negative, positive, or no effect on African mammal behaviour? 2) Is the literature biased towards studying particular species, behaviours, or forms of human disturbance? and 3) Do tourists negatively affect the behaviour of African mammals?

2.2 Methods

2.2.1 Literary Search

I found primary scientific articles that investigated the effects of human disturbance on mammal behaviour and manually filtered for studies that included African species in African countries. Human disturbance is a broad term encompassing many mechanisms of disturbance such as human presence, tourism, hunting, settlements, agriculture, roads, and any other forms of infrastructure. These mechanisms have been shown to have non-equivalent effects on mammal behaviour (Nickel et al 2020), thus all forms of human disturbance on wildlife are included in my review to be as comprehensive as possible. I followed protocol of previous meta-analyses on fear behaviour in wildlife (Preisser et al 2005; Zanette & Clinchy 2020), to search the Web of Science for the terms "behav*," "respons*," "flight initiation distance," "social disruption," "determine*," "distinguish," and "vigilance" in combination with "human*," "anthro*," "hunt*," "cull*," "*tourism*," "human-wildlife," "human voice*," "human vocal*," "fear," "fear of human," "fear of humans," and "fear of the human." I manually filtered my initial search results of 2,563 papers by title to exclude secondary articles as well as primary articles that did not appear relevant to the study of human disturbance on African mammal behaviour. To limit the analysis to free-living wildlife, I excluded studies that measured the effect of humans or human disturbance in domesticated or zoo animals. Lastly, I reviewed the citations of my paper collection and included any additional papers from the citations that were pertinent.

2.2.2 Data Collection

I categorized studies by factors including study species (carnivores, primates, ungulates, elephants (*Loxodonta africana*), other), study location (North, South, West, East, Central Africa), study design (experimental, observational), human disturbance type (presence/tourism, hunting, infrastructure, agriculture, other), behaviour (fleeing, vigilance, foraging, movement, boldness, vocalizations, other), and study methodology. I categorized study methodology of observational studies by the use of direct observation, surveying, GPS tracking, or camera traps to collect behavioural data, meanwhile I further categorized experimental methods on whether the authors implemented auditory playbacks, attracted wildlife with food patches or decoys ("baiting"), or approached wildlife to manipulate their behaviour. For human disturbances: I included humans approaching wildlife on foot, tourists viewing wildlife from vehicles at close quarters, and auditory playbacks of human vocalizations as examples of human presence or tourism; I included comparisons of hunting and non-hunting areas, comparisons of hunted and non-hunted populations within a species, and comparisons of hunting and non-hunting time periods as examples of hunting; I included comparisons between urban and rural/edge-of-urban areas, comparisons between areas of low and high human densities, the presence of roads, and noise produced by roads; examples of agriculture included comparisons between cultivated and non-cultivated areas as examples of infrastructure; and finally I included logging and the direct feeding of wildlife by humans as other disturbances. I categorized behaviours as follows: fleeing behaviours that were measured by recording fleeing frequencies or flight initiation distances (FID); vigilance behaviours that were measured by vigilance scanning rates or time spent vigilant; foraging behaviours that were measured by time spent foraging or hunting prey, giving up densities, changes in diet, or time spent drinking or feeding; movement behaviours were measured by distance moved, movement speed, and frequency of initiating movements from a resting state; vocalizations that were measured by the frequency of calling (call rate); boldness that was measured by distance to a conspecific decoy (Turner et al 2020), count of contacts with humans or human food, and contact duration with humans. Other behaviours, including resting and grooming, that were measured by time spent resting and frequency of grooming events.

For behavioural comparisons between subcategories within each factor, I recorded means for the treatment and control groups and calculated the effect size as ln(mean for treatment/mean for control) to provide effect sizes that can be easily interpreted as approximate proportional differences from 0 (where 0 indicates no effect on behaviour). This method has been used in past reviews when a considerable portion of collected studies do not report the standard deviation or variance needed to calculate Hedges' *d* (Salo 2010; Zanette & Clinchy 2020). For articles that investigated multiple behavioural responses to human disturbance, I estimated an effect size for each behaviour. For articles that reported multiple estimates of the same type of behaviour, I recorded separate effect sizes if they involved different species (up to 5 species) or if a species was assessed in different environments or types of human disturbance. If multiple estimates were given for the behaviour of a single species to one type of human disturbance, I averaged effects to produce a single estimate and calculated one effect size. I took data directly from text, tables, or I estimated data points by measuring figures. I excluded any studies where means of treatment and control groups were not stated or presented as an effect size could not be calculated. Furthermore, I excluded experimental studies without an obvious control group.

2.2.3 Statistical Analyses

When calculating effect sizes, I considered estimates associated with little to no disturbance as the control mean and estimates associated with human disturbance as the treatment mean. However, the direction of the signs of these calculated effect sizes often did not reflect the effect of disturbance on wildlife. To facilitate consistent and clear interpretation across different types of behaviour, I inverted the expected direction of some effect sizes to ensure that all positive signs indicated a positive effect of humans on wildlife behaviour and negative signs indicated a negative effect (after Coetzee & Chown 2016; Tables 2.1 & 2.2). Human-induced behaviours that I inverted the direction of the effect size included: increased (+) vigilance behaviours, more (+) frequent fleeing, greater (+) flight initiation distances (FID), more (+) frequent alarm calls, more (+) frequent foraging during more risky times of day such as moonlight or night, lower (-) giving up densities (GUD), less (-) boldness in hyenas [as less bold individuals are modeled to have greater survivorship (Greenberg & Holekamp 2017; Turner et al 2020)], and increased (+) movement speed or distance to areas away from human disturbance.

To investigate the direction of effects without consideration of magnitude, I conducted paired-samples sign tests to determine the proportion of effect sizes that report a positive or negative ecological effect of humans, evaluating significance with a Z score ($\alpha = 0.05$). In addition to analyzing 77 individual effect sizes, I also performed this analysis on the averaged effect size of each study to represent the overall directional effect of human disturbance on mammal behaviour presented by the authors for each paper.

To determine if effect sizes were influenced by certain factors within the study design, I compared averaged effect sizes between experimental and observational studies as well as across species, methodologies, human disturbance types, and behaviours. Given the non-normal distribution of effect sizes, I used non-parametric Kruskal-Wallis and Mann-Whitney U tests to compare levels within each factor. Levels that contained less than three effect sizes were excluded from analyses to meet the assumptions of the Kruskal-Wallis test. For analyses, I combined disturbance types of presence and tourism were combined as both forms of disturbance involve the presence of humans, as well as camera traps, surveying, and observation as all three methods involve observing and recording behavioural data. When groups significantly differed, I conducted Holm-Bonferroni corrected comparisons ($\alpha = 0.05$).

Lastly, I investigated if the averaged effect size of the entire dataset, along with the averaged effect sizes of factor levels, represented true positive or negative effects of human disturbance. To determine whether an effect size was significantly different from zero, I calculated standard errors and 95% confidence intervals (CI) for median values of the dataset and individual factor levels by performing bootstrapping with a sample size of

1000. I recorded means, medians, standard errors, upper confidence limits (UCL), lower confidence limits (LCL), and counts (Appendix C). If the UCL of a negative effect was less than zero, I considered the effect as significant; likewise, if the LCL of a positive effect was greater than zero, I considered the effect as significant. I performed all statistical analyses using IBM SPSS (2020).

2.3 Results

In total, I found 31 journal articles that investigated the effects of human disturbance on the behaviour of free-living 48 African mammal species (Figure 2.1). I found 13 experiments reporting significant behavioural effects in response to human disturbance in a total of 32 species (Table 2.1). Additionally, I found and listed the effect sizes of 18 observational studies that contrasted sites, time periods, or wildlife populations to investigate the behavioural effects of similar forms of human disturbance on a total of 25 species (Table 2.2). Mammal species that were studied using both experimental and observational methods included elephants, impalas (*Aepyceros melampus*), leopards (*Panthera pardus*), African wild dogs (*Lycaon pictus*), greater kudu (*Tragelaphus strepsiceros*), lions (*Panthera leo*), giraffes (*Giraffa camelopardalis*), wildebeest (*Connochaetes taurinus*), and zebras (*Equus burchelli*).

When examining the directional effect of human disturbance on behaviour, I found that significantly more studies reported a negative effect (N = 25) than a positive effect (N = 6; Sign: $Z = 3.48$, $p < 0.001$). Furthermore, 87% of individual effect sizes indicated a negative effect of humans, with a total of 67 negative effect sizes and 10 positive effect sizes ($Z = 6.38$, $p < 0.001$). Both experiments and observational studies reported significantly more negative effects than positive effects, with 86% of experiments ($Z = 4.17$, $p < 0.001$; Table 2.1) and 88% of observational studies ($Z = 4.69$, $p < 0.001$; Table 2.2) reporting a negative effect of humans.

All disturbance types led to negative behavioural reactions (Figure 2.2), though effect sizes differed significantly amongst disturbance types (Kruskal-Wallis: $H_3 = 7.88$, $p = 0.048$; Figure 2.2). Studies that investigated behaviour in response to human presence and tourism (median = -1.15, SE = 0.27) reported greater negative effects in behaviour than those that investigated the effects of agriculture (median = -0.21, SE = 0.22; $p = 0.01$). Methods of collecting behavioural data also differed ($H_4 = 0.93$, $p = 0.043$; Figure 2.3), whereby baiting resulted in greater positive effects (median = 0.27, SE = 0.32) compared to approaching subjects (median = -1.07, SE = 0.40; p – 0.01) or using auditory playback systems (median = -0.86, SE = 0.18; $p = 0.01$). There were no significance differences among behaviours, species groups, or between study designs.

When analyzing the significance of the direction of effect sizes for the entire data collection, I found that the current literature reports a significantly negative effect of human disturbance on African mammal behaviour (median = -0.70, SE = 0.12, UCL = -0.55). When I averaged effect sizes by the 22 subcategories within disturbance type (N = 4), study design (N = 2), species group (N = 5), methodology (N = 5), and behaviour type (N = 6), the majority of averaged effect sizes (18/22) were significantly negative (Appendix C). Four averaged effect sizes that were not significantly different from zero and do not represent a significant directional effect were behaviours in response to agriculture (median

= -0.21, LCL = -0.55, UCL = 0.31), behaviours of carnivores (median = -0.52, LCL = -1.52, UCL = 0.22), behaviours that were manipulated using bait (median = 0.27, LCL = -0.55, UCL = 0.56), and behaviours related to boldness (median = 0.33, LCL = -0.59, UCL = 0.69).

Figure 2.1: Number of studies conducted on each subcategory of study site, species, human disturbance, behaviour, and methodology among all studies (column 1), experiments (column 2), and observational studies (column 3) that investigated human disturbance on behaviour of free-living African mammals.

Reference	Species	Method	Behavioural Measure	Effect Size ^{a}	Corrected Effect Size ^{b}
Hunting					
Greenberg & Holekamp 2017	Spotted hyena (*Crocuta crocuta*)	Artificial food patch in hunting & non-hunting areas	Exploration score	0.69	0.69
			Boldness score	-0.56	0.56
Bshary 2001	Diana monkey (*Cercopithecus diana*)	Auditory playbacks of predator's call (P), imitation predator's call (IP), & imitation conspecific distress call (ICD) in poaching & non-poaching areas	Call rate to P	-0.22	-0.22
			Call rate to IP	-0.59	-0.59
			Call rate to ICD	-2.08	-2.08
			Fear to P	-0.07	-0.07
			Fear to IP	-0.92	-0.92
			Fear to ICD	-0.69	-0.69
Shannon et al 2013	Elephant (*Loxodonta africana*)	Auditory playbacks of elephants to hunted & non-hunted populations	Bunching (family)	-1.82	-1.82
			Bunching (age)	-1.61	-1.61
McComb et al 2014	Elephant (*Loxodonta africana*)	Auditory playbacks of vocalizations of hunting & non-hunting tribes	Bunching	0.55	-0.55
Nyahongo 2008	Impala *(Aepyceros melampus)*	Approaching subjects with vehicle in poaching and non-poaching areas	Fear (FID)	1.35	-1.35
	Gazelle *(Gazella thomsonii)*		Fear (FID)	1.97	-1.97
	Korrigum (*Damaliscus korrigum)*		Fear (FID)	1.61	-1.61
	Zebra *(Equus burchelli)*		Fear (FID)	1.66	-1.66
	Wildebeest (*Connochaetes taurinus*)		Fear (FID)	1.61	-1.61
Frizzelle et al (unpub)	26 mammal species	Auditory playbacks of human vocalizations (HV) & hunting sounds in hunting (HS) and non-hunting areas	Fear (fleeing freq.) to HS	0.18	-0.18
			Fear (fleeing freq.) to HV	0.37	-0.37
Human Presence					
Nowak et al 2014	Samango monkey (*Cercopithecus albogularis*)	Artificial food patch when followed by humans	Feeding (food remaining at site)	-0.27	0.27
Soltis et al 2014	Elephant (*Loxodonta africana*)	Auditory playbacks of white noise & human vocalizations	Movement (dist.)	0.80	-0.80
			Fear (vigilance)	0.86	-0.86
			Call rate	0.61	-0.61
Frizzelle et al (unpub)	26 mammal species	Auditory playbacks of bird & human vocalizations	Fear (fleeing freq.) across areas	1.26	-1.26
			Fear (fleeing freq.) in hunting area	1.48	-1.48
			Fear (fleeing freq.) in no-hunt area	1.04	-1.04

Table 2.1: Summary of species, methods, behavioural measures, and effect sizes of 13 experiments that demonstrated effects of human disturbance on behaviour of free-living African mammals.

Reference	Species	Method	Behavioural Measure	Effect Size [a]	Corrected Effect Size [b]
Human Settlements					
Turner et al 2020	Spotted hyena (*Crocuta crocuta*)	Conspecific decoy in areas of low and high human density	Fear behaviours Bold behaviours Boldness (Dist. to decoy)	0.55 -0.22 0.44	-0.55 0.22 0.44
Hicks et al 2012	Chimpanzee (*Pan troglodytes*)	Approaching subjects on foot near and away from settlements	Fear (fleeing) Boldness (# contacts) Boldness (contact time)	0.58 -0.79 -0.39	-0.58 -0.79 -0.39
Kaplan et al 2011	Chacma baboon (*Papio ursinus*)	Articifial food patch outside of urban area	Feeding (% use of urban land)	-1.12	-1.12
Road Noise					
Morris-Drake et al 2017	Dwarf mongoose (*Helogale parvula*)	Auditory playbacks of ambient sound & road noise	Fear (time vigilant) Fear (vigilance scan rate)	1.85 1.10	-1.85 -1.10
Agriculture					
McLennan & Hill 2010	Chimpanzee (*Pan troglodytes*)	Approaching subjects on foot in dense forest and gardens	Fear (vigilance to humans) Fear (retreating from humans)	0.69 0.40	-0.69 -0.40

a Effect size calculated as ln(mean for fear treatment/mean for control), after Salo et al. (2010).

b Sign (+/-) of effect size corrected to reflect positive (+) or negative (-) effect of humans on behaviour, as reported by original authors

Table 2.1 (continued): Summary of species, methods, behavioural measures, and effect sizes of 13 experiments that demonstrated effects of human disturbance on behaviour of free-living African mammals.

Reference	Species	Method	Behavioural Measure	Effect Size [a]	Corrected Effect Size [b]
Hunting					
Rasmussen & MacDonald 2012	African wild dog *(Lycaon pictus)*	GPS tracking of subjects in no hunting vs hunting areas	Hunting in morn. Hunting in eve. Hunting at moonlight	-0.52 -0.15 1.01	-0.52 -0.15 -1.01
Setsaas et al 2007	Impala *(Aepyceros melampus)*	Transect surveying in no hunting vs hunting areas	Fleeing Resting Movement Vigilance Feeding	1.36 -0.89 -0.54 -0.36 -1.12	-1.36 -0.89 -0.54 0.36 -1.12
Ihwagi et al 2018	Elephant *(Loxodonta africana)*	GPS tracking of subjects before vs during poaching period	Movement (night-day speed ratio)	0.21	-0.21
Kiffner et al 2014	Elephant *(Loxodonta africana)* & 7 ungulate species	Road surveying in no hunting vs hunting areas	Fear (vigilance, fleeing, alarm calls)	0.92	-0.92
Topp-Jorgensen et al 2008	Eastern tree hyrax (Dendrohyrax validus)	Directly observed behaviour in low vs moderate hunting areas	Call rate	-0.39	-0.39
Muposhi et al 2016	Impala *(Aepyceros melampus)* Greater kudu *(Tragelaphus strepsiceros)* Sable *(Hippotragus niger)*	Directly observed behaviour in no hunting vs hunting areas	Fear (FID) Fear (FID) Fear (FID)	0.61 0.57 0.70	-0.61 -0.57 -0.70
Tarakini et al 2014	Impala *(Aepyceros melampus)* Greater kudu *(Tragelaphus strepsiceros)*	Directly observed behaviour in no hunting vs hunting areas	Fear (FID) Fear (FID)	0.50 0.40	-0.50 -0.40
Crosmary et al 2012a	Impala *(Aepyceros melampus)* Greater kudu *(Tragelaphus* Sable *(Hippotragus niger)*	Directly observed behaviour in no hunting vs hunting areas	Fear (time vigilant) Fear (time vigilant) Fear (time vigilant)	0.96 0.23 0.80	-0.96 -0.23 -0.80
Crosmary et al 2012b	Impala *(Aepyceros melampus)* Greater kudu *(Tragelaphus* Sable *(Hippotragus niger)*	Directly observed behaviour in no hunting vs hunting areas	Drinking at night Drinking at night Drinking at night	1.53 3.00 1.61	-1.53 -3.00 -1.61
Henschel et al 2011	Leopard *(Panthera pardus)*	Camera traps & skat analysis in no hunting vs hunting areas	Feeding (diet)	-2.86	-2.86
Croes et al 2007	5 monkey species 4 duiker species	Transect surveying in no hunting vs hunting areas	Fear (FID) Fear (fleeing freq.) Fear (alarm call)	0.24 3.32 0.83	-0.24 -3.32 -0.83

Table 2.2: Summary of species, methods, behavioural measures, and effect sizes of 18 observational studies reporting effects of human disturbance on behaviour of free-living African mammals.

Reference	Species	Method	Behavioural Measure	Effect Size [a]	Corrected Effect Size [b]
Tourism & Feeding of Wildlife					
Hayward & Hayward 2009	Lion *(Panthera leo)*	GPS tracking & directly observed behaviour in absence and presence of tourists	Movement Grooming Vigilance	1.67 -3.00 1.52	-1.67 -3.00 -1.52
Altmann & Muruthi 1988	Yellow baboon (*Papio*	Directly observed behaviour in areas where humans fed vs did not feed subjects	Feeding (diet) Resting	-1.05 1.50	-1.05 1.50
Human Settlements & Roads					
Hicks et al 2013	Chimpanzee *(Pan troglodytes)*	Transet surveying in remote areas vs areas with human settlement	Call rate	-1.12	-1.12
Abrahms et al 2016	African wild dog *(Lycaon pictus)*	GPS tracking of subjects that used vs did not use roads for travelling	Movement (speed)	0.30	0.30
Schuette et al 2013	Lion *(Panthera leo)*	GPS tracking in areas of low vs high human density	Habitat selection (dense cover) Habitat selection (conservation area)	0.40 1.56	-0.40 -1.56
Graham et al 2009	Elephant *(Loxodonta africana)*	GPS tracking of subjects in areas of low vs high human density	Habitat selection	-2.59	-2.59
Logging					
Henschel et al 2011	Leopard *(Panthera pardus)*	Camera traps & skat analysis in no hunting vs hunting areas	Feeding (diet)	-0.51	-0.51
Agriculture					
Bryson-Morrison et al 2017	Chimpanzee *(Pan troglodytes)*	Directly observed behaviour in non-cultivated vs cultivated areas	Foraging Movement Resting Socializing	-0.09 0.09 -0.32 0.53	-0.09 0.09 -0.32 0.53

a Effect size calculated as ln(mean for fear treatment/mean for control), after Salo et al. (2010).

b Sign (+/-) of effect size corrected to reflect positive or negative effect of humans on behaviour, as reported by original authors

Table 2.2 (continued): Summary of species, methods, behavioural measures, and effect sizes of 18 observational studies reporting effects of human disturbance on behaviour of free-living African mammals.

