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Modelling and monitoring the behaviour of predators and prey in the context of anthropogenic risk

MSc (by Research) in Zoology



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Acknowledgements

Thank you to my supervisors, David Macdonald and Mike Bonsall, for providing constant support and guidance throughout this degree. They have been endlessly understanding through difficult times and have given me the confidence and advice I needed to keep going. They did not give up on me, even when I nearly did. I will always be grateful to them for helping me accomplish this feat.

For their guidance and assistance in completing Chapter Two, I thank Tutilo Mudumba, Sophia Jingo, Bob Montgomery, Petero Luhonda, Herbert Kasozi, Patience Ariyo, Cresent Rugumyangabo, Rosemary Alinda, Nulu Nangobi, Shukran Iwutung, Wyclef Wako, Enock Nankwatsa, Derrick Akampurira, Matthew Chun, Michael Zhu Chen, and Matthew Rogers. I am particularly grateful to everyone who worked with me in the field and supported me as friends and teachers during a trying season. This work would never have been possible without them, and I am so lucky to have worked alongside them. Thank you to the Uganda Wildlife Authority for allowing this research to be conducted and for their support in the field.

My field work was funded by the Sir Peter Elworthy Research Grant, The Emma Eisenstein Foundation, and Merton College. I was funded as a student by the Rhodes Trust. I'm grateful to Mary Eaton and Elizabeth Kiss for cheering me on, for helping me navigate tough times, and for believing in me.

Andrew Loveridge made it possible for me to access an incredible database regarding the lions of Hwange National Park, and without that generosity, I would not have been able to pursue the ideas that inspired me the most and this work could not have been done. For their kind support during the creation of Chapter Three, including offerings of advice, coding solutions, raster files, and shared data, thanks to Lara Sousa, Egil Dröge, Beth Preston, and Lisanne Petracca. The research that created the Hwange National Park database was funded by Panthera, The Recanati-Kaplan Foundation, and The Robertson Foundation.

For their valuable guidance and their thorough assessment of my work during my Transfer of Status and Viva Voce, I thank Paul Johnson, Jonathan Green, and Dan Parker.

Thank you to Sean Roberts and Tyler Silvestri, my dear patient friends, for helping me proofread in the final hours. I'm also indebted to the host of friends I made in Oxford, who were like family to me when I was far from home. David, Jay, Dylan, Eric, Nayani, Jean, Nadine, and too many others to list – thank you.

Thank you to Matt, who has been my sunshine on dark and cloudy days.

Thank you to my parents for their endless love and support and for everything they've done to help get me where I am. I am enormously lucky to have been raised by them and to know they'll always have my back.

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Abstract

Predator-prey dynamics help shape the populations and behavioural interactions of wildlife at all trophic levels. Risk effects are animals' behavioural responses to the risk of predation and their associated costs. Humans impose risk effects on both predators and prey, and it's important to understand those effects when developing conservation strategies. Here I examine the behaviours of Uganda kob (*Kobus kob thomasi*) and African lions (*Panthera leo*), both living in carnivore-ungulate systems within human-dominated landscapes. By recording kobs' flight distances relative to road networks and snare poaching activity, I find that kobs' antipredator responses do not seem to be affected by proximity to roads or local snaring intensity. However, sexual differences in flight distance may suggest intraspecific competition influences kobs' risk tolerance. I also develop a model of lions' energy expenditure over space and time as a result of habitat covariates. The construction of behavioural decision-making models could allow researchers to identify how lions and other carnivores perceive anthropogenic risk, given enough data to distinguish risk effects from other variables influencing their decisions. The aim of this thesis is to better understand the extent to which humans influence the behaviours of predators and prey and how human activities influence other animals' perceptions of risk in dynamic ways.

Chapter One

Introduction

On Risk Effects

Entire ecosystems can be shaped by the interactions between predators and their prey. In addition to the lethal effects of predation on prey populations, predators influence prey behaviour via risk effects (Werner *et al.* 1983; Brown *et al.* 1999; Creel 2018). Risk effects are the behavioural changes made by animals in response to the risk of predation and their associated costs (Lima and Dill 1990). These risk-based effects alter interactions within and across trophic levels and can thus have effects that ripple throughout an ecosystem (Brown 1999; Ford *et al.* 2014).

For prey, there is usually a trade-off between avoiding predation and engaging in other behaviours such as finding food and/or mates. These trade-offs require prey species to vary their behaviours over space and time to minimize the risk of predation while maximizing the benefits from other activities like foraging and reproducing (Abrams 1984; Brown *et al.* 1999; Brown and Kotler 2004; Creel 2018). Sometimes predation risk produces costly non-consumptive effects that compromise the fitness of an animal, usually by hindering its abilities to forage or reproduce or by inducing prolonged stress (see Boonstra *et al.* 1998). When antipredator responses are costly, prey will adapt to use those responses when the immediate risk of predation is high and the increased level of protection is therefore worth the costs incurred (Lima and Bednekoff 1999). This variation in antipredator behaviours is dependent on the prey's ability to perceive and respond to various levels of predation risk. Prey species alter antipredator responses based on a variety of cues (e.g. auditory and olfactory), habitat features, and temporal patterns that indicate elevated levels of risk (Lima 1998; Creel *et al.* 2008; Parsons *et al.* 2016; Courbin *et al.* 2018). Due to the trade-offs associated with responding to risk, it is advantageous for those responses to be

dynamic – that is, for individuals to adjust their perceptions of risk based on past experiences and to tailor their decisions using updated information, thus improving their fitness.

As ecological 'super-predators', humans and their activities influence many species via risk effects (Darimont *et al.* 2015; Clinchy *et al.* 2016; Smith *et al.* 2017; Zbyryt *et al.* 2018; Shamoon *et al.* 2018; Suraci *et al.* 2019). Non-human animals are affected by the changes in resource availability and predation risk that humans and their modified environments cause (Griffiths and Van Schaik 1993; Oriol-Cotterill *et al.* 2015a; Clinchy *et al.* 2016; Blecha *et al.* 2018; Suraci *et al.* 2019) and their individual responses to human-induced stimuli can change over time (Whittaker and Knight 1998). An example of a dynamic response to the risk that humans pose is the process of habituation (McNay 2002; Marino and Johnson 2012; Braimoh *et al.* 2018). This process is loosely defined as a loss of fear caused by repeated and consistently inconsequential exposures to certain stimuli and can have many different outcomes. In predators, for example, habituation can lead to interactions with humans that can be potentially lethal for both parties (McNay 2002).

The dynamism of risk effects is particularly relevant when examining the relationship between humans and large carnivores. While humans have the capacity as a species to decimate the populations of even the largest apex predators, the same predators can pose substantial threats to the safety and livelihoods of people living near them (Ripple *et al.* 2014). In this way, depending on the scale at which one observes the interactions between humans and large carnivores, either species may be a predator imposing risk on the other. Large carnivores are some of the most threatened species on the planet (Ripple *et al.* 2014), making it critical to understand factors that allow for attainable coexistence, conservation, and preservation.

An Abridged Review of Predator-Prey Dynamics Preceding the 21st Century

The interactions between predators and prey have piqued the interest of ecologists for over a hundred years. For many years, this interest focused on how the populations of eating and eaten species influenced one another. Darwin in his seminal work speculated that local populations of game species were predominantly limited by predation rather than the availability of food and emphasized that predation by 'vermin' far outweighed the impacts of human hunting activities (Darwin 1872). He also credited predator-prey interactions and other forms of interspecific competition with the defined geographic ranges of species, noting that much of an animal's range is decided not by gradually varying physical changes in the landscape but by relationships with other distinct living