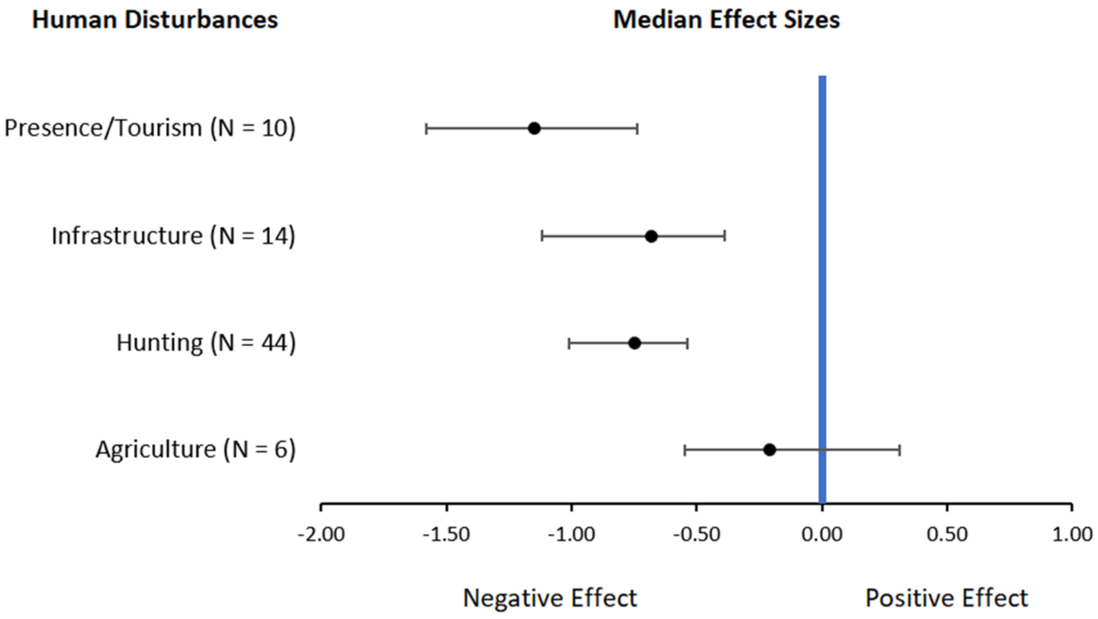

Figure 2.2: Median effect sizes (± 95% CI) of African mammal behaviour among different types of human disturbance.

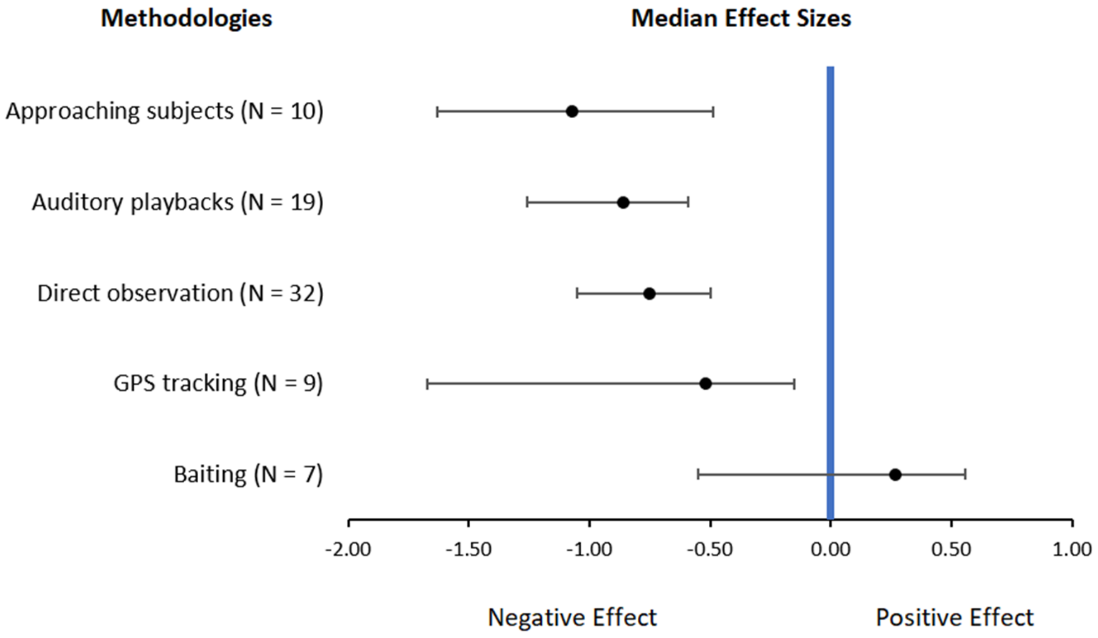

Figure 2.3: Median effect sizes (± 95% CI) of African mammal behaviour among different methods of collecting data.

2.4 Discussion

My literature search has revealed that the vast majority of journal articles (27/31) and effect sizes (67/77) report that humans negatively affect the behaviour of free-living African mammals. Nearly half (30/77) of the effect sizes had a magnitude of 1.00 or greater, demonstrating very strong effects of human disturbance (Salo et al 2010; Zanette & Clinchy 2020). When accounting for two studies that explored effects of more than one disturbance type, I found that more than half of studies (17/31) investigated the effects of hunting, one quarter of studies (8/31) investigated the effects of infrastructure, and the remaining quarter of studies (8/31) investigated the effects of agriculture (N = 2), tourism (N = 1), logging (N = 1), feeding of wildlife (N = 1), and human presence (N = 3). Consistent with Nickel and colleagues' (2020) previous findings, I observed a trend that suggests that different forms of disturbance elicit different strengths of effect size, with tourism eliciting the strongest negative effect and agriculture eliciting the smallest effect on African mammal behaviour (Figure 2.2). Additionally, baiting methods yielded an effect size significantly more positive than auditory playbacks and approaching (Figure 2.3); however, neither GPS tracking nor observation differed from any of the aforementioned methods, indicating that experimental studies yield similar effect sizes as observational studies. The majority of behaviours studied in African mammals fell into one of four categories: fleeing (N = 11), vigilance (N = 9), foraging (N = 8), and movement behaviours (N = 8). Fourteen studies investigated additional behaviours including vocalizations (N = 7), boldness (N = 3), and resting and grooming (N = 4).

My meta-analysis and review clearly demonstrate a consistent and frequently large negative impact of humans on the behaviour of African mammals, accurately reflecting the common use of the term “human disturbance” in scientific literature. These effects can be considered substantial in magnitude as previous comparative meta-analyses on wildlife behaviour (Salo et al 2010; Zanette & Clinchy 2020) have reported much smaller effect sizes (2/24 & 1/36 effect sizes above 1.0 in magnitude, respectively). However, there is a great need for more research to be conducted as a total of 31 studies does not suffice in representing the behavioural effects of humans on mammals for a *continent*.

Many species that are endemic to Africa are at-risk (Rosser & Mainka 2002; Ripple et al 2016), yet my review demonstrates that current research only focuses on a relatively small number of charismatic species; for example, Africa is home to 20% of all bat species in the world (Herkt et al 2016) and not a single behaviour of theirs has been studied in relation to human disturbance. Therefore, we are currently missing the big picture of how African mammals respond to human disturbance, especially of species endemic to northern African countries as my literary search did not record any study sites located north of Guinea. In addition to studying more species, more forms of human disturbance need to be addressed and studied, as more than half of studies (17/31) focused on the behavioural effects of hunting. In comparison, despite eliciting the strongest effect sizes of all the forms of disturbances that I sampled, only four studies addressed the effects of tourism or human presence on African mammal behaviour. Ecotourism is a crucial industry that centers around Africa’s wildlife and contributes billions of dollars to the continent’s GDP (WTTC 2019; IMF 2021); thus, more research needs to be conducted on tourism to understand the effects of humans' mere presence so that tourism organizations can implement practices, such as guiding smaller groups of tourists or greater buffer zones between tourists and wildlife (Johns 1996; Rodgers & Smith 1997), to better conserve wildlife behaviour.

Observational studies often suggest that changes in mammal behaviour are due to the presence or absence of given human disturbance between time periods or locations (Zanette & Clinchy 2020); however, many human disturbances are intercorrelated, so it is difficult to isolate which disturbances, if not a combination of all, are affecting wildlife behaviour. In contrast, experiments provide quantifiable data directly associated with one isolated form of human disturbance by manipulating behavioural responses in wildlife with the presence and absence of that disturbance (Zanette & Clinchy 2020), yielding more informative results. For the remainder of the discussion, I will go over the documented effects of human disturbances on each of the aforementioned behaviours, focusing particularly experimental results, beginning with the most commonly studied behaviour – fleeing.

2.4.1 Fleeing Behaviours

The effects of human disturbance on fleeing behaviours were experimentally tested in six studies on various species of ungulates, primates, and carnivores. Three studies collected behavioural data by approaching subjects either on foot or in a vehicle and recording the frequency of fleeing as well as flight initiation distance (FID) (Nyahongo 2008; Hicks et al 2012; McLennan & Hill 2010). All three studies reported negative effects of humans on impalas, gazelles (*Gazella thomsonii*), korrigums (*Damaliscus korrigum*), zebras, and wildebeest. Each species fled at shorter distances to approaching vehicles on the outside of a protected park (where hunting occurs) compared to the inside of the park (Nyahongo 2008). Chimpanzees (*Pan troglodytes*) fled more frequently to approaching humans on agricultural land (McLennan & Hill 2010) and near human settlements (Hicks et al 2012) compared to their natural habitats away from human settlements.

Two studies used auditory playbacks to determine if mammals displayed more fearfulness in hunting areas than non-hunting areas (Bshary 2001; Frizzelle, Chapter 3). Bshary (2001) used playbacks of a common predator (eagle), a human imitation of eagle calls, and a human imitation of a conspecific alarm call, and found consistent results among all three treatments such that Diana monkeys (*Cercopithecus diana*) fled and called less in the hunting area compared to the non-hunting area. Instead of showing a direct fear of human presence, this finding demonstrates that Diana monkeys reduce their antipredator response to non-human predators in areas of human hunting, trading off the benefits of warning conspecifics of a nearby eagle and fleeing to safety to reduce detection by humans from revealing their location (Bshary 2001). Contrastingly, Frizzelle (Chapter 3) tested a direct fear of human presence by using playbacks of hunting sounds (dog (*Canis familiaris*) vocalizations and gunshots) as well as human voices to elicit a fleeing response in a mammal community consisting of 26 mammal species. My experimental findings demonstrated that the community not only feared human presence more in the hunting area than the non-hunting area, but also demonstrated that human voices elicited a greater fleeing response when compared to the community’s natural predator – the lion (Frizzelle, Chapter 3).

Most experiments that baited wildlife used food as an attractant, whereas Turner and colleagues (2020) used a unique approach to testing fleeing responses in hyenas (*Crocuta crocuta*) by deploying a conspecific decoy in areas of low and high human density. Similar to the findings of Hicks and colleagues (2012), hyenas fled more frequently in the area of high human density (Turner et al 2020). This study is unique not only in its experimental design, but also in their findings as the previous five studies demonstrated greater fearfulness of humans in areas of greater human disturbance, but Turner and colleagues (2020) demonstrated that human disturbance may also affect how mammals perceive members of their own species, potentially also negatively affecting socialization behaviours.

Five additional observational studies investigated the effects of hunting on fleeing behaviour by directly observing the frequency of fleeing or by recording FID when surveying areas of high and low hunting intensity (Setsaas et al 2007; Croes et al 2007; Tarakini et al 2014; Kiffner et al 2014; Muposhi et al 2016). All five studies reported that fleeing behaviour was more persistent in areas where hunting occurred more frequently, demonstrating a relationship between hunting intensity and fearfulness in monkeys, elephants, and various ungulate species.

2.4.2 Vigilance Behaviours

Vigilance behaviours of elephants were manipulated using auditory playbacks in three studies to investigate the effects of hunting and human presence (Shannon et al 2013; McComb et al 2014; Soltis et al 2014). Soltis and colleagues (2014) exposed elephants to playbacks of human voices, buzzing bees, and white noise and observed that individuals displayed greater scan rates to humans than to white noise but similar scan rates in response to humans and bees, demonstrating that elephants may perceive human presence as a predatory risk. Furthermore, it was demonstrated that elephants could not only distinguish human voices from non-threats, but elephants could distinguish different human languages, as elephants elicited stronger bunching behaviour in response to the language of a local hunting tribe than a non-hunting farming tribe (McComb et al 2014). Lastly, in addition to short-term behavioural effects of hunting, Shannon and colleagues demonstrated that hunting could have long lasting effects on the social behaviour in elephants, as elephants that were exposed to culling operations displayed less recognition of familial vocalizations (as determined through observation of bunching behaviour) compared to those that were not exposed to culling, *decades* after culling operations had ceased.

Two additional studies investigated the effects of human disturbance on vigilance behaviour of African mammals (McLennan & Hill 2010; Morris-Drake et al 2017). Using auditory playbacks of road noise and ambient noise, Morris-Drake and colleagues (2017) found greater scanning rates and more time spent vigilant in Dwarf mongooses (*Helogale parvula*) when exposed to road noise. Meanwhile, McLennan and Hill (2010) approached chimpanzees in croplands and outside of croplands to record their vigilance towards human presence and found that chimpanzees displayed greater vigilance and were more fearful of approaching humans in croplands. Both studies demonstrate that human-induced land use change to provide us with food and transportation can also have negative effects on wildlife behaviour.

Three observational studies explored the relationship of hunting and tourism in impala, greater kudu, sable antelopes (*Hippotragus niger*), and lions (Setsaas et al 2007; Hayward & Hayward 2009; Crosmary et al 2012a). Hayward and Hayward (2009) measured how often lions are disturbed and alerted from slumber and found that lions displayed more alertness when in the presence of tourists. When comparing a hunting area and a protected area, Crosmary and colleagues (2012a) observed that impalas, greater kudu, and sable antelopes spent more time displaying vigilance where hunting occurred. This finding contrasts the results of the third observational study, as Setsaas and colleagues (2017) reported that impalas displayed less vigilance in an area of hunting compared to an area without the occurrence of hunting. However, more fleeing behaviour was displayed in the hunting area, which may suggest that individuals in the hunting area were very fearful and immediately displayed fleeing behaviour to avoid perceived threats rather than spend time to first detect and assess the threat (Setsaas et al 2007).

2.4.3 Movement & Foraging Behaviours

Only two experimental studies have investigated how human disturbance affects foraging behaviour in African mammals (Kaplan et al 2011; Nowak et al 2014). Both studies used baiting to measure the amount of food remaining and assess foraging behaviour in natural habitat compared to areas of human settlements (Kaplan et al 2011) or human presence (Nowak et al 2014); however, their study design slightly differed. Kaplan and colleagues (2011) introduced a food patch outside an urban area that chacma baboons (*Papio ursinus*) and found that baboons preferred the artificial food patch to human waste and spent less time within the urban area. Meanwhile, Nowak and colleagues (2014) compared the foraging behaviour of Samongo monkeys (*Cercopithecus albogularis*) in a site with no human hunting when humans were present or not present. They found that without humans present, lower canopies showed greater giving up densities (GUD) than the higher levels, indicating a vertical axis of fear whereby monkeys low to the ground were at greater risk of predation by natural predators; in comparison, when humans were present, all levels of canopies reduced their GUDs, demonstrating that monkeys recognize that natural predators avoid areas with humans, reducing their risk of predation and allowing more time to be spent foraging (Nowak et al 2014). Therefore, these two studies provide conflicting results whereby one showcases how human waste negatively alters the diet of primates away from natural resources (Kaplan et al 2011), although the latter demonstrates a positive effect of human presence allowing for primates to forage for longer periods of time (Nowak et al 2014).

Six observational studies explored the effects of hunting, logging, feeding, and agriculture on African mammal foraging or feeding behaviour and all reported negative effects of humans (Altmann & Muruthi 1988; Setsaas et al 2007; Henschel et al 2011; Rasmussen & MacDonald 2012; Crosmary et al 2012b; Bryson-Morrison et al 2017). Two studies explored the temporal changes that mammals exhibited in response to hunting pressure, such that when human hunting pressure was high, mammals were more often observed hunting for prey or drinking from watering holes at night (Rasmussen & MacDonald 2012; Crosmary et al 2012b). This shift towards nocturnality suggests that these animals would rather expose themselves to higher predation risk from large carnivores during the night in order to reduce their risk of being hunted by humans in the daytime (Gaynor et al 2018). Furthermore, human disturbance has been observed to reduce feeding in impalas (Setsaas et al 2007) and chimpanzees (Bryson-Morrison et al 2017) as well as alter natural diet preferences of leopards (Henschel et al 2011) and baboons (Altmann & Muruthi 1988).

Human-induced movement patterns of African mammals has only been experimentally tested once; whereby auditory playbacks of human voices induced greater movement of elephants away from the stimulus in comparison to white noise (Soltis et al 2014). Two studies observed movement alterations in impalas (Setsaas et al 2007) and baboons (Bryson-Morrison et al 2017) but reported contrasting results. Setsaas and colleagues (2007) reported decreased movement of impalas as a negative effect of hunting, as impalas more often fled where hunting occurred, rather than walking from patch to patch. Yet, Bryson-Morrison and colleagues (2017) considered a reduction of movement in baboons as a positive effect of agriculture, given that these individuals did not have to expend energy to forage for food as croplands provided abundant food in one location. The remaining observational studies used GPS tracking to measure movement patterns and found that humans negatively affected these mammals' behaviour such that elephants moved faster at night (Ihwagi et al 2018) and altered their habitat selection (Graham et al 2009), lions increased their frequency of movements (Hayward & Hayward 2009) and altered their habitat selection (Schuette et al 2013), and African wild dogs increased their overall travel speed (Abrahms et al 2016).

2.4.4 Other Behaviours

Five other behaviours were investigated in relation to how they were affected by human disturbance: boldness, vocalizing, resting, grooming and socialization. The effects of humans on boldness differed between species, such that human hunting and settlements induced less bold behaviours exhibited in hyenas and chimpanzees; however, less bold hyenas are predicted to have better survival rates (Greenberg & Holekamp 2017; Turner et al 2020) whereas this relationship has not yet been determined in chimpanzees so less boldness was considered as an indication of a fear of humans which may negatively affect these primates' survivorship (Hicks et al 2012). Similar to the findings of Bshary's (2001) study, a reduced alarm call rate was recorded in Eastern tree hyraxes in response to human hunting (Topp-Jorgensen et al 2008) and in chimpanzees nearby human settlements (Hicks et al 2013), as a reduction in calling may increase predation risk of natural predators but may also increase chances of detection by humans. However, the opposite has also been observed in duikers (Croes et al 2007) and elephants (Soltis et al 2014) such that these species will increase their call rates in response to human hunting or presence, perhaps indicating that these species determine that this trade off exhibited by primates and hyraxes is not advantageous for them. When observing behaviours that indicate a lack of fearfulness, such as grooming, socialization, and resting, the form of human disturbance seemed to play a key role in whether humans elicited a positive or negative effect. Impalas in areas of persistent hunting exhibited fewer resting behaviours (Setsaas et al 2007), lions in the presence of tourists exhibited fewer grooming behaviours (Hayward & Hayward 2009), and chimpanzees in croplands exhibited fewer resting behaviours (Bryson-Morrison et al 2017). However, baboons that were hand-fed by tourists exhibited more frequent resting behaviours (Altmann & Muruthi 1988) and chimpanzees in croplands exhibited more frequent socialization behaviours with conspecifics (Bryson-Morrison et al 2017), as these individuals did not have to spend extra time foraging for food.

2.4.5 Concluding Remarks

Overall, an effect of human disturbance that is both negative and consistently large suggests that African mammals may fear humans as predators and actively engage in energetically costly antipredator behaviours to avoid human presence. Within the 31 reviewed papers, African mammals have been shown to trade off behaviours crucial to survival and fecundity – for example, reducing the frequency of foraging or the quality of their diets – with an increase in behaviours such as fleeing and vigilance. Thus, conducting further research in this field will not only reveal how human disturbance affects mammal behaviour, but will also provide us with a better understanding of how these behaviours drive changes in population sizes and distributions across Africa, resulting in more informed conservation and management practices.

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Chapter 3

3 A South African Mammal Community Fear the Human "Super Predator"

3.1 Introduction

As the global human population grows and overconsumption of goods and services increases (Wilting et al 2017), wildlife are increasingly subjected to human activity, resulting in profound detrimental effects on wildlife behaviour. In addition to contributing to habitat loss by converting natural habitats to agricultural land, building more infrastructure, and logging of old-growth forests (Tilman et al 2017), humans kill wildlife for meat, trophies, medicine, and sport in many places on Earth (Wilkie & Carpenter 1999; Corlett 2007; Darimont et al 2015). The human "super-predator" kills animals of all sizes, taxa, and trophic levels and globally exploits large carnivores and medium sized (meso-) carnivores at 4 to 9 times the rate of non-human predators (Darimont et al 2015). To avoid humans, mammals alter their movement patterns by proactively reducing activity in areas of high human disturbance (Ordiz et al 2011, Tucker et al 2018; Suraci et al 2019a; Nickel et al 2020) or by reactively fleeing when a human is detected nearby (Stankowich 2008; Smith et al 2017). In doing so, mammals either momentarily leave behind food resources and mating opportunities (Stankowich & Blumstein 2005) or completely shift home ranges when human-induced predation risk increases during hunting seasons (Lemke 1975; Root et al 1988; Stillfried et al 2015; Lone et al 2015). When spatial avoidance is not possible, such as in areas of high human footprint where movement barriers are abundant (Tucker et al 2018), mammals become more nocturnal (Ordiz et al 2013; Wheat & Wilmers 2016;

Gaynor et al 2018; Nickel et al 2020). Increased nocturnal activity decreases one's likelihood of detection by humans but also predisposes wildlife to increased vulnerability to large carnivores (Rasmussen & MacDonald 2012; Bonnot et al 2020; Haswell et al 2020). However, given that an increase in nocturnality in response to human disturbance has been observed in over 60 species across the globe (Gaynor et al 2018), mammals may collectively perceive this trade off as advantageous. By restricting the natural habitats of mammals and killing or invoking fear in individuals when interactions do occur, perceived human presence has been observed to reduce feeding and foraging behaviours (Smith et al 2017; Clinchy et al 2016; Suraci et al 2019a) as well as increase vigilance and fleeing behaviours (Taylor & Knight 2003; Stankowich 2008; Nyahongo 2008; Soltis et al 2014), resulting in potential consequences of lowered reproduction and survival rates (Frid & Dill 2002; Tuomainen & Candolin 2011; Tablado & Jenni 2017).

While it is widely known that human disturbance negatively impacts wildlife behaviour, these detrimental effects may be more pervasive than originally thought. A pervasive fear of humans is the likely driving mechanism to explain findings from two global meta-analyses, whereby over 60 mammal species were observed to alter their nocturnality (Gaynor et al 2018) and movement (Tucker et al 2018) behaviours in response to human activity and footprint. Recent experiments on the fear of human presence complement this proposed global-scale mechanism by demonstrating a fear of humans that exceeds a fear of natural predators (if any) in cougars (*Puma concolor*) and white-tailed deer *(Odocoileus virginianus)* in North America (Suraci et al 2019a; Crawford et al, in press), badgers (*Meles meles*) in Europe (Clinchy et al 2016), and elephants (*Loxodonta* *africana*) in Africa (McComb et al 2014; Soltis et al 2014). A fear of humans can also carry long-term changes in wildlife behaviour, as demonstrated in elephants who displayed hyper-aggression (Bradshaw et al 2005) or experienced significant impairment in fundamental social skills (Shannon et al 2013) as a result of extensive poaching from decades prior. In addition to directly invoking fear in wildlife, human-induced behavioural effects can indirectly pervade multiple trophic levels, such that fear behaviours elicited by species in higher trophic levels have been shown to influence behavioural modifications in lower trophic levels and release prey from predation risk (Hebblewhite et al 2005; Berger 2007; Muhly et al 2011; Suraci et al 2019a; Haswell et al 2020). Specifically, a fear of humans drives away large carnivores from occurrences of high human activity, providing increased foraging opportunities to prey species by reducing the spatial or temporal overlap of predator and prey distributions (Hebblewhite et al 2005; Berger 2007; Muhly et al 2011; Haswell et al 2020). Suraci and colleagues (2019a) experimentally demonstrated a fear-induced behavioural trophic cascade by invoking fear in cougars with playbacks of human vocalizations. In their study, carnivores responded by avoiding areas where the voices could be heard, becoming more elusive, and reducing foraging, meanwhile small mammals increased habitat use and foraging in response to a lowered perceived predation risk in the now cougar-free environment (Suraci et al 2019a). However, this benefit to species in lower trophic level may only be short-term, as human presence may decrease wariness and increase boldness in these species over time, resulting in greater vulnerability to natural predators if humans suddenly decrease activity or abandon sites (Geffroy et al 2005).

The pervasiveness of a fear of humans suggests that the strength of antipredator responses elicited by mammals may be influenced by more than predator-induced kill rates (Creel and Christianson 2008). Recent studies have found that the strength of antipredator behaviours elicited by ungulates do not correlate with the species-specific kill rates of large carnivores (Thaker et al. 2011; Creel et al. 2017; Makin et al. 2017; Creel et al. 2019; Packer and Palmer 2021). This finding suggests that prey species must be considering another important factor in addition to predator-induced kill rates for assessing the threat level of predators. To follow the safest strategy in surviving a predator encounter, mammals must consider both the specific-species kill rates *and* the killing success rate of a predator (Bouskila & Blumstein 1992; Creel et al 2019; Palmer and Packer 2021). Two important factors that prey often consider when assessing the threat level of a predator is their body size and the number of individuals present, as an increase in both of these factors can improve hunting success (Werner & Gillium 1984; Bouskila and Blumstein 1992; Fanshawe & Fitzgibbon 1993; Funston et al 2001; MacNulty et al 2009). However, humans have acquired an additional factor in improving hunting success: technology. In Africa, a human with a gun (72%, Rogan et al 2017) has a much higher average success rate of killing herbivores than all large carnivores (leopard (*Panthera pardus*) = 18%, Bothma & Coertze 2004; lion (*Panthera leo*) = 22%, African wild dog (*Lycaon pictus*) = 37%, hyena (*Crocuta crocuta*) = 29%, cheetah (*Acinonyx jubatus*) = 40%, Palmer & Packer 2021). Thus, regardless of how often humans kill members of their species, mammals may recognize humans' exceptionally high killing success rate and engage in the safer strategy of avoiding detection by humans all together (Stankowich 2008); thus, a fear of humans has the potential to pervade entire mammal communities.

My research objective was to experimentally test the pervasiveness of perceived human presence and hunting on the fear behaviour across an entire mammal community. I chose South Africa as an optimal study location as this country greatly profits from tourism, boasting the largest hunting-related tourism industry of the continent (Lindsey et al 2007). To achieve this objective, I conducted a bi-factorial experiment in which I manipulated fear by broadcasting auditory playbacks of human vocalizations, gunshots, dog (*Canis familiaris*) vocalizations, lion vocalizations, and bird vocalizations. Measuring both fleeing and vigilance behavioural responses, I evaluated and compared how mammal species in a South African community responded to these playbacks in two reserves of contrasting hunting intensity: high-intensity hunting in Klaserie Private Nature Reserve and low-intensity hunting in Thornybush Game Reserve. I predicted that (1) the community will perceive humans as ultra-lethal "super-predators" and as a result would respond most to human vocalizations than any other predator playback (McComb et al 2014; Soltis et al 2014); (2) the community will perceive humans' killing success rate as equal between the two reserves and consequentially would respond to human vocalizations equally between the two reserves (Gaynor et al 2018; Montgomery et al 2020); (3) in comparison to Thornybush, the community would respond more to gunshots and dog vocalizations in Klaserie, as hunting cues are perceived as more threatening where hunting occurs (Laundré et al 2010; Tarakini et al 2014).

3.2 Methods

3.2.1 Site Description

My manipulations were conducted in two adjacent reserves within the Greater Kruger National Park (GKNP), South Africa during June and July of 2018 by colleagues Dr. Zanette and Dr. Clinchy (Appendix D). The first reserve, Klaserie Private Nature Reserve (24.203S, 31.179E), is a reserve that encourages many forms of hunting, including trophy hunting (Pierce 2021). Contrastingly, the second reserve, Thornybush Private Game Reserve (24.467S, 31.150E), is a reserve that prohibits hunting, with human presence being primarily associated with ecotourism (Pierce 2021). The mammal community within the GKNP is diverse yet well-studied, with the most common mammal species being the impala and elephant (Sutherland et al 2018). All species can move freely between both reserves (Child et al 2013), allowing me to investigate if the community alters their behaviour according to differences in predation threat between reserves of high and low hunting pressure.

3.2.2 Experimental Design

I used a bi-factorial experiment to investigate the mammal community's antipredator responses to the presence of humans and hunting in two areas of contrasting hunting intensity. To determine if the mammal community adjusts their antipredator response according to hunting intensity, I monitored and manipulated the behaviours exhibited by the community in two adjacent reserves: one with a high intensity of hunting and one with very minimal hunting. I conducted manipulations with an Automated

Behavioural Response (ABR) system, comprised of a motion-activated camera and a speaker (Suraci et al 2017). I exposed the community to playbacks of hunting sounds (gunshots and dog vocalizations), human vocalizations (conversations), lion vocalizations, and the negative control of birdsongs at set intervals (details below). I included lion vocalizations as a basis to gauge responses to humans, as lions are the top non-human predators and have been previously found to invoke the most fear this mammal community (Rigoudy et al, in review). Since the ABR system includes both playback treatments and controls at each site, each site represents a replicate of the same experiment (Suraci et al 2017), providing large sample sizes (N > 50) of most species in the community. I scored behaviours of individuals captured by the ABRs before and after the initiation of the playback. I recorded whether individuals fled after the playback, as fleeing is the most unambiguous measure of fear (Stankowich & Blumstein 2005), as well as vigilance behaviours in species groups that did not flee more than 20% of the time. I compared fleeing and vigilance responses across playback treatments, across reserves, and across species within the community.

3.2.3 Automated Behavioural Response (ABR) System

Dr. Zanette and Dr. Clinchy deployed 21 ABRs across 11 sites in Klaserie and 10 sites in Thornybush for 49 consecutive 24-hour periods (Figure 3.1). At each site, they attached a camera trap to a tree 2m above ground and strapped the speaker 0.5m above the camera, ensuring a 100% detection rate at 8m directly in front of the camera with an overall detection range of the camera's motion sensor as 15m in front of the camera. At all sites, the ABRs were facing watering holes (dams), as water is a limiting resource during the dry season in South Africa and therefore acts as a natural “bait” to attract predators and prey alike in front of the ABRs (de Boer et al 2010). Following protocol from previous ABR experiments (Smith et al 2017; Suraci et al 2017), They initiated recording once motion was detected and broadcasted a 10s playback after a 3s delay. They recorded 30s videos during daytime while videos at night were 20s in length, as video length was restricted by the camera’s design. They programmed the ABRs with a minimum of 9 exemplars of each of the five playback treatments: human speech (14), dog vocalizations (11), gunshots (11), lion vocalizations (9), and birdsong (24). They included three audio variations within the birdsong playback treatment to match natural presence in the environment: African hoopoe (*Upupa africana*) for daytime, Pearl-spotted owlet (*Glaucidium perlatum*) for dawn and dusk, and African wood owl (*Strix woodfordii*) for nighttime, as well as four languages of human speech to represent the most common languages spoken in the GKNP: English, Northern Sotho, Afrikaans, and Tsonga. They standardized the occurrence of each playback treatment using two playlists, such that treatments played for 15 minute blocks and exemplars were randomized within each block (Appendix B). All playbacks were broadcasted at 80db at 1m away from the camera.

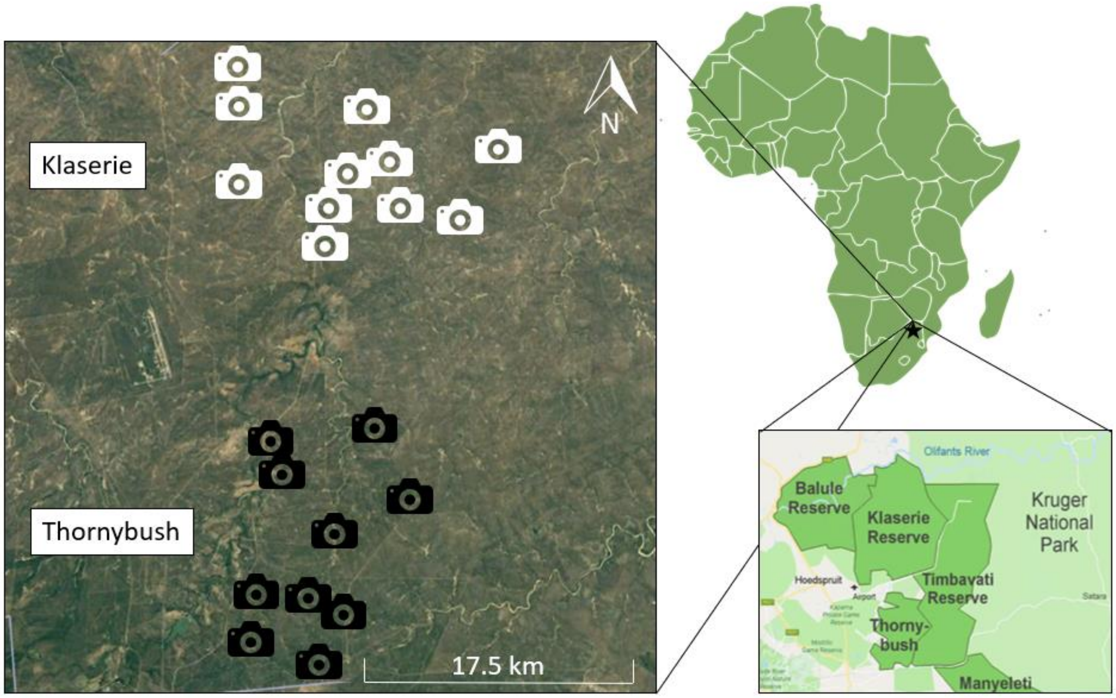

Figure 3.1: Placement of 21 ABRs in Klaserie and Thornybush reserves, South Africa.

3.2.4 Classification & Scoring of Behaviour

Over 49 days, my manipulation generated 15,425 videos of 30 South African mammals responding to my auditory stimuli. For each video, I recorded species, date, time of day, reserve, site, playback treatment, and exposure type as either first or repeat. I conservatively classified videos as first exposure when >60 minutes have passed from the last video with the same species present at the same site broadcasting the same playback treatment (Suraci et al 2017; Chandler et al 2018). Overall, I classified 3,989 videos of 30 mammal species as first exposure videos (Appendix B), of which 3,931 were categorized into species groups for analysis. I classified 18 species groups once carnivores were combined and bushbuck (*Tragelaphus sylvaticus*) (N = 8), porcupines (*Hystrix* *africaeaustralis*) (N = 4), chacma baboons (*Papio ursinus*) (N = 21), and vervet monkeys (*Chlorocebus pygerythrus*) (N = 25) were removed due to low sample sizes. My community dataset consisted of 4 large carnivores (≥ 15 kg), 8 mesocarnivores (< 15 kg), 10 herbivores (≤ 1000 kg), and 4 megaherbivores.

I recorded behaviours of the closest five individuals to the camera at each frame (0.03s) of each video using a computer coding software (*solomon.andraspeter.com*). I recorded whether the subjects *Fled* after the playback as a behavioural measure of fear (Stankowich & Blumstein 2005). Additionally, for individuals that did not flee, I recorded whether the subjects *Looked* at the camera after the playback as a measure of vigilance. Performing fleeing and vigilance behaviours result in a costly trade-off to an individual as it can limit foraging opportunities (Lima & Dill 1990; Clinchy et al 2016; Suraci et al 2019a). I scored additional movement and attention behaviours of these five individuals throughout each video using behaviour descriptions used in previous studies (Appendix E): head up, head down, stand, and walk.

3.2.5 Additional Ecological Variables

I collected additional ecological variables that may influence animal behaviour to explore if any other variables were important predictors for fleeing behaviour in my experimental design. For each study species, I recorded herbivory, trophic level, and average body size (as a proxy for home range size (Lindstedt et al 1986)); for each video, I recorded herd size, presence of offspring, and time of day; for each camera site, I recorded vegetation cover, large carnivore presence, human presence, and water availability; and for each individual, I recorded sex and age when possible (Appendix F). For vegetation cover, I calculated the total percentage of land covered by trees, bushes, or shrubs immediately around each camera site as well as in the surrounding area of the dam using Google Earth. To calculate large carnivore presence, I averaged the number of days that hyenas, leopards, lions, and wild dogs were captured by my ABRs for each camera site by total days that cameras were functional. Lastly, I identified sexes and ages of my mammal subjects using the "Mammals of Africa" encyclopedia by Kingdon et al (2013a); however, I did not include these data in statistical analyses as they are individual-based data that could not be averaged to produce one informative data point per video. Instead, sex and age data were used for collaborating projects.

3.2.6 Statistical Analyses

I evaluated the antipredator responses of the community to human-related playbacks in two ways: 1) I compared the reactions to the playback treatments for the community as a whole; and 2) I compared the reactions to the playback treatments for each species group in the community separately.

I first examined antipredator responses as either fleeing or not fleeing after playbacks, then examined vigilance responses of videos where subjects did not flee for species groups in which fleeing occurred less than 20% of the time (using median value of closest 5 individuals). I developed separate generalized linear models (glms) with binomial distributions (logit link) to assess *Fled* and *Looked* as binary response variables. I evaluated categorical responses with a Wald test ($\alpha = 0.05$) and examination of standard error (SE) of beta estimates. For community-level analyses of *Fled*, I included camera site and species group as random intercepts in my initial models, and then additionally included species group as a random slope to determine response differences to playback treatments across species groups. For analyses of *Looked,* I included species group as a random intercept.

I determined if the community were more likely to flee or exhibit vigilance after each human-related playback by modeling *Fled* and *Looked* separately with the fixed effect *Treatment* with negative control of birdsong as the reference category. I reported likelihoods of fleeing and vigilance in comparison to birdsong with odds ratios, meanwhile I reported absolute means percentages of fleeing behaviour and vigilance using pairwise contrasts. Next, I evaluated variation in responses between species by comparing all species groups. To test whether responses differed between hunting intensities, I compared *Fled* and *Looked* responses to human-related playbacks in Klaserie to *Fled* and *Looked* responses in Thornybush. To determine if the community's responses varied by specific playback treatments between high hunting intensity and low hunting intensity sites, I compared *Fled* and *Looked* responses in Klaserie with birdsong to 1) birdsong in Thornybush, 2) dog vocalizations in Klaserie, 3) dog vocalizations in Thornybush, 4) gunshots in Klaserie, 5) gunshots in Thornybush, 6) lion vocalizations in Klaserie, 7) lion vocalizations in Thornybush, 8) human speech in Klaserie, and 9) human speech in Thornybush. I evaluated the categorical responses with a Wald test (α = 0.05) and examination of standard error of beta estimates. I performed all glms using IBM SPSS (2020).

I used a classification tree analysis to predict fleeing behaviour from my ecological data (Breiman et al 1984). I chose this method of classification as trees are highly suited for categorical and complex ecological data and are more effective in finding meaningful patterns from data compared to most other exploratory and statistical modeling techniques (De'ath & Fabricius 2000). The tree grows recursively from the complete dataset to nodes of homogeneous subsets of data (Scull et al 2005). I used an Exhaustive Chi-squared Automatic Interaction Detector as my growing algorithm since my dependent variable of fleeing was categorical (Kass 1980; TIBCO 2020). This algorithm cycles through predictor variables by computing Chi-square tests and splitting the data by the predictor variable with the smallest Bonferroni-adjusted p-value (must be < 0.05); this procedure repeats for up to 3 maximum levels of nodes or until no further splits can be performed and results in only two categories for each predictor (TIBCO 2020). I used cross-validation with 10 sample folds to validate the model, as this technique makes use of all of the data in the dataset, minimizes noise, and allows for random subsampling (Bishop 2006).

3.3 Results

3.3.1 Fleeing Response of Community to Human-related Vocalizations

Playback treatment significantly affected fleeing behaviour in the mammal community ($F_{4,3921} = 16.32$, $p < 0.001$), with all predator treatments eliciting a significantly stronger fear response than bird vocalizations. Relative to birds, the community was 3.23 times more likely to flee to dogs ($\beta = 1.17$, SE = 0.24, $p < 0.001$), 4.00 times more likely to flee to gunshots ($\beta = 1.39$, SE = 0.24, $p < 0.001$), 4.47 times more likely to flee to lions

($\beta = 1.50$, SE = 0.26, $p < 0.001$), and 9.18 times more likely to flee to humans ($\beta = 2.22$, SE = 0.36, $p < 0.001$; Figure 3.2). My findings demonstrate that the community were *twice* as likely to flee to human vocalizations than to lion vocalizations.

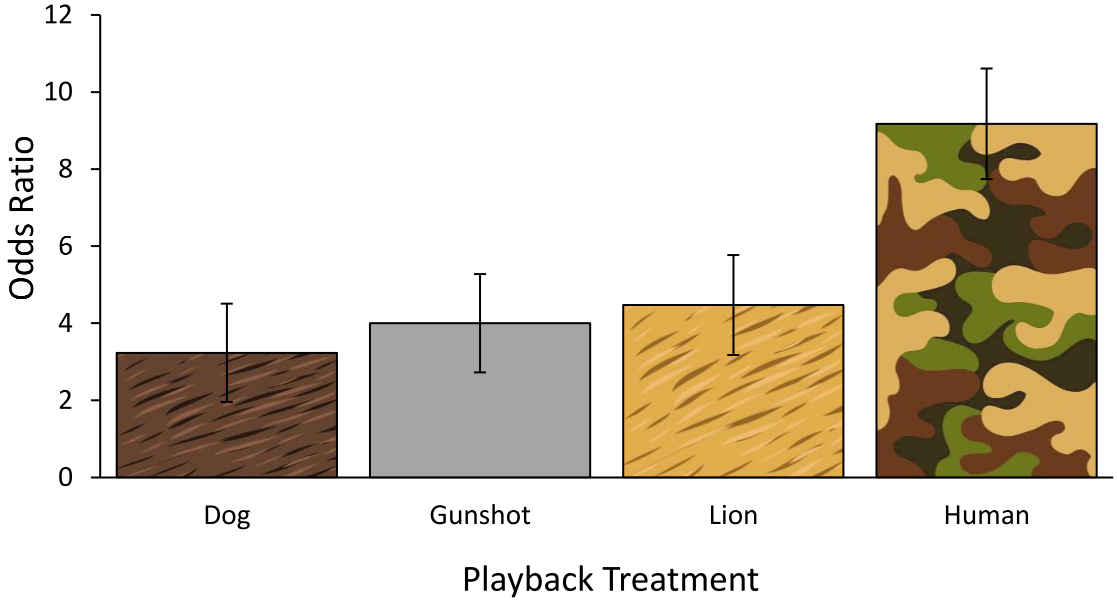

Figure 3.2: Odds ratios ± SE of fleeing behaviour for predator treatments relative to control treatment of birdsong in a South African mammal community. N = 3931.

Across all five treatments, reserve type did not significantly affect fleeing behaviour ($F_{1,142} = 0.02$, $p = 0.88$); however, relative to birdsong, the community was significantly *more likely* to flee in the hunting reserve than the non-hunting reserve (OR = 1.93, SE = 1.29, $p < 0.01$; Figure 3.3). Therefore, the community is more likely to exhibit fearfulness where they are more likely to be hunted. In both reserves, humans elicited the strongest fear response, followed by lions and then hunting sounds. Relative to birdsong, the community was significantly more likely to flee to lions (OR = 1.82, SE = 1.31, $p = 0.03$) and dogs (OR = 1.88, SE = 1.31, $p = 0.02$) in the hunting reserve than the non-hunting reserve. The contrast in likelihood of fleeing between the reserves was particularly great in response to the human treatment (OR = 2.77, SE = 1.28, $p < 0.001$), resulting in a significant interaction of playback treatment and reserve type ($F_{4,3921} = 5.64$, $p < 0.001$; Figure 3.4). Furthermore, the community were more likely to flee in response to human vocalizations than lion vocalizations in the hunting reserve (OR = 2.52, SE = 1.26, $p < 0.001$), than the non-hunting reserve (OR = 1.67, SE = 1.24, $p = 0.02$; $t = 2.17$, $p = 0.03$). This indicates that humans elicit an exceptionally greater fear response where hunting occurs compared to where hunting is prohibited.

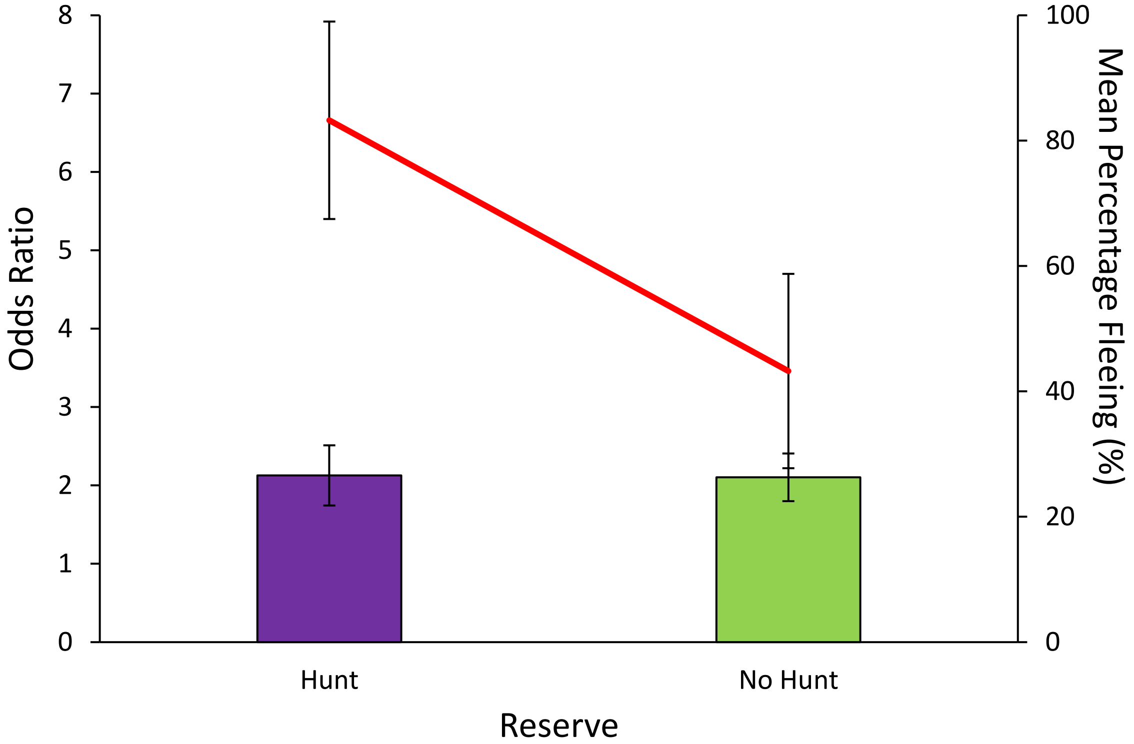

Figure 3.3: Odds ratios ± SE of predator treatments relative to control treatment of birdsong between hunting and non-hunting reserves (line) and mean percentage fleeing (%) ± SE of all treatments between hunting and non-hunting reserves (bar).

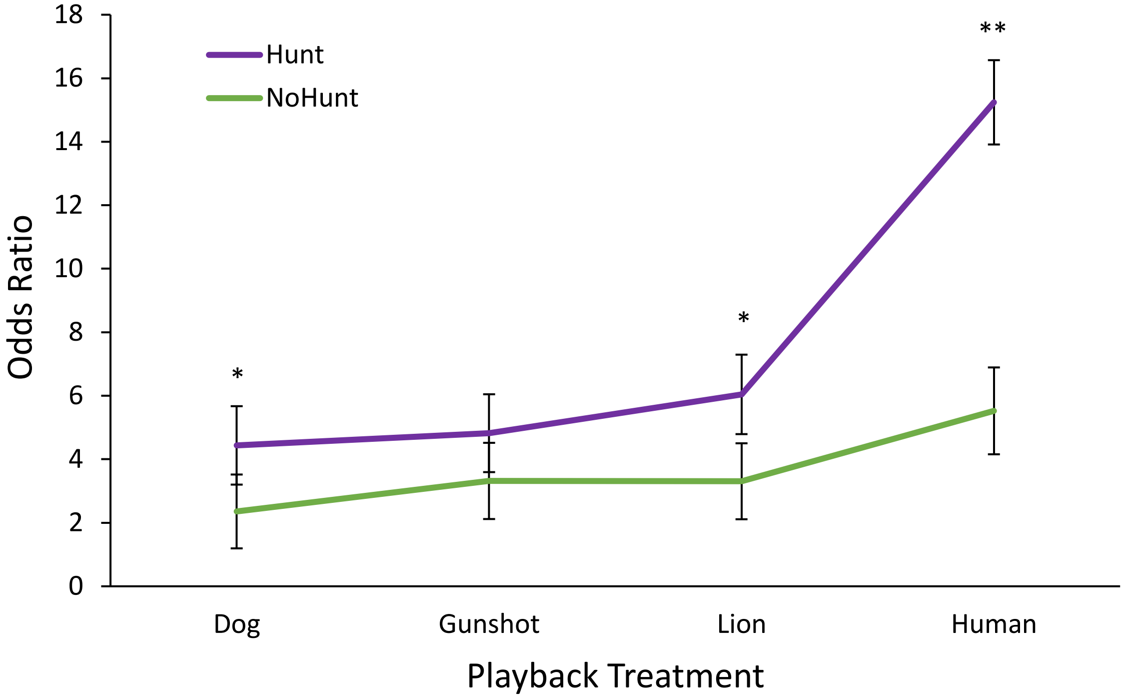

Figure 3.4: Odds ratios ± SE of predator treatments relative to control treatment of birdsong in a South African mammal community between a hunting (N = 1783) and non-hunting reserve (N = 2148). Asterisks indicate significance at the 0.05 level (*) and 0.001 level (**).

3.3.2 Effect of Species on Fleeing Response of Community

The random intercept of species group was significant (Z = 2.57, p = 0.01), revealing that some species ran more than others to my playback treatments. For example, some species were very responsive, such as the warthog (*Phacochoerus africanus*) which fled 60.4% of the time, while buffalo (*Syncerus caffer*), duikers (*Sylvicapra grimmia*), elephants, hippopotamuses (*Hippopotamus amphibius*), lions, wild dogs, and leopards fled less than 20% of the time (Figure 3.5). For classification purposes, the latter group were denoted as “non-runners”. When species groups as a random slope across treatments was investigated, the effect was also significant (Z = 2.39, p = 0.02), indicating that there were some species in the community that do not demonstrate the same hierarchy of fleeing responses across predator treatments as at the community-level. Hence, species-level analyses were required to investigate how the relationship of species group and treatment affects fleeing behaviour further.

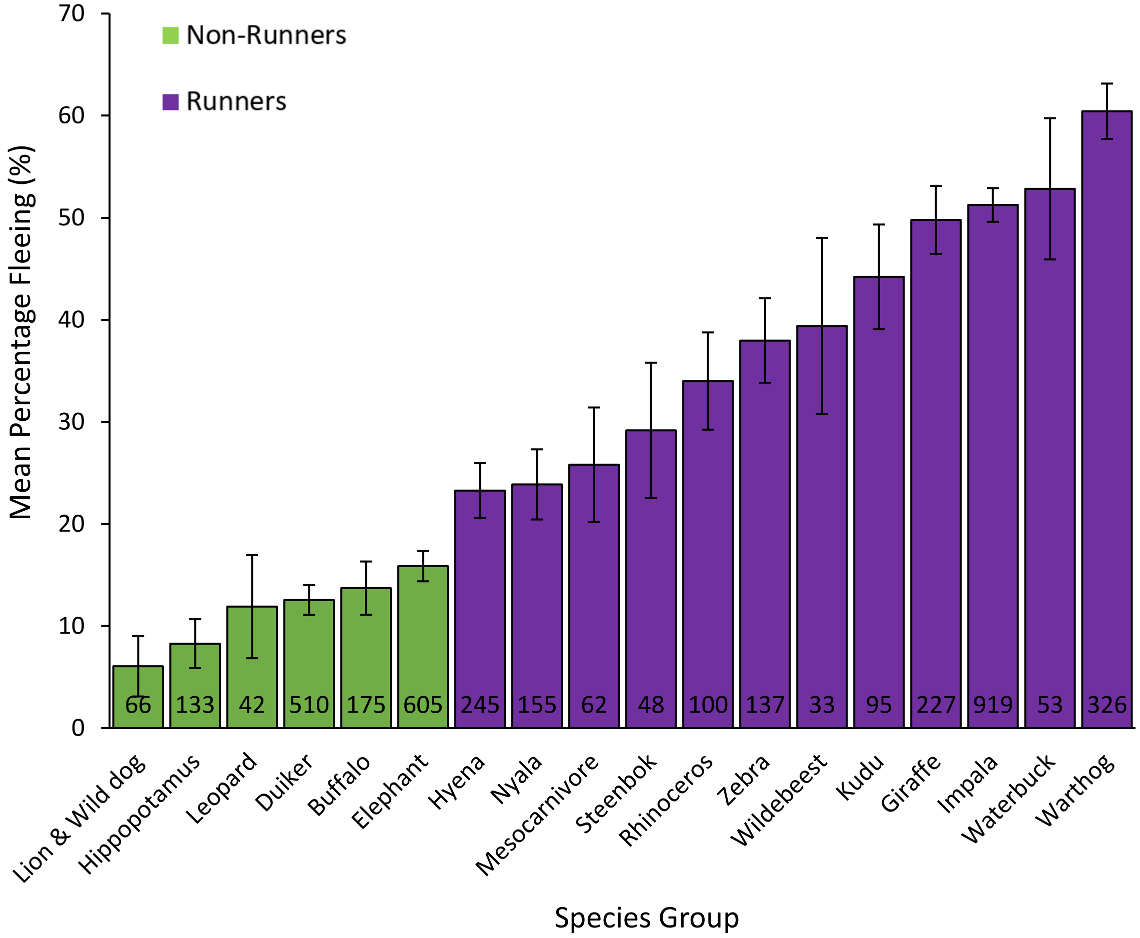

Figure 3.5: Mean percentage of fleeing (%) ± SE of runners and non-runners (< 20%) in 18 South African mammal species groups to five playback treatments. N values are present in bars.

3.3.3 Fleeing Response of Species to Human-related Vocalizations

Species-level analyses confirm my findings at the community-level with the majority of the species (13/18) fleeing most to humans than any other predator treatment (Figure 3.6). Eight species groups fled significantly more to humans than the control treatment of birdsong (Figure 3.7), with waterbuck (*Kobus ellipsiprymnus*), wildebeest (*Connochaetes pygerythrus*), nyala (*Tragelaphus angasii*), elephants, lions, and wild dogs fleeing most to lions or to a hunting treatment. A significance in the random slope of playback treatment and species group in my model may be explained by different predators eliciting the most fleeing among different species. Furthermore, playback treatment significantly affected the fleeing behaviour of 7 of the 18 species groups (Table 3.1); however, effect sizes differ among species groups between responses to birds and humans as shown in Figure 3.6. Therefore, a significance in the random slope of playback treatment and species group may also be representative of this variation in effect sizes among species groups.

Additionally, reserve type was not a significant predictor for the majority of the community's species (16/18). Reserve significantly affected the fleeing behaviour of only 2 species groups, with hyenas fleeing more in the non-hunting reserve than the hunting reserve (W = 10.1, p = 0.002) and zebras (*Equus quagga*) fleeing more in the hunting reserve than the non-hunting reserve (W = 8.2, p = 0.004; Figure 3.6). However, it is worth noting that fleeing responses between reserves in wildebeest (p = 0.06) and giraffes (*Giraffa camelopardalis*) (0.05) trended towards significance and waterbuck were excluded as they were only present in one reserve.

Species	Wald's test	Df	P value
Impala (*Aepyceros melampus*)	128.42	4	<0.001*
Common warthog (*Phacochoerus africanus*)	40.00	4	<0.001*
Giraffe (*Giraffa camelopardalis*)	22.02	4	<0.001*
Plains zebra (*Equus quagga*)	15.31	4	0.004*
Greater kudu (*Tragelaphus strepsiceros*)	15.22	4	0.004*
Southern white rhinoceros (*Ceratotherium simum*)	13.43	4	0.01*
Spotted hyena (*Crocuta crocuta*)	12.22	4	0.02*
Blue wildebeest (*Connochaetes pygerythrus*)	6.48	4	0.17
African elephant (*Loxodonta africana*)	6.31	4	0.18
Common duiker (*Slyvicapra grimmia*)	5.06	4	0.28
Nyala (*Tragelaphus angasii*)	4.36	4	0.36
Hippopotamus (*Hippopotamus amphibius*)	3.80	4	0.43
African buffalo (*Syncerus caffer*)	3.46	4	0.48
Steenbok (*Raphicerus campestris*)	1.15	4	0.89
Mesocarnivore	1.14	4	0.89
Waterbuck (*Kobus ellipsiprymnus*)	1.10	4	0.90
Lion (*Panthera leo*) & African wild dog (*Lycaon pictus*)	0.57	4	0.97
Leopard (*Panthera pardus*)	0.00	4	1.00

Table 3.1: Wald’s test for playback treatment across reserves for 19 South African species.

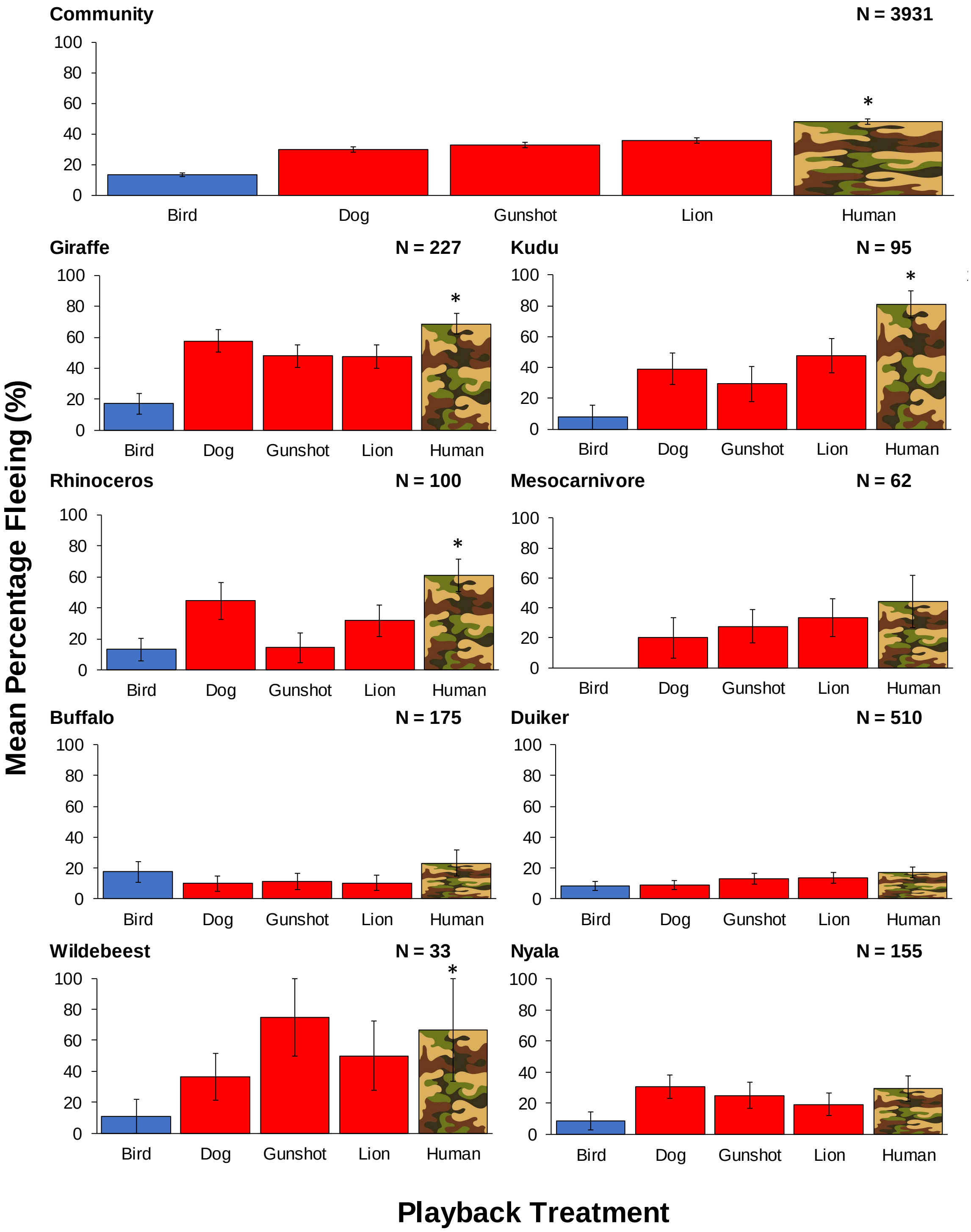

Figure 3.6: Mean percentage of fleeing (%) ± SE of 18 South African mammal species groups to five different playback treatments. Asterisks (*) denote significance of human treatment compared to negative control of birdsong at the 0.05 level.

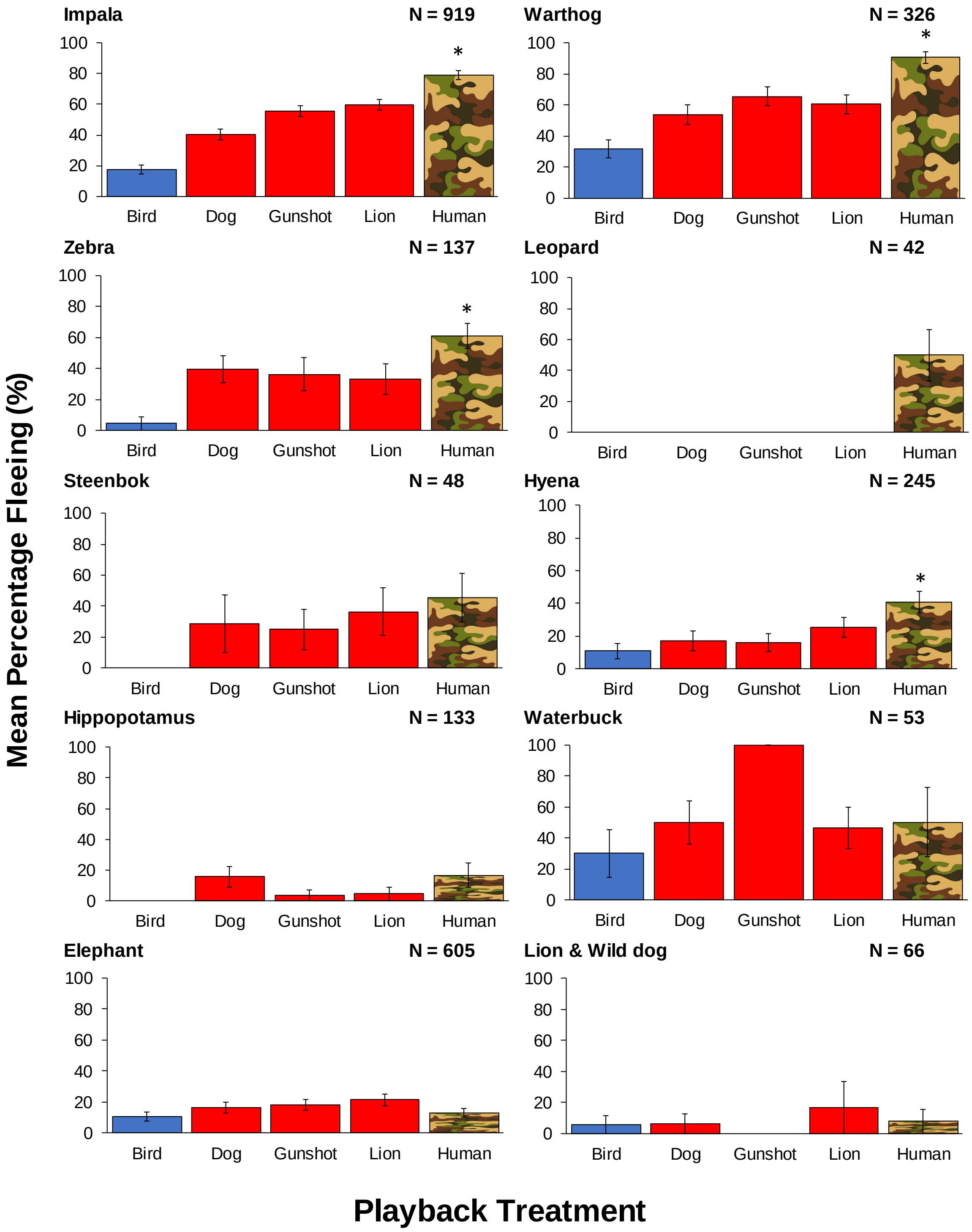

Figure 3.6 (continued): Mean percentage of fleeing (%) ± SE of 18 South African mammal species groups to five different playback treatments. Asterisks (*) denote significance of human treatment compared to negative control of birdsong at the 0.05 level.

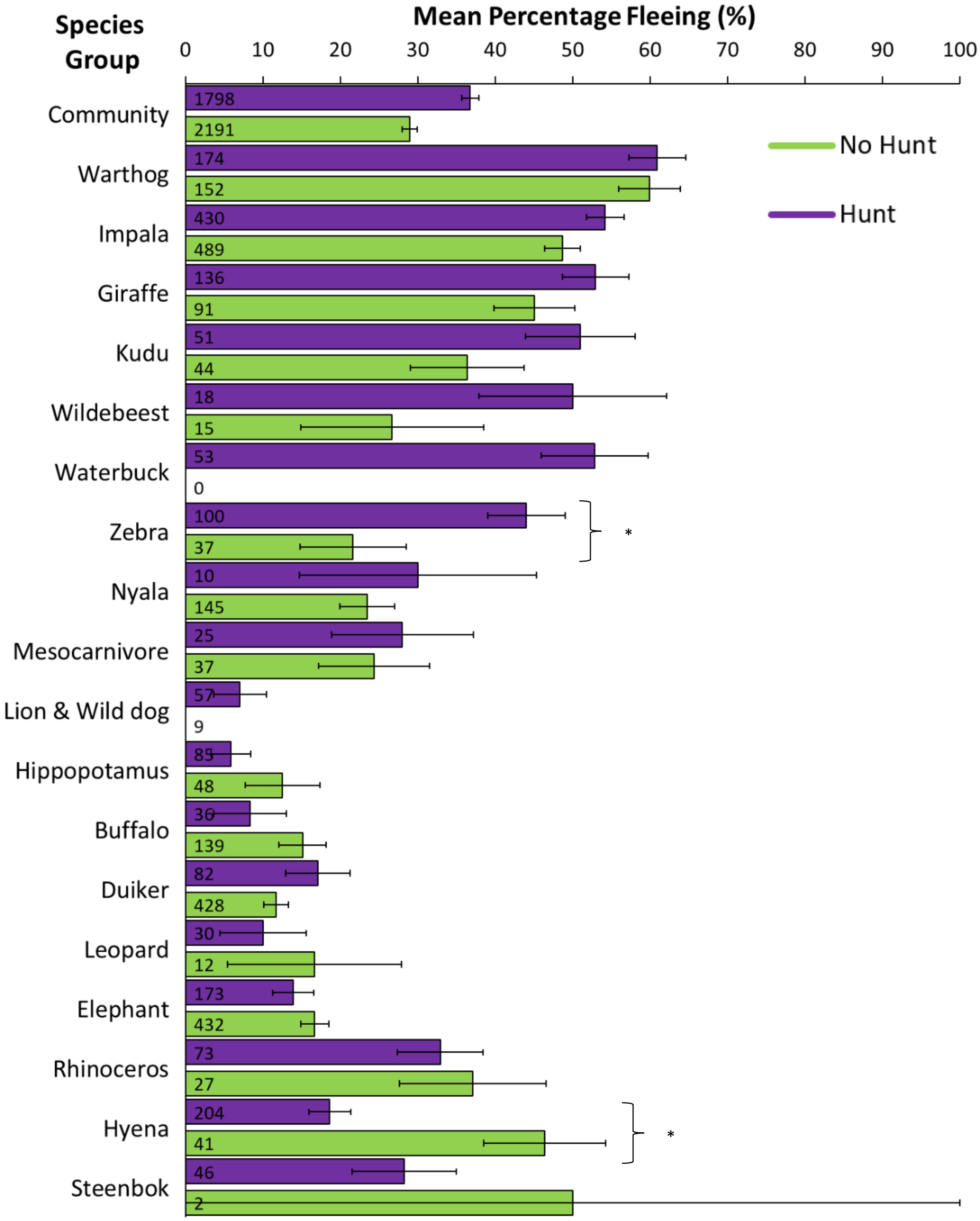

Figure 3.7: Mean percentage of fleeing (%) ± SE of 18 South African mammal species groups to five playback treatments between two reserves: one hunting and one non-hunting. Asterisks denote significant differences at the 0.05 level between reserves. N values are present in bars.

3.3.4 Effect of Ecological Variables on Fleeing Response of Community

My classification tree revealed that the most important factor for predicting fleeing response in the community is species group, with the community splitting into 5 nodes ($\chi^2 = 582.13$, df = 4, $p < 0.001$). These nodes ranged from my “non-runner” species, fleeing an average of only 13.3% of the time, to warthogs which fled 60.4% of the time (Figure 3.8).

The second most important factor to predicting fleeing in the majority (3/5) of the nodes was playback treatment, with individuals fleeing most to humans and least to birds (node 1: $\chi^2 = 181.22$, df = 3, $p < 0.001$; node 4: $\chi^2 = 33.66$, df = 2, $p < 0.001$; node 5: $\chi^2 = 47.63$, df = 2, $p < 0.001$; Appendix G). Nodes 2 and 3, which included the species that fled the least to my playback treatments (24.3% and 13.3% respectively), split by vegetation cover next; however, there was no observable linear pattern seen to describe this relationship of percentage fleeing and percentage vegetation cover. Tertiary-level predictors of fleeing behaviour included playback treatment, distance to the nearest building, abundance of nearby roads, time of day, and vegetation cover at camera sites (Appendix G). Overall, environmental variables had little effect on fleeing behaviour of the community as species group and playback treatment were the most important predictive factors for the majority of species.

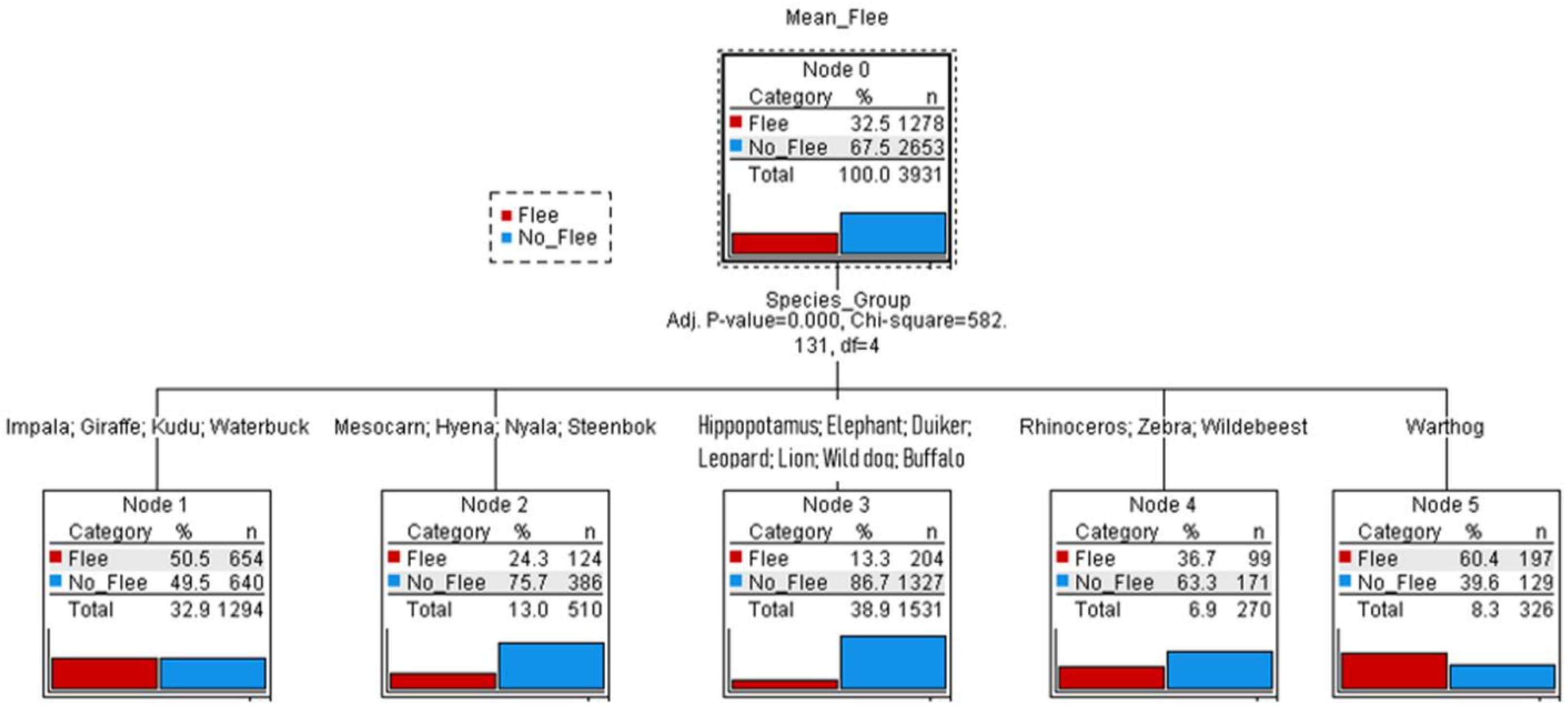

Figure 3.8: Classification tree of both experimental and environmental variables for South African mammal community binary fleeing response, N = 3931.

3.3.5 Vigilance of "Non-Runners" to Human-related Vocalizations

Playback treatment significantly affected the looking behaviour of the "non-runners" ($F_{4,1003}$ = 98.83, $p < 0.001$), with lion and human vocalizations eliciting a significantly stronger fear response than the negative control. Relative to birdsong, "non-runners" were 3.17 times more likely to look to lions ($\beta = 1.15$, SE = 0.51, $p < 0.001$) and 3.53 times more likely to look to humans ($\beta = 1.26$, SE = 0.53, $p < 0.001$; Figure 3.9). My findings demonstrate that "non-runners" were just as likely to look towards human voices as the positive control of lion vocalizations and were nearly twice as likely to look to human voices than to hunting sounds. Across treatments, reserve type did not significantly affect looking behaviour ($F_{1,1003}$ = 0.54, $p = 0.46$). Playback treatment and reserve type did not significantly interact ($F_{4,4}$ = 2.99, $p = 0.16$).

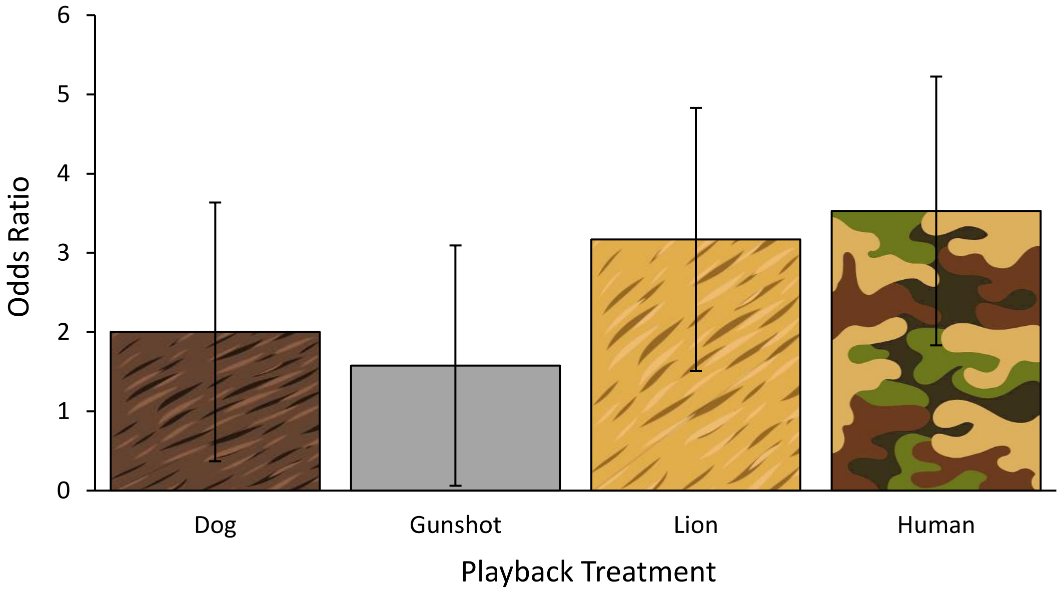

Figure 3.9: Odds ratios ± SE of looking behaviour for predator treatments relative to control treatment of birdsong of 6 "non-runners" in a South African mammal community. N = 1013.

3.4 Discussion

My fear manipulation demonstrated that the South African mammal community were most afraid of humans as they were *twice* as likely to flee to human vocalizations than to vocalizations of their non-human predator – the lion (Figure 3.2). A recent meta-analysis considers humans as highly lethal "super predators" due to our globally exploitative hunting of wildlife, killing almost two times more prey than all other terrestrial predators combined (Darimont et al 2015). My results suggest that consequently, the mammal community perceive humans as the most threatening and lethal predator in the Greater Kruger National Park (GKNP). Human vocalizations elicited the greatest fear response in both hunting and non-hunting reserves, followed by lion vocalizations, gunshots, and dog vocalizations, demonstrating a "hierarchy of fear" whereby greater perceived threats elicit greater fear responses in the community (Rigoudy et al, in review). Despite differences in humans' ecological role as a hunter in Klaserie or a tourist in Thornybush, human presence was perceived as exceedingly threatening, providing further evidence that humans' inordinate killing success rate influences the community's fear response (Darimont et al 2015). However, predator type and hunting intensity did interact, with the community nearly twice as likely to flee to dog and lion vocalizations and nearly three times as likely to flee to human vocalizations in the hunting than the non-hunting reserve (Figure 3.3). While lions hunt in both reserves, my data show that lions were nearly four times more populous in Klaserie (M = 4.3 lions/site/day) compared to Thornybush (M = 1.2 lions/site/day), likely indicating that more wildlife are killed by lions in Klaserie than Thornybush. Therefore, this interaction suggests the presence of a predator-induced “landscape of fear”, whereby lions and humans are more likely to elicit fear responses in the hunting reserve since they are perceived as a greater threat by wildlife in areas where their kill rates are higher (Lima & Dill 1990; Laundré et al 2010; Ciuti et al 2012). I further demonstrated that a fear of humans is pervasive across the entire community as the majority of species groups (13 of 18) within the community fled most to human vocalizations across reserves when analyzed independently (Figures 3.6 & 3.7). Six species groups in the community fled less than 20% of the time to all predator types including lion vocalizations (Figure 3.5); however, these “non-runners” were more likely to look towards the source of lion and human vocalizations than bird vocalizations (Figure 3.9), indicating that these species may initially display increased vigilance in response to predation threats to minimize fleeing from false alarms (Beauchamp & Ruxton 2007).

A handful of recent studies have investigated how human presence may affect mammal behaviour; however, my experiment provides novel experimental evidence of a fear of humans in a mammal community. Two meta-analyses have alluded to human-induced changes in movement (Tucker et al 2018) and nocturnality (Gaynor et al 2018) of mammals at the global scale. Tucker and colleagues (2018) determined that mammals residing in areas with a higher human footprint displayed reduced movements compared to those in areas of lower human footprint. Although, this relationship is most likely attributed to human infrastructure creating movement barriers, croplands providing high abundance of food resources, and the exclusion of species with long-range movements, as human footprint was mainly categorized by the presence of agriculture and infrastructure rather than human presence. In contrast, Gaynor and colleagues (2018) attributed fear of humans as the likely cause of increased nocturnality, with mammals becoming more active at night to avoid human presence during the day in areas of high human disturbance. Human disturbance is a broad term that encompasses human presence, infrastructure, and hunting, resulting in uncertainty of which mechanism is causing the change in behaviour. Three experimental studies to date have investigated the direct effect of human presence on mammal behaviour using auditory playbacks of human vocalizations (Clinchy et al 2016; Smith et al 2017; Suraci et al 2019a). These studies have demonstrated a fear of human presence in five different persecuted medium- and large-carnivore species. I show consistent results, as the majority of species in the community fled most to human vocalizations across both reserves. Therefore, I have provided experimental evidence that hunted as well as non-hunted mammal species fear the human "super-predator" more than their natural predator. A pronounced fear response of non-hunted species towards human presence supports that these mammals do not fully rely on the actuarial risk of being preyed upon, but also consider the danger that humans pose in their inordinately high hunting success rate (Creel et al 2019; Palmer & Packer 2021).

Assessing the extent by which prey species fear their predators is crucial to understanding how population sizes and behaviours are regulated within a community (Zanette & Clinchy 2020), as heightened fear responses can result in detrimental cascading effects of reduced foraging, altered movement patterns, and reduced fecundity for populations within the community (Preisser & Bolnick 2008; Suraci et al 2016; Suraci et al 2019a; Atkins et al 2019). My results demonstrated that human vocalizations elicited a fleeing response twice that of lion vocalizations in the community (Figure 3.2).

Importantly, a strong fear of humans was evident in both the hunting and the non-hunting reserves, suggesting that humans were most feared in both reserves regardless of the difference in hunting intensity. Establishing whether hunting intensity influences fear of humans in wildlife provides further insight into whether wildlife can distinguish hunters from non-hunters (McComb et al 2014) or instead generalize all humans as lethal predators (Darimont et al 2015). Nyahongo (2008) experimentally tested differences in fleeing behaviour of wildlife in response to tourists in a national park and non-tourists at the edge of the park, where (illegal) hunting occurs, and found that flight initiation distances (FID) of five ungulates species were greater when individuals were approached outside the park compared to inside the park. Similarly, I found that the mammal community in the GKNP were more likely to flee in response to human vocalizations in the hunting reserve than non-hunting reserve (Figure 3.3), supporting past literature that report African mammals displaying greater FIDs (Croes et al 2007; Tarakini et al 2014; Muposhi et al 2016) or exhibiting more frequent fleeing and vigilance (Setsaas et al 2007; Croes et al 2007; Crosmary et al 2012a; Kiffner et al 2014) in hunting areas compared to national parks and other non-hunting areas. However, unlike Nyahongo's (2008) study, I also compared these fear responses to a natural predator in both reserves to determine if still unclear if the less threatening tourist still elicits more fear than a non-human predator. The community fled more to lions in the hunting reserve than the non-hunting reserve, which is most likely due to a higher abundance of lions present in Klaserie than Thornybush; however, despite this difference, the effect sizes between the responses to humans compared to lions were still greater in the hunting reserve than the non-hunting reserve. I demonstrated that in the hunting reserve, where the community may perceive humans as highly threatening and lethal hunters, mammals were 2.5 times more likely to respond to human vocalizations than lion vocalizations. Meanwhile in the non-hunting reserve, where the community may perceive humans as ecotourists, of whom are still lethal but less likely to kill and thus less threatening, the community were only 1.7 times more likely to response to human vocalizations than lion vocalizations (Figure 3.4).

Additionally, hunting sounds were perceived as a predation threat by the community, eliciting a fleeing response that was three-to-four times that of bird vocalizations (Figure 3.2). Despite increased fear responses to the perceived presence of nearby hunters in Klaserie, the community were less than half as likely to respond to actual cues of ongoing hunting. Furthermore, when comparing responses to gunshots and dog vocalizations, the community were more likely to flee to dog vocalizations in the hunting reserve than the non-hunting reserve, whereas the likelihood of fleeing to gunshots did not differ between reserves (Figure 3.4). The community have learned that human presence is strongly associated with mortality; however, a gunshot is an indistinct loud noise that can only be associated to human-induced mortality by nearby conspecifics of a targeted individual (Olsson & Phelps 2007; Sih et al 2010). Frequent occurrences of both lethal (gunshots) and benign (i.e., thunder) loud explosive sounds have been shown to be generalized in mammals (Blackwell et al 2013), thus the community may be less likely to respond to gunshots than human presence to avoid regularly responding to false positives (Beauchamp & Ruxton 2007). Therefore, the community as a whole may not recognize that gunshots are associated with humans' superior kill rates, which may explain similar fear responses between reserves (Laundré et al 2010; Ciuti et al 2012). Unlike gunshots, the barking of domestic dogs is easily distinguishable from the squeaky yips of African wild dogs and the cackles of hyenas. The presence of domestic dogs have been previously shown to elicit strong behavioural effects in birds and mammals such as increased vigilance (Randler 2006; Gingold et al 2008; Lenth et al 2008), reduced feeding (Mahlaba et al 2017), increased fleeing (Sweeney et al 1971; Miller et al 2001; Gingold et al 2008; Sastre et al 2009; Fernandez-Juricic & Telleria 2010) and reduced movement activity (Lenth et al 2008) in addition to habitat displacement (Sweeney et al 1971; Banks & Bryant 2007; Lenth et al 2008; Silva-Rodriguez & Sieving 2012; Parsons et al 2016); however, in the few studies that have compared the behavioural effects of dog versus human presence, humans elicited a stronger response in wildlife (Miller et al 2001; Sastre et al 2009; Fernandez-Juricic & Telleria 2010; Parsons et al 2016). My community also responded stronger to perceived human presence than dog presence, indicating that the community may recognize that the killing success rate of humans with guns (72%) is much greater than that of hunting dogs (56%; Rogan et al 2017). Given that dogs in Thornybush do not hunt, the community may not associate dogs with humans in the non-hunting reserve (Suraci et al 2019b). Consequently, the community may elicit a lesser fear response in Thornybush than Klaserie to match the lower (or non-existent) kill rates of family pets compared to hunting dogs.

Lastly, seven species in the community did not flee more than 20% of the time to humans or lion vocalizations, but instead displayed vigilance in response to my playbacks (Figure 3.5). These species included lions, wild dogs, mesocarnivores, leopards, duikers, elephants, and hippopotamuses. Despite exhibiting a different fear behaviour, "non-runners" responded with a hierarchy congruent to fleeing in which most looked to human vocalizations, followed by lion vocalizations and hunting sounds (Figure 3.9). Freezing rather than fleeing may be a more successful strategy for species active at night, as avoiding detection of predators in low light conditions and dense vegetation requires less energy than fleeing away and provides more time to assess the threat (Lima & Dill 1990; Ydenberg & Dill 1986; Beauchamp & Ruxton 2007). This may be especially true for the meso- and large carnivores in the community as these species are primarily nocturnal and prefer to avoid detection when hunting (Kingdon 2013b, p. 33, 41, 121, 151, 162, 234, 258, 344, 450). Unlike most other carnivores in my community, hyenas were an exception as some individuals fled from my playbacks while others displayed vigilance. This variation in the display of fear behaviours has been previously studied, where Watts and colleagues (2010) observed considerable interindividual variation in vigilance behaviours of hyenas in response to lion vocalizations. It is hypothesized that this sizable variation may be due to hyenas' unique scavenging behaviour, as they perceive other predators as both a threat and a source of food. Large and heavy megaherbivores may also prefer to display vigilant behaviours than fleeing as species such as elephants, hippopotamuses, and rhinoceroses (*Ceratotherium simum*) have no natural predators once they reach their adult size (Hayward & Kerley 2005). However, rhinoceroses have poor vision and are unable to identify motionless threats more than 15 meters away (Kingdon 2013b, p. 449), thus fleeing is likely a more successful strategy for avoiding predation of their offspring than attempting to detect the source of the threat. Lastly, duikers are known to initially freeze when threatened and then sprint away and dive into thick cover, earning their name of “duiker” which translates to “diver” in Afrikaans (Kranz & Ralls 1984; Barnes et al 2002). Given that my videos were only 20-30 seconds long, it is possible that the characteristic diving behaviour of these antelopes sometimes occurred only after the ABR had stopped filming.

In conclusion, my study provides experimental evidence that humans elicit a greater fear response than lions in a South African mammal community, demonstrating that humans’ pervasive presence and exploitative hunting has altered wildlife communities to fear humans as a “super-predator”.

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Chapter 4

4 Discussion

In this thesis, I explored the effects of human presence and hunting on the fear behaviour of African mammals. In Chapter 1, I reviewed the overexploitation of wildlife by humans and the effects that hunting and human presence can have on wildlife behaviour. I described various measures that are used to quantify human-induced behavioural changes in mammals, highlighting fleeing behaviour, vigilance, and foraging behaviour. In Chapter 2, I collected, assessed, and reviewed the current literature to identify what is currently known about how human disturbance affects mammal behaviour in Africa. I focused on several factors which may have influenced the results of these studies, including study species, experimental design, methodology for collecting behavioural data, behaviour, and type of human disturbance that was investigated by the authors. In Chapter 3, I conducted an experiment in South Africa's Greater Kruger National Park (GKNP) to investigate if human presence and hunting affected the fleeing behaviour and vigilance behaviour of 30 mammal species within a community. I used a combination of cameras, motion sensors, and playback speakers to manipulate the community's behaviour in response to several human-related and non-human-related auditory playbacks. I compared behaviour between these auditory treatments as well as between areas of high and low hunting intensity. Additionally, I determined if any external ecological variables explained or influenced these mammal's behavioural responses to my stimuli. In this final chapter, I will summarize how my work provides insight into the pervasive impacts of human disturbance on wildlife, as well as I explore potential future directions in research to support suitable management strategies to better conserve these species.

4.1 A Fear of Humans can Pervade Entire Communities

My results from Chapter 2 bring us closer to understanding the true extent of how human disturbance can impact wildlife communities. The majority of primary articles that investigated the effects of human disturbance on African mammal behaviour reported that humans negatively altered multiple types of behaviour including fleeing, vigilance, movement, and foraging. Therefore, it is evident that humans negatively impact wildlife behaviour on the global scale, outside of Antarctica (Coetzee & Chown 2016), as this result has been reported in other meta-analyses and reviews that focused on American, Eurasian, and/or Australian fauna (such as Boyle & Samson 1985; Stankowich 2008; Vistnes & Nellemann 2008; Steven et al 2011; Lowry et al 2012; Weston et al 2012). When comparing between different forms of disturbance, tourism and general presence of humans elicited the strongest negative behavioural responses in African mammals. This result suggests that mere human presence is the most powerful human disturbance in terms of altering wildlife behaviour, most likely due to the perception of humans as ultra-lethal "super-predators" (Darimont et al 2015; Zanette & Clinchy 2020). Studies from non-African countries also describe prominent behavioural changes in mammals in response to human presence, as recreational activities such as hiking and biking have been observed to alter movement patterns of nearby ungulates, bears, and cougars (Taylor & Knight 2003; Stankowich 2008; Smith et al 2012; Ordiz et al 2013, 2019; Morrison et al 2014).

In Chapter 3, experimentally testing for the effects of perceived human presence and hunting in an African mammal community demonstrated that human vocalizations elicit the strongest fear responses, as the community were more likely to flee to human vocalizations than to gunshots or the vocalizations of lions (*Panthera leo*) or dogs (*Canis familiaris*). This result suggests that the community perceive humans as a predation threat (Murphy 1978; Lima & Dill 1990) and is consistent with past studies that have demonstrated prominent behavioural changes in mammals when exposed to human vocalizations (Clinchy et al 2016; Smith et al 2017; Suraci et al 2019). A fear of humans across the majority of species within the community corroborates observational studies that have suggested that the negative impacts of human presence can pervade at scales much larger than that of a targeted individual or group (Gaynor et al 2018; Tucker et al 2018). Hunting intensity minimally affected fear behaviour in the community; however, the community were more likely to flee to human vocalizations where hunting is prominent compared to an area where hunting is limited to culling. This finding suggests that while the community may not perceive the hunting reserve as a higher risk area than the non-hunting reserve in general, the community may recognize that humans kill more frequently in the hunting reserve and adjust their behaviour in response to human presence.

4.2 Implications for Conservation

Understanding the extent to which wildlife fear humans is crucial to maintaining ethical management of wildlife within the hunting and tourism industries. Zanette and colleagues (2011) experimentally demonstrated the how fear of a predator can elicit a reduction in foraging in fearful individuals, lowering their fecundity as well as the survivorship of their offspring. Given that the overkilling of wildlife by humans is considered a prominent threat to hundreds of mammal species (Rosser & Mainka 2002; Ripple et al 2016), a pervasive fear of humans may indirectly contribute to the further population declines of these species by affecting the individuals that escaped from the hunter. In addition to Southeast Asia, Africa hosts the most species threatened by hunting (Ripple et al 2016) due to the continent's large dependence on the wildlife tourism industry to generate revenue (Lindsey et al 2007; WTTC 2019; UN 2021) as well as high rates of illegal hunting for ivory and other animal products (Rogan et al 2017). Thus, gaining a better understanding of how humans both directly and indirectly affect wildlife populations may help biologists determine the true risks associated with threatened species and provide more evidence to policymakers to implement further regulations on hunting.

Furthermore, determining the magnitude of a community's fear behavioural response to humans can help provide land managers with information of where hunting occurs most. Previous research has demonstrated that hunted populations display a significant difference in behaviour than non-hunted populations (Caro 1999; Novack et al 2005; Shannon et al 2013; Zanon-Martinez et al 2016). In Chapter 3, I quantified behavioural responses between high and low hunting intensity in multiple mammal species and demonstrated a difference in the likelihood of exhibiting fleeing behaviour. By collecting and comparing additional behavioural data from other areas of varying hunting intensity, a scaled guideline can be formulated to indicate the amount of hunting that occurs in an area when given the fear responses of its residents. Accordingly, these data can be collected in areas where illegal hunting intensity is unknown and provide land managers with a reliable estimate of hunting intensity, allowing for better informed delegation of conservation and management efforts.

Lastly, understanding the effect that human presence can have on wildlife behaviour is important to reduce any harm or stress in wildlife caused by tourists and tourism activities. In my study, the majority of South African mammals (many of which attract tourists) were fearful of human voices when humans were perceived to be within 15 meters. This finding suggests that a buffer zones (of much greater than 15 meters) should be implemented between tourists and wildlife at all times in the Greater Kruger National Park to reduce the frequency of fear behaviours elicited by these mammals (Rodgers & Smith 1997). Protocols to reduce human-wildlife conflicts are especially important in national parks, as animals are often contained within the park's boundaries and are limited in spatial opportunities to avoid humans throughout the day (McInturff et al 2020).

4.3 Future Directions

My meta-analysis revealed that the majority of literature that investigates the effects of human disturbance on mammal behaviour are focused on North American or European species, similar to findings of other meta-analyses on wildlife ecology (Martin et al 2012; Nuñez et al 2019; Montgomery et al 2020; Christie et al 2020), as only 31 studies from my initial collection of 2,563 papers when location was not yet filtered. Thirty-one studies do not suffice in providing enough information to understand how human disturbance affects the behaviour of an entire continent's endemic mammal species, thus further research is needed. More specifically, I found that biases occur within the studies that have investigated this relationship in Africa, with some factors being very under-represented. Areas within the study of human disturbance on African behaviour that require further investigation include: 1) studies in Central Africa and/or West Africa; 2) studies on species that do not fall under the categorization of ungulates, carnivores, elephants (*Loxodonta africana*), or primates (such as rodents or bats); 3) studies that investigate the effects of agriculture and/or tourism; 4) studies that investigate the effects of human disturbance on vocalization, habitat selection, mating, and/or grooming behaviours.

My experiment demonstrated that a fear of humans can have pervasive effects across a wildlife community. Thus, it is possible that a fear of humans can also induce cascading effects in this community by altering the foraging and movement patterns of lower trophic levels when large carnivores exhibit fear behaviours. Predator-induced trophic cascades in wildlife behaviour have been previously demonstrated (Preisser et al 2005; Laundre et al 2010; Suraci et al 2016); however, a human-induced trophic cascade in behaviour has only been experimentally tested once to date in Californian species (Suraci et al 2019). It would be interesting to determine if a pervasive fear of humans results in similar trophic cascades that are induced by Africa’s large carnivores, especially in megaherbivores as they have been demonstrated to counteract the effects of trophic cascades as adults are less fearful of predation (le Roux et al 2018), yet I have shown that they are fearful of humans and thus may behave differently.

Furthermore, the majority of studies focus on the short-term behavioural changes that wildlife display in response to humans, meanwhile the long-term effects are largely unknown. Previous research have demonstrated that exposure to predation risk can result in long-term neurological effects in chickadees (*Poecile atricapillus*) and cowbirds (*Molothrus ater*) (Witterick 2017; Zanette et al 2019) as well as lower fecundity and offspring survival in various bird and mammal species (Zanette & Clinchy 2020). However, these studies have not been replicated with humans as the perceived predation risk, as the effects of human disturbance on wildlife demography have only been reported using observational data (Gill et al 2001) and thus cannot attribute changes in population size as a direct result of human-induced behavioural changes. Thus, an informative future direction of research would be to experimentally test how human-induced behaviour in wildlife can directly cause demographic changes at the population level.

Lastly, I investigated if environmental factors influence the fleeing behaviour of a mammal community in response to perceived human presence and found that there were no factors that strongly predicted fleeing behaviour. Although I did not see an effect of the immediate environment on behaviour, previous research has demonstrated that environmental factors, such as vegetation cover, time of day, and distance to cover, do influence fleeing behaviour (Dill & Houtman 1989; Roberts 1996; Matson et al 2005; Reimers et al 2006). Contrastingly, there is limited research on how human-induced behaviour can affect the environment. Ford and colleagues (2014) demonstrated that antipredator behaviour elicited by herbivores can alter the landscape, such that areas with abundant predation risk of large carnivores consisted of less thorny vegetation than areas with lower levels of risk. Thus, in addition to humans directly contributing to habitat loss via agriculture, infrastructure, and logging (Tilman et al 2017), invoking antipredator behaviours in herbivores or ecosystem engineers (such as elephants) may also result in environmental changes or further loss of habitat. Brodie and Gibbs (2009) describe how overexploitation of wildlife may further act as a climate threat, as the removal of seed dispersers would result in a reduction of growth in tropical forests and deplete important carbon sinks that help mitigate climate change. Given that mammal species have been shown to avoid human presence, it would be interesting to determine if areas where seed dispersers were driven away or extirpated due to human disturbance are less forested.

4.4 References

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Appendices

Appendix A: List of all study species and number of videos collected for each species.

Species		Video Count	Trophic Level
Common Name	**Scientific Name**		
Impala	*Aepyceros melampus*	919	Herbivore
African elephant	*Loxodonta africana*	605	Megaherbivore
Common duiker	*Sylvicapra grimmia*	510	Herbivore
Common warthog	*Phacochoerus africanus*	326	Herbivore
Spotted hyena	*Crocuta crocuta*	245	Large Carnivore
Giraffe	*Giraffa camelopardalis*	227	Megaherbivore
African buffalo	*Syncerus caffer*	175	Herbivore
Nyala	*Tragelaphus angasii*	155	Herbivore
Plains zebra	*Equus quagga*	137	Herbivore
Hippopotamus	*Hippopotamus amphibius*	133	Megaherbivore
Southern white rhinoceros	*Ceratotherium simum*	100	Megaherbivore
Greater kudu	*Tragelaphus strepsiceros*	95	Herbivore
Waterbuck	*Kobus ellipsiprymnus*	53	Herbivore
Steenbok	*Raphicerus campestris*	48	Herbivore
Leopard	*Panthera pardus*	42	Large Carnivore
African wild dog	*Lycaon pictus*	41	Large Carnivore
Blue wildebeest	*Connochaetes taurinus*	33	Herbivore
Vervet monkey	*Chlorocebus pygerythrus*	25	Omnivore
Lion	*Panthera leo*	25	Large Carnivore
African civet	*Civettictis civetta*	23	Mesocarnivore
Chacma baboon	*Papio ursinus*	21	Omnivore
Black-backed jackal	*Canis mesomelas*	11	Mesocarnivore
Side-striped jackal	*Canis adustus*	9	Mesocarnivore
Bushbuck	*Tragelaphus sylvaticus*	8	Herbivore
White-tailed mongoose	*Ichneumia albicauda*	6	Mesocarnivore
Honey badger	*Mellivora capensis*	5	Mesocarnivore
Banded mongoose	*Mungos mungo*	4	Mesocarnivore
African crested porcupine	*Hystrix africaeaustralis*	4	Omnivore
Large spotted genet	*Genetta maculata*	3	Mesocarnivore
Slender mongoose	*Galerella sanguinea*	1	Mesocarnivore

Appendix B: Playlists for Automated Behavioural Response systems (ABR).

Playlist 1

TimeStart	TimeEnd	Treatment
0:00	0:16	Dog
0:16	0:32	Gunshot
0:32	0:48	Lion
0:48	1:04	Human
1:04	1:20	African Wood Owl
1:20	1:36	Dog
1:36	1:52	African Wood Owl
1:52	2:08	Gunshot
2:08	2:24	Lion
2:24	2:40	Human
2:40	2:56	African Wood Owl
2:56	3:12	Lion
3:12	3:28	Gunshot
3:28	3:44	Human
3:44	4:00	Dog
4:00	4:16	Gunshot
4:16	4:32	Human
4:32	4:48	Lion
4:48	5:04	Dog
5:04	5:20	Pearl-Spotted Owlet
5:20	5:36	Dog
5:36	5:52	Gunshot
5:52	6:08	Pearl-Spotted Owlet
6:08	6:24	Human
6:24	6:40	Lion
6:40	6:56	Gunshot
6:56	7:12	Lion
7:12	7:28	Dog
7:28	7:44	Pearl-Spotted Owlet
7:44	8:00	Human
8:00	8:16	Dog
8:16	8:32	Human
8:32	8:48	Lion
8:48	9:04	African Hoopoe
9:04	9:20	Gunshot
9:20	9:36	Human
9:36	9:52	African Hoopoe
9:52	10:08	Gunshot
10:08	10:24	Dog
10:24	10:40	Lion
10:40	10:56	Dog
10:56	11:12	Human
11:12	11:28	African Hoopoe
11:28	11:44	Lion
11:44	12:00	Gunshot

Playlist 2

TimeStart	TimeEnd	Treatment
0:00	0:16	Human
0:16	0:32	African Wood Owl
0:32	0:48	Gunshot
0:48	1:04	Lion
1:04	1:20	Dog
1:20	1:36	Lion
1:36	1:52	Human
1:52	2:08	African Wood Owl
2:08	2:24	Gunshot
2:24	2:40	Dog
2:40	2:56	Lion
2:56	3:12	African Wood Owl
3:12	3:28	Human
3:28	3:44	Gunshot
3:44	4:00	Dog
4:00	4:16	Gunshot
4:16	4:32	Pearl-Spotted Owlet
4:32	4:48	Dog
4:48	5:04	Human
5:04	5:20	Lion
5:20	5:36	Human
5:36	5:52	Lion
5:52	6:08	Gunshot
6:08	6:24	Pearl-Spotted Owlet
6:24	6:40	Dog
6:40	6:56	Pearl-Spotted Owlet
6:56	7:12	Human
7:12	7:28	Lion
7:28	7:44	Dog
7:44	8:00	Gunshot
8:00	8:16	Human
8:16	8:32	African Hoopoe
8:32	8:48	Dog
8:48	9:04	Lion
9:04	9:20	Gunshot
9:20	9:36	Human
9:36	9:52	African Hoopoe
9:52	10:08	Gunshot
10:08	10:24	Dog
10:24	10:40	Lion
10:40	10:56	Dog
10:56	11:12	Human
11:12	11:28	Gunshot
11:28	11:44	Lion
11:44	12:00	African Hoopoe

Playlist 1

TimeStart	TimeEnd	Treatment
12:00	12:16	Lion
12:16	12:32	Gunshot
12:32	12:48	Dog
12:48	13:04	Human
13:04	13:20	African Hoopoe
13:20	13:36	Human
13:36	13:52	Gunshot
13:52	14:08	African Hoopoe
14:08	14:24	Dog
14:24	14:40	Lion
14:40	14:56	Human
14:56	15:12	Dog
15:12	15:28	Lion
15:28	15:44	African Hoopoe
15:44	16:00	Gunshot
16:00	16:16	Lion
16:16	16:32	Dog
16:32	16:48	Gunshot
16:48	17:04	Pearl-Spotted Owlet
17:04	17:20	Human
17:20	17:36	Gunshot
17:36	17:52	Human
17:52	18:08	Pearl-Spotted Owlet
18:08	18:24	Lion
18:24	18:40	Dog
18:40	18:56	Gunshot
18:56	19:12	Pearl-Spotted Owlet
19:12	19:28	Dog
19:28	19:44	Human
19:44	20:00	Lion
20:00	20:16	Dog
20:16	20:32	Human
20:32	20:48	Lion
20:48	21:04	African Wood Owl
21:04	21:20	Gunshot
21:20	21:36	African Wood Owl
21:36	21:52	Human
21:52	22:08	Gunshot
22:08	22:24	Lion
22:24	22:40	Dog
22:40	22:56	Human
22:56	23:12	Dog
23:12	23:28	Lion
23:28	23:44	African Wood Owl
23:44	0:00	Gunshot

Playlist 2

TimeStart	TimeEnd	Treatment
12:00	12:16	Dog
12:16	12:32	African Hoopoe
12:32	12:48	Gunshot
12:48	13:04	Human
13:04	13:20	Lion
13:20	13:36	Gunshot
13:36	13:52	Dog
13:52	14:08	Human
14:08	14:24	Lion
14:24	14:40	African Hoopoe
14:40	14:56	Dog
14:56	15:12	Human
15:12	15:28	African Hoopoe
15:28	15:44	Gunshot
15:44	16:00	Lion
16:00	16:16	Pearl-Spotted Owlet
16:16	16:32	Human
16:32	16:48	Gunshot
16:48	17:04	Dog
17:04	17:20	Lion
17:20	17:36	Gunshot
17:36	17:52	Lion
17:52	18:08	Pearl-Spotted Owlet
18:08	18:24	Human
18:24	18:40	Dog
18:40	18:56	Lion
18:56	19:12	Gunshot
19:12	19:28	Human
19:28	19:44	Pearl-Spotted Owlet
19:44	20:00	Dog
20:00	20:16	Human
20:16	20:32	Dog
20:32	20:48	Lion
20:48	21:04	Gunshot
21:04	21:20	African Wood Owl
21:20	21:36	Lion
21:36	21:52	Dog
21:52	22:08	Human
22:08	22:24	Gunshot
22:24	22:40	African Wood Owl
22:40	22:56	Gunshot
22:56	23:12	Lion
23:12	23:28	African Wood Owl
23:28	23:44	Human
23:44	0:00	Dog

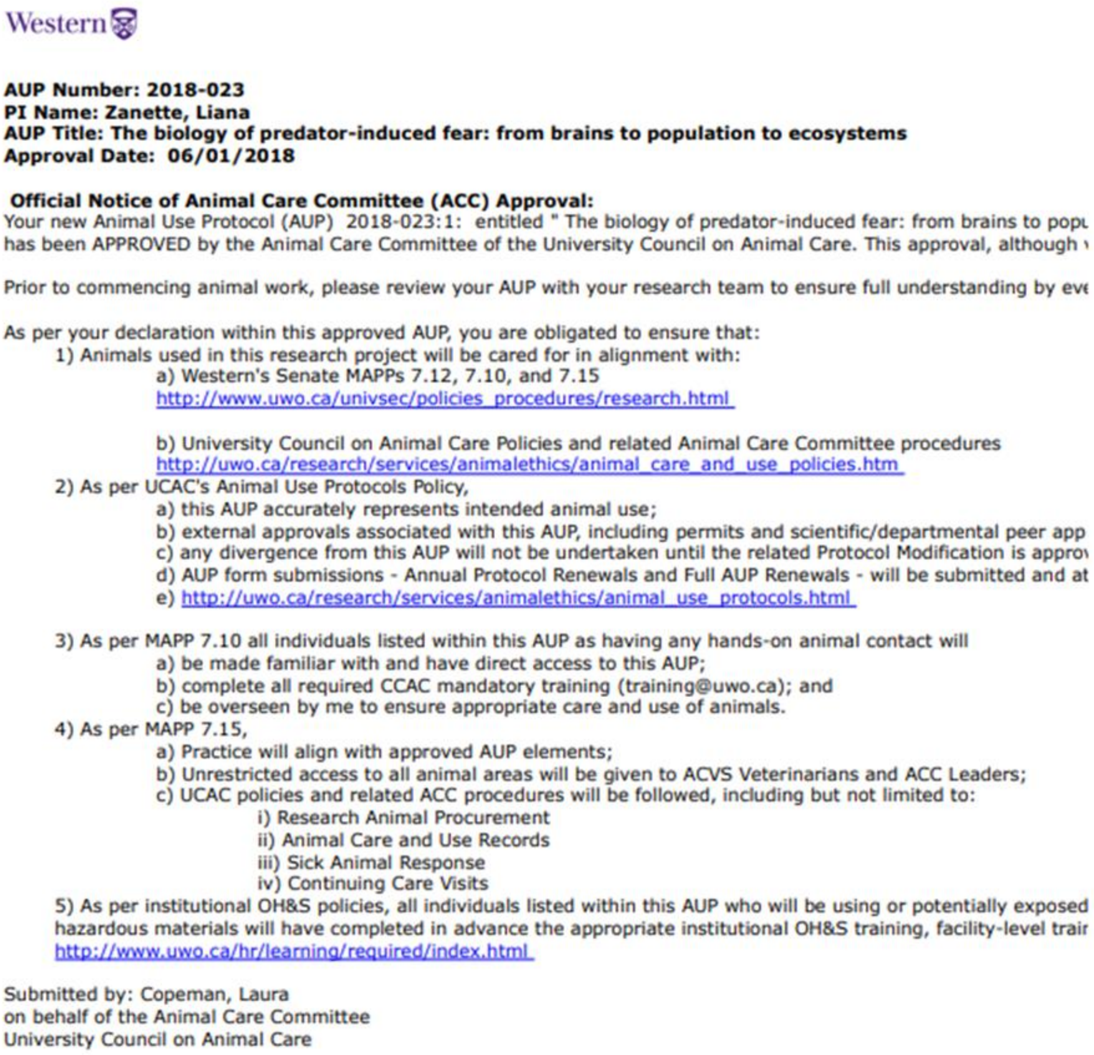
Appendix C: Descriptive statistics of effect sizes of African mammal behaviour in response to human disturbance.

Variable	Count (N)	Mean (M)	Standard Error (SEM)	Lower CI	Upper CI	Median	Standard Error (SE)	Lower CI	Upper CI
Overall									
	77	-0.84	0.10	-1.04	-0.65	-0.70	0.12	-0.96	-0.55
Human Disturbance Type									
Agriculture	6	-0.15	0.17	-0.47	0.18	-0.21	0.22	-0.55	0.31
Hunting	44	-0.93	0.13	-1.19	-0.66	-0.75	0.15	-1.01	-0.54
Infrastructure	14	-0.79	0.23	-1.27	-0.35	-0.68	0.30	-1.12	-0.39
Presence / Tourism	10	-1.20	0.27	-1.76	-0.69	-1.15	0.27	-1.58	-0.74
Study Design									
Experimental	36	-0.80	0.12	-1.04	-0.53	-0.74	0.16	-1.11	-0.54
Observational	41	-0.89	0.16	-1.23	-0.60	-0.70	0.16	-1.03	-0.50
Species Group									
Carnivores	16	0.29	0.28	-1.26	-0.19	-0.52	0.36	-1.52	0.22
Elephants	8	-1.13	0.28	-1.72	-0.60	-0.83	0.41	-1.82	-0.55
Ungulates	23	-1.16	0.18	-1.52	-0.86	-0.96	0.24	-1.57	-0.70
Primates	21	-0.43	0.16	-0.73	-0.12	-0.40	0.16	-0.74	-0.16
Multiple groups present	6	-0.88	0.21	-1.29	-0.47	-0.98	0.31	-1.48	-0.18
Methodology									
Approaching subjects	10	-1.11	0.19	-1.50	-0.77	-1.07	0.40	-1.63	-0.49
Baiting	7	0.07	0.25	-0.46	0.51	0.27	0.32	-0.55	0.56
Auditory playbacks	19	-0.95	0.14	-1.23	-0.71	-0.86	0.18	-1.26	-0.59
GPS tracking	9	-0.87	0.31	-1.53	-0.31	-0.52	0.45	-1.67	-0.15
Direct observation	32	-0.89	0.18	-1.24	-0.54	-0.75	0.15	-1.05	-0.50
Behaviour									
Boldness	6	0.12	0.24	-0.36	0.57	0.33	0.34	-0.59	0.69
Feeding	13	-1.10	0.27	-1.60	-0.62	-1.05	0.30	-1.53	-0.33
Fleeing	21	-1.04	0.17	-1.38	-0.75	-0.70	0.31	-1.48	-0.55
Vigilance	12	-0.97	0.19	-1.36	-0.57	-0.91	0.26	-1.61	-0.55
Movement	9	-0.82	0.31	-1.44	-0.26	-0.54	0.42	-1.67	-0.06
Vocalizations	7	-0.83	0.23	-1.33	-0.44	-0.61	0.24	-1.23	-0.39

Note: Effect size calculated as ln(mean for fear treatment/mean for control), after Salo et al. (2010).

Note: Sign (+/-) of effect size adjusted to reflect positive or negative effect of humans on behaviour, as reported by original authors

Appendix D: Ethics approval form for experiment on South African mammals



Western

AUP Number: 2018-023
PI Name: Zanette, Liana
AUP Title: The biology of predator-induced fear: from brains to population to ecosystems
Approval Date: 06/01/2018

Official Notice of Animal Care Committee (ACC) Approval:
Your new Animal Use Protocol (AUP) 2018-023:1: entitled " The biology of predator-induced fear: from brains to popu
has been APPROVED by the Animal Care Committee of the University Council on Animal Care. This approval, although

Prior to commencing animal work, please review your AUP with your research team to ensure full understanding by eve

As per your declaration within this approved AUP, you are obligated to ensure that:

1) Animals used in this research project will be cared for in alignment with:
    a) Western's Senate MAPPs 7.12, 7.10, and 7.15
    http://www.uwo.ca/univsec/policies_procedures/research.html

    b) University Council on Animal Care Policies and related Animal Care Committee procedures
    http://uwo.ca/research/services/animalethics/animal_care_and_use_policies.htm
2) As per UCAC's Animal Use Protocols Policy,
    a) this AUP accurately represents intended animal use;
    b) external approvals associated with this AUP, including permits and scientific/departmental peer app
    c) any divergence from this AUP will not be undertaken until the related Protocol Modification is appro
    d) AUP form submissions - Annual Protocol Renewals and Full AUP Renewals - will be submitted and at
    e) http://uwo.ca/research/services/animalethics/animal_use_protocols.html

3) As per MAPP 7.10 all individuals listed within this AUP as having any hands-on animal contact will
    a) be made familiar with and have direct access to this AUP;
    b) complete all required CCAC mandatory training (training@uwo.ca); and
    c) be overseen by me to ensure appropriate care and use of animals.
4) As per MAPP 7.15,
    a) Practice will align with approved AUP elements;
    b) Unrestricted access to all animal areas will be given to ACVS Veterinarians and ACC Leaders;
    c) UCAC policies and related ACC procedures will be followed, including but not limited to:
        i) Research Animal Procurement
        ii) Animal Care and Use Records
        iii) Sick Animal Response
        iv) Continuing Care Visits
5) As per institutional OH&S policies, all individuals listed within this AUP who will be using or potentially exposed
hazardous materials will have completed in advance the appropriate institutional OH&S training, facility-level trai
http://www.uwo.ca/hr/learning/required/index.html

Submitted by: Copeman, Laura
on behalf of the Animal Care Committee
University Council on Animal Care

Appendix E: Behavioural ethogram using to score fear behaviours of South African mammals.

Behaviour	Operational Definition
Movement	
Standing	The animal is in an upright position and is remaining in one location. The animal can make three or less steps in any direction to scan.
Walking	The animal took more than three consecutive steps in a single direction. Left and right legs alternate.
Running	The animal took more than three consecutive steps in a single direction at speed greater than walking. Left and right legs move together.
Retreating	The animal took more than three consecutive steps backwards. Left and right legs alternate.
Approaching	The animal changed direction and walked towards the camera with its head also turned towards the camera.
Attention	
Head-up standing	The animal was standing with its head above the shoulders. The head could move for scanning.
Head-down	The animal was standing or walking with its head below the shoulders. The head could move for foraging.
Looking at camera	The animal was standing or walking with its head raised up and looking directly at the camera with both eyes visible.
Wallowing	The animal is laying down in the mud with limited attention of its surroundings.

Appendix F: Methodology for additional factor collection

Time of Day

I calculated time of day using the length of the videos captured by the ABR, as the length of video is determined by the amount of visible light in the environment (with a range of 19.98 – 30.48 sec). Thus, day videos were videos that were 30 sec or longer in length, and night videos were videos that were less than 30 sec in length. I recorded the information for the phase of the moon for each night during July and August 2018 from the NASA Moon Phase and Libration website, *https://svs.gsfc.nasa.gov/4604.*

Vegetation Cover

I calculated the percentage of vegetation cover immediately surrounding the camera set up as well as surrounding the perimeter of the nearby dam. First, I obtained aerial photographs of the camera locations during the 2018 dry season using Google Earth. Using ImageJ, I drew a grid centered around the camera and parallel to the dam's shoreline closest to the camera. The grid 20 m long, 15 m wide, and contained 12 5m x 5m squared within it (Figure D1). To calculate vegetation cover, I used a point system for each square, such that: if 0% of the square had vegetation, the square received 0 points; if 1% - 49% of the square had vegetation, the square received 1 point; if 50%-99% of the square had vegetation, the square received 2 points; and if 100% of the square had vegetation, the square received 3 points. Therefore, the total vegetation coverage a camera site could have is 30 points = 100%.

To calculate the percentage of vegetation cover surrounding the dam, I first calculated the position of the centroid of the dam itself using ImageJ. This centroid provides an unbiased, repeatable center for the dams regardless of their shape and size. I created a transect starting at the outer, most northern edge of the dam's perimeter, aligning with the centroid, going northwards. This transect was 10 m wide, 100 m long, and had 10 m intervals along its length to total ten 10 m x 10 m boxes. This transect was repeated for S, W, E, NW, NE, SW, and SE directions (Figure D2) to provide an approximate vegetation cover percentage within a 100 m radius of the dam's perimeter. Within each box, I categorized percentage cover using the same method as for the camera set, so that the total vegetation coverage a transect could have is 30 points = 100% and the total vegetation coverage the dam perimeter could have is 300 points = 100%.

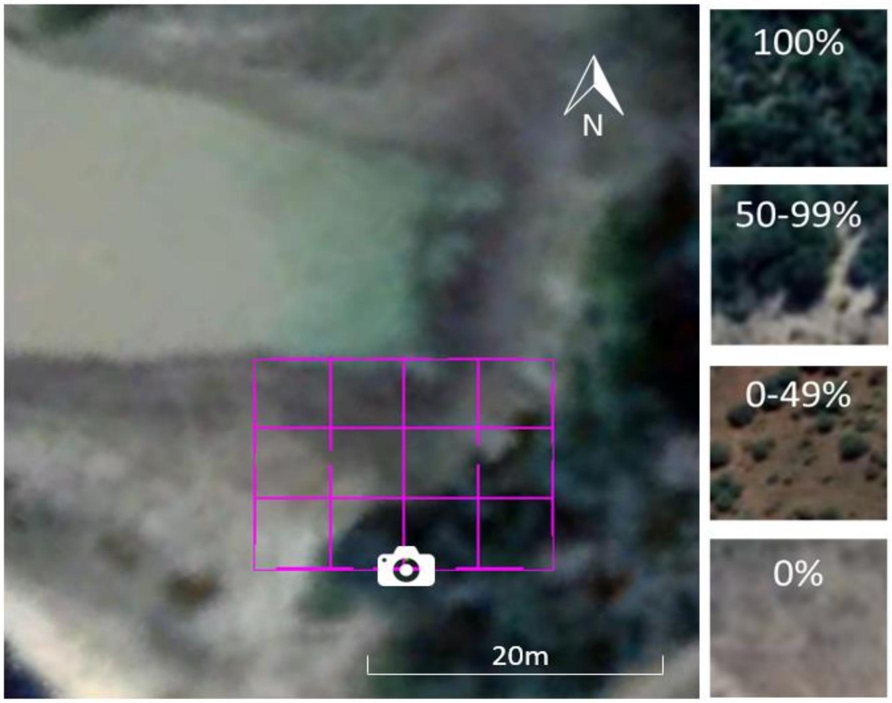


Figure D1: Quadrat method to calculating vegetation cover surrounding camera site.

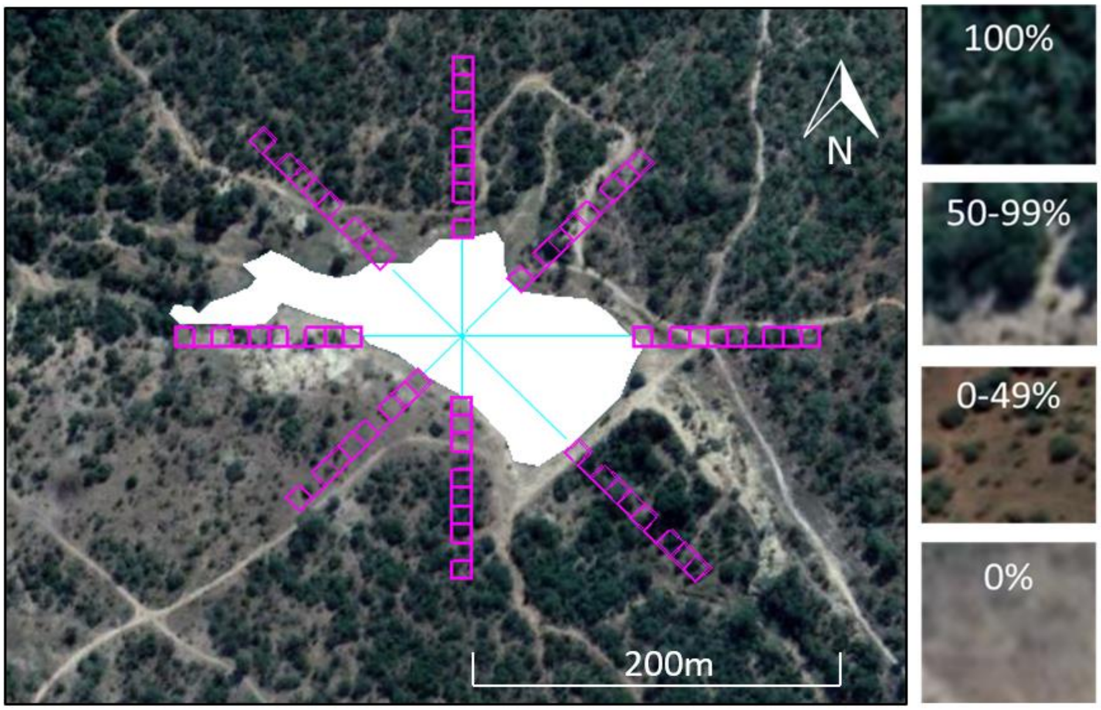


Figure D2: Quadrat method to calculating vegetation cover surrounding dam site.

Large carnivore presence and human presence

To determine if nearby large carnivores were influencing the behaviour of the subjects, I recorded both the presence and intensity of the large carnivores in the area: lions (*Panthera leo*), leopards (*Panthera pardus*), and hyenas (*Crocuta crocuta*). Presence is defined as how often a large carnivore appeared on video at a given camera location. For example, to calculate lion presence, I summed the number of times that I captured a first exposure video of a lion at a given camera site, and then divided that sum by the number of days that the camera was functional and at the site. I repeated this protocol each camera site. In addition to lion presence, I also calculated leopard presence, hyena presence, and overall large carnivore presence which was the sum of the presence of all three large carnivores. Similar to presence, intensity also accounts for how many large carnivores there were in total that appeared on video at each camera location. To calculate lion intensity, I summed the number of individuals that were spotted at a given camera site, and then divided that sum by the number of days that the camera was functional and at the site. Again, this procedure was repeated for each camera site and each large carnivore.

To represent the potential influence of human presence, I referenced two current maps of Klaserie and Thornybush with information about the buildings and roads within the reserves. I determined three different measures of human presence: number of nearby buildings to camera site, distance of nearest building to camera site, and the length of nearby roads. I calculated these measurements by uploading the provided maps onto ImageJ. To calculate the number of nearby buildings, I drew a 1 km^2 square around a given camera site and counted the number of buildings placed within this square. To calculate the distance of the nearest building, I drew a straight line from the nearest building to the camera site and measured the distance. Lastly, to determine the length of the nearby roads, I measured and summed the distance of each road within the same 1 km^2 square around each camera site. One kilometer was used as a guideline because the camera sites were placed a minimum of 2 km apart; hence, 1 km allowed for non-overlapping human presence information between camera sites.

Age and sex

I recorded sex for species that were visibly sexual dimorphic on camera: antelopes, giraffes, rhinoceroses, warthogs, lions, buffalo, and elephants (Figure D3). For antelopes, males have horns while females do not (Kingdon 2013d, p. 120). Due to their height, I sexed giraffes solely based on their genitalia. I also sexed rhinoceroses based on genitalia, in addition to the shape and thickness of their horn since males have bigger and thicker horns than females and often have a large muscular bulge at the base of their neck to compensate for their larger head and horn (Kingdon 2013c, p. 447). I sexed warthogs based on their genitalia, the presence of facial warts only seen in males, the thickness of their mane, and the size of their tusks (Kingdon 2013d, p. 54). If offspring were nearby a warthog without obvious male traits, then I presumed the individual as female. I used genitalia along with mane colour and thickness to sex lions (Kingdon 2013c, p. 145). I used the position of the horns to sex buffalo as females have a space on their head between their horns while males do not, with male horns forming a "boss" (Kingdon 2013d, p. 126). Lastly, I sexed elephants by their genitalia (where possible) or by the presence of absence of mammary glands that are visible in females. If these sex organs were not visible on camera, then I examined their head shape as males have rounder heads with eyes that bulge out while females have squarer heads; males also have larger tusks and have an underside that slopes up towards the front legs while the underside of females is parallel to the ground (Kingdon 2013b, p. 182). I did not record sex for species that are not visibly sexually dimorphic on camera: hyenas, zebras, hippopotamuses, wild dogs, leopards, wildebeest, vervet monkeys, baboons, civets, mongooses, jackals, badgers, porcupines, and genets.

I classified all study species into two age groups: adults and offspring. In most species, I defined offspring as being noticeably smaller in size compared to their adult counterparts. In species where this difference in size is not as obvious, such as rhinoceroses and elephants, I used more precise definitions. In rhinoceroses, I aged calves based on their shoulder height in comparison to their mother: calves with a shoulder height level with the mother's groin are 0-3 months of age, calves with a shoulder height slightly about the mother's underside are 1-2 years of age, and calves with a shoulder height at approximately three quarters of the mother's shoulder height are 2-3.5 years of age (Adcock 2020). Regardless of age, I considered all calves as offspring if they close by an adult female and have not yet developed a horn (Kingdon 2013c, p. 452). In elephants, I used shoulder height in relation to the offspring's mother to indicate the age of the elephant. I decided that elephants of 8 years or younger would be considered offspring because calves will remain close to their mothers until they are 6-8 years old, while sexual dimorphism in offspring doesn't become apparent until age 10 (Lee & Moss 1986; Lee & Moss 1995). To identify a calf of 8 years or less in age, the calf's shoulder height must be equal or less than three quarters of the height of its mother (Shrader et al 2006; Stoeger et al 2014).

Species	Male	Female	Offspring
Common Warthog *Phacochoerus africanus*			
Nyala *Tragelaphus angasii*			*male sub-adult 

Figure D3: Guide to distinguish sexes and offspring in sexually dimorphic species.

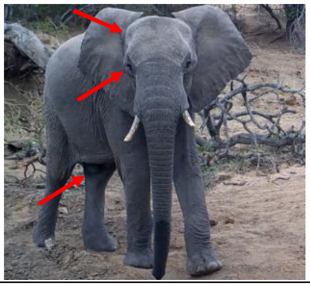
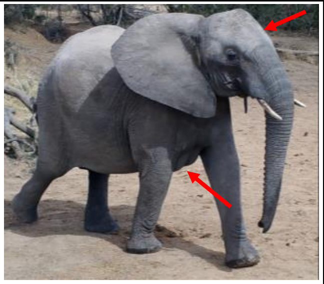
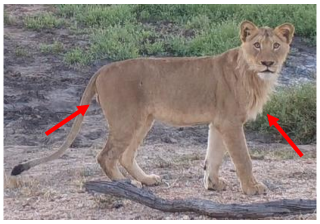
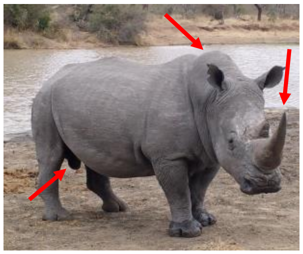
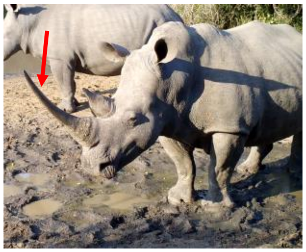
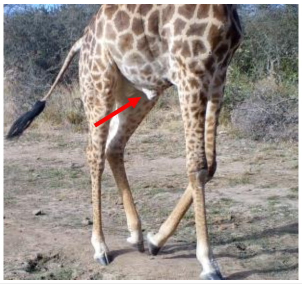
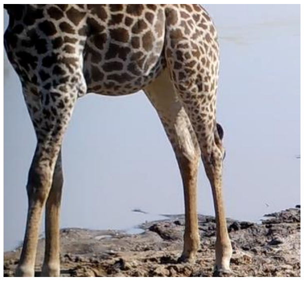
Species	**Male**	**Female**	**Offspring**
African elephant *Loxodonta africana*			
African buffalo *Syncerus caffer*			
Lion *Panthera leo*			*young male 
Southern white rhinoceros *Ceratotherium simum*			
Giraffe *Giraffa camelopardalis*			

Figure D3 (continued): Guide to distinguish sexes and offspring in sexually dimorphic species.

Herd Size

I collected information on average body size, body size range, and trophic level for each species from "*Mammals of Africa*" (Kingdon 2013a). I categorized herd size into three groups: small, medium, and large, comprising of 1 individual, 2-7 individuals, and 8+ individuals, respectively. I based the differentiation between medium and large groups on impala herding composition, where a group of 7 or less are more likely to be a group of bachelors whereas a group of 8+ are more likely to be breeding herds (Shorrocks & Cokayne 2005).

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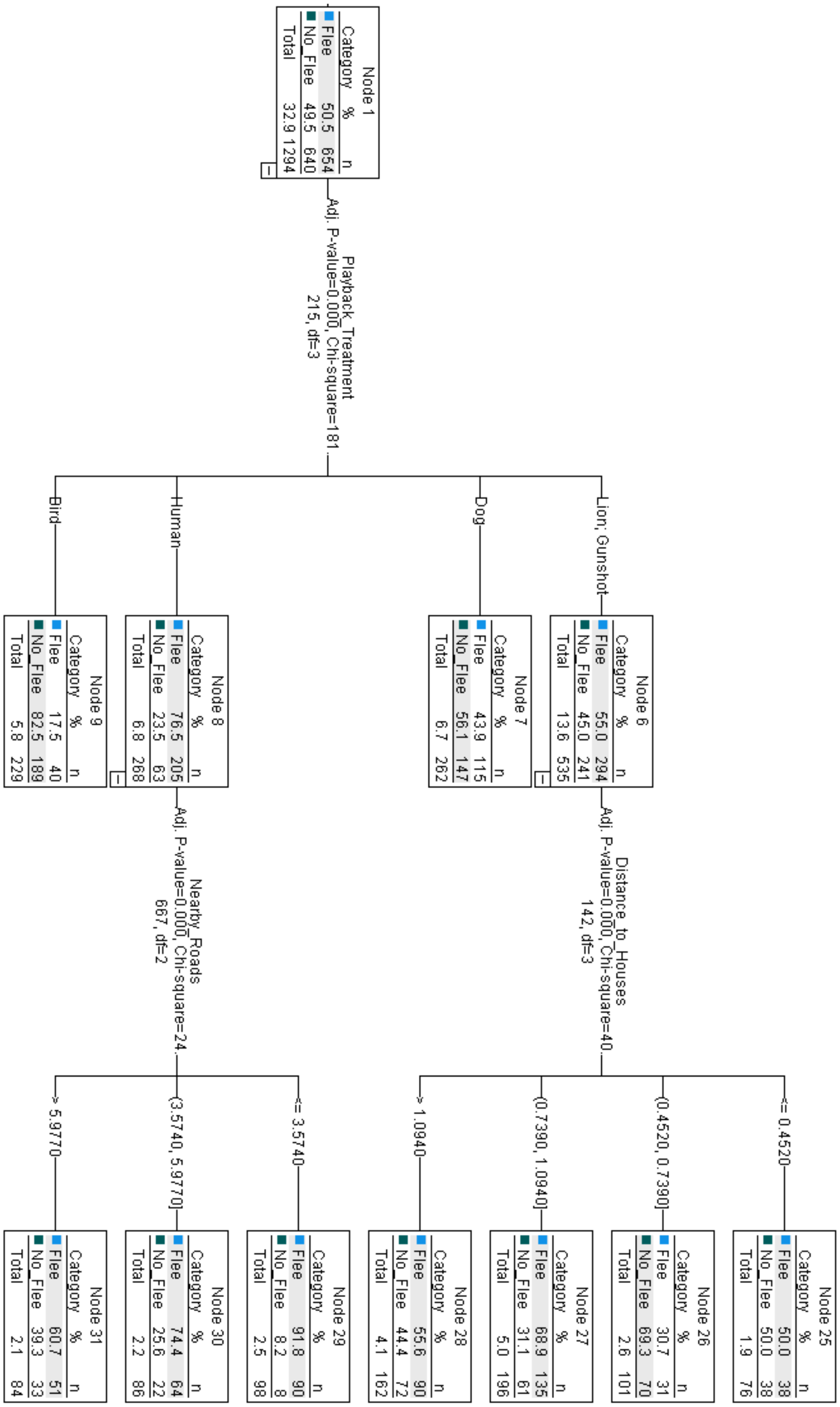
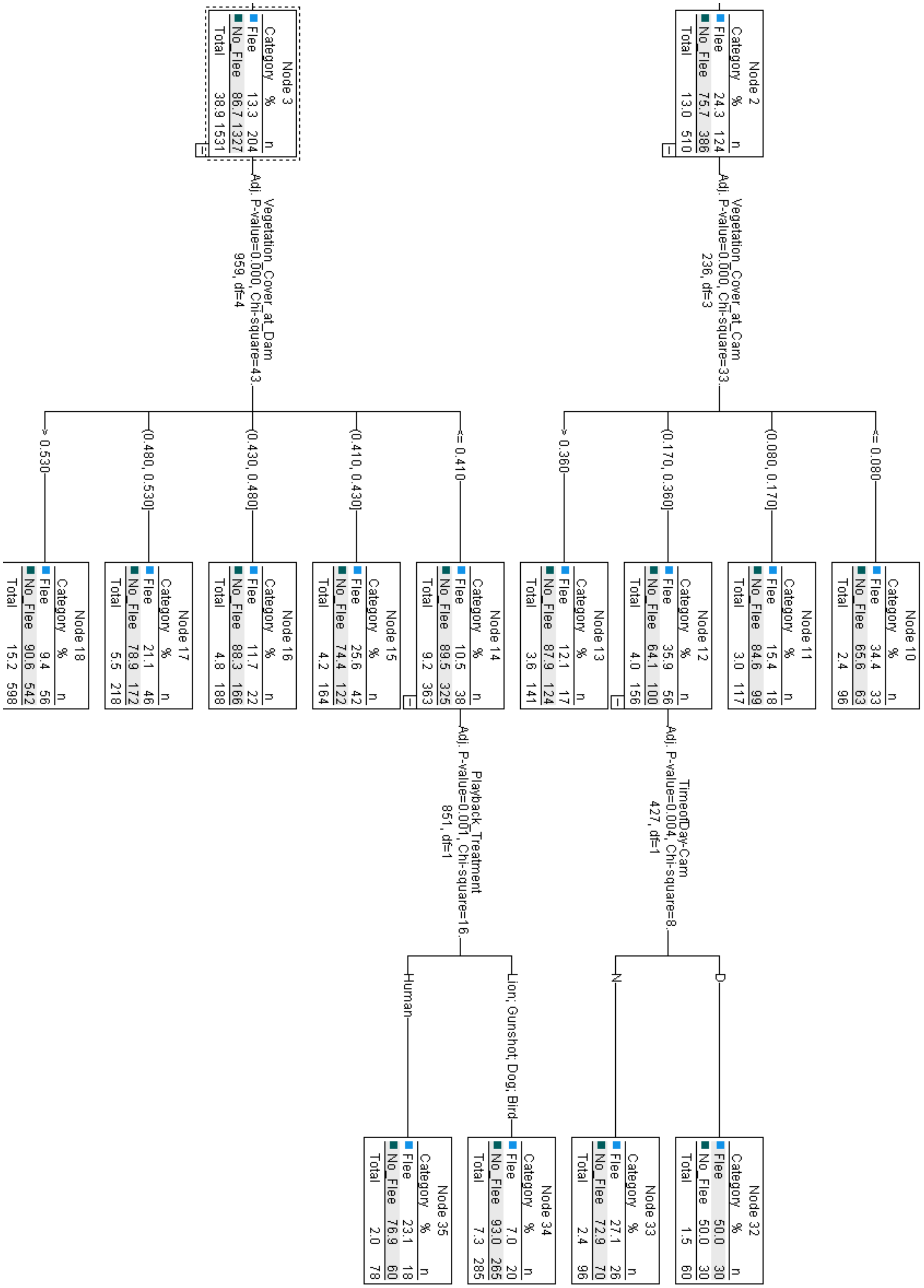
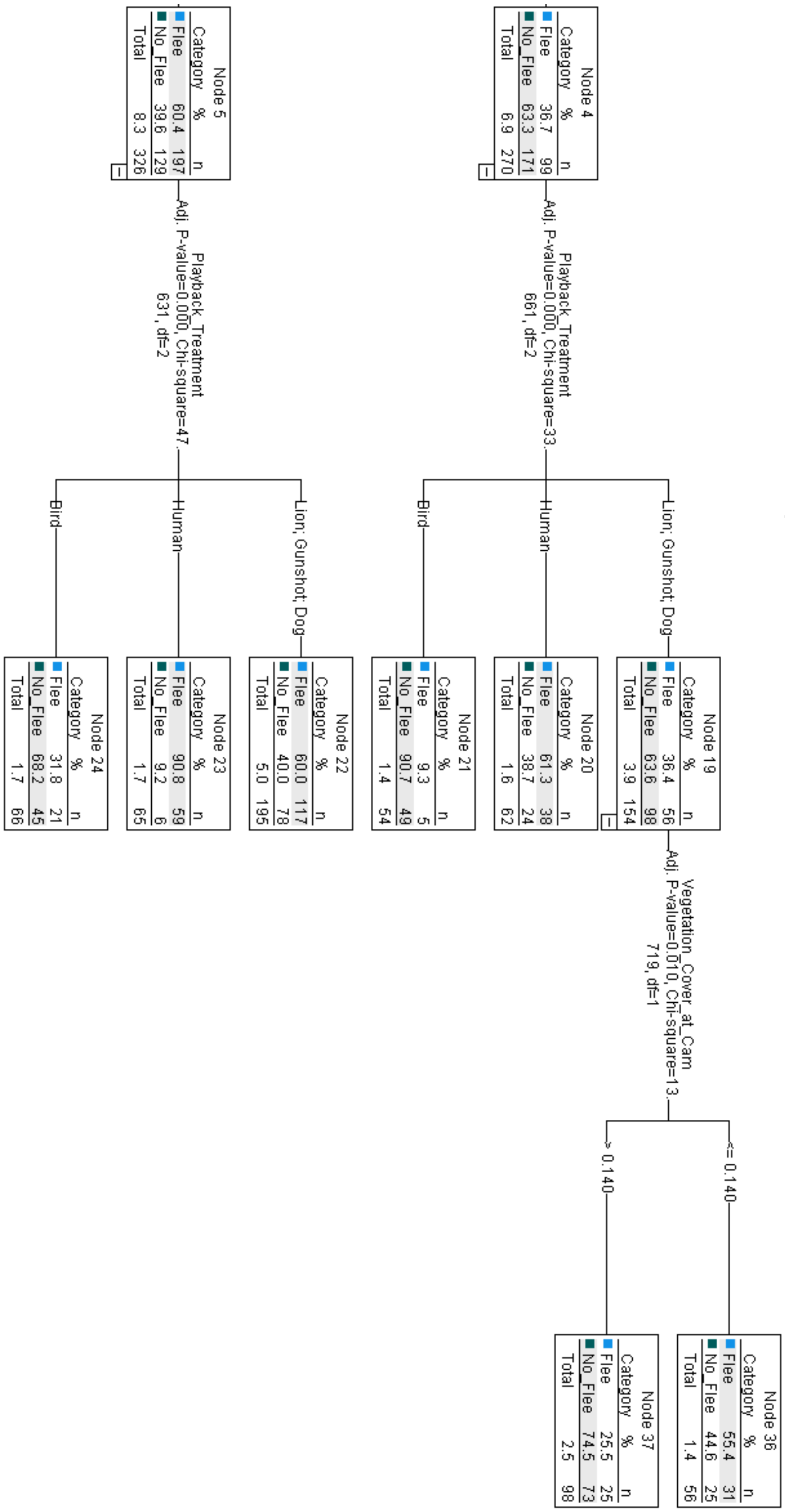
Appendix G: Secondary and tertiary ecological predictors for fleeing in a South African mammal community.




Node 2
Category % n
Flee 24.3 124
No_Flee 75.7 386
Total 13.0 510
Vegetation_Cover_at_Cam
Adj. P-value=0.000, Chi-square=33.236, df=3
<= 0.080
(0.080, 0.170]
(0.170, 0.360]
> 0.360
Node 10
Category % n
Flee 34.4 33
No_Flee 65.6 63
Total 2.4 96
Node 11
Category % n
Flee 15.4 18
No_Flee 84.6 99
Total 3.0 117
Node 12
Category % n
Flee 35.9 56
No_Flee 64.1 100
Total 4.0 156
Node 13
Category % n
Flee 12.1 17
No_Flee 87.9 124
Total 3.6 141
TimeofDay-Cam
Adj. P-value=0.004, Chi-square=8.427, df=1
D
N
Node 32
Category % n
Flee 50.0 30
No_Flee 50.0 30
Total 1.5 60
Node 33
Category % n
Flee 27.1 26
No_Flee 72.9 70
Total 2.4 96
Node 3
Category % n
Flee 13.3 204
No_Flee 86.7 1327
Total 38.9 1531
Vegetation_Cover_at_Dam
Adj. P-value=0.000, Chi-square=43.959, df=4
<= 0.410
(0.410, 0.430]
(0.430, 0.480]
(0.480, 0.530]
> 0.530
Node 14
Category % n
Flee 10.5 38
No_Flee 89.5 325
Total 9.2 363
Node 15
Category % n
Flee 25.6 42
No_Flee 74.4 122
Total 4.2 164
Node 16
Category % n
Flee 11.7 22
No_Flee 88.3 166
Total 4.8 188
Node 17
Category % n
Flee 21.1 46
No_Flee 78.9 172
Total 5.5 218
Node 18
Category % n
Flee 9.4 56
No_Flee 90.6 542
Total 15.2 598
Playback_Treatment
Adj. P-value=0.001, Chi-square=16.851, df=1
Lion; Gunshot; Dog; Bird
Human
Node 34
Category % n
Flee 7.0 20
No_Flee 93.0 265
Total 7.3 285
Node 35
Category % n
Flee 23.1 18
No_Flee 76.9 60
Total 2.0 78


Node 4
Category % n
Flee 36.7 99
No_Flee 63.3 171
Total 6.9 270
Playback_Treatment
Adj. P-value=0.000, Chi-square=33.661, df=2
Lion; Gunshot; Dog
Human
Bird
Node 19
Category % n
Flee 36.4 56
No_Flee 63.6 98
Total 3.9 154
Node 20
Category % n
Flee 61.3 38
No_Flee 38.7 24
Total 1.6 62
Node 21
Category % n
Flee 9.3 5
No_Flee 90.7 49
Total 1.4 54
Vegetation_Cover_at_Cam
Adj. P-value=0.010, Chi-square=13.719, df=1
<= 0.140
> 0.140
Node 36
Category % n
Flee 55.4 31
No_Flee 44.6 25
Total 1.4 56
Node 37
Category % n
Flee 25.5 25
No_Flee 74.5 73
Total 2.5 98
Node 5
Category % n
Flee 60.4 197
No_Flee 39.6 129
Total 8.3 326
Playback_Treatment
Adj. P-value=0.000, Chi-square=47.631, df=2
Lion; Gunshot; Dog
Human
Bird
Node 22
Category % n
Flee 60.0 117
No_Flee 40.0 78
Total 5.0 195
Node 23
Category % n
Flee 90.8 59
No_Flee 9.2 6
Total 1.7 65
Node 24
Category % n
Flee 31.8 21
No_Flee 68.2 45
Total 1.7 66

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Master of Science (Biology) 2019-2021
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BIO 3440A: Ecology of Populations	2020
BIO 3442F: Conservation Biology	2020

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Western Summer 2020 Student Fellowship	2020
Queen Elizabeth II Graduate Scholarship in Science & Technology	2020
Canadian Society of Zoologists: Helen I Battle Award	2019
Western's Dean's Honour Roll	2019
Western's Scholarship of Excellence	2015

RESEARCH CONFERENCE PRESENTATIONS

May 17, 2021. A South African mammal community fears the human "super predator". Oral. *International Student Symposium on Animal Behaviour & Cognition.* Western University (virtual), London, Ontario, Canada.

October 18, 2019. Dispersal ability & flight morphology of the Rocky Mountain Apollo butterfly. Poster. *Biology Graduate Research Forum.* Western University, London, Ontario, Canada.

May 15, 2019. Dispersal ability & flight morphology of the Rocky Mountain Apollo butterfly. Poster. *Canadian Society of Zoologists Conference*. University of Windsor, Windsor, Ontario, Canada.

May 14, 2019. Dispersal ability & flight morphology of the Rocky Mountain Apollo butterfly. Mini talk. *Canadian Society of Zoologists Conference*. University of Windsor, Windsor, Ontario, Canada.

March 29, 2019. Dispersal ability & flight morphology of the Rocky Mountain Apollo butterfly. Poster. *Western Student Research Conference*. Western University, London, Ontario, Canada.

March 23, 2019. Dispersal ability & flight morphology of the Rocky Mountain Apollo butterfly. Oral. *Ontario Biology Day*. Western University, London, Ontario, Canada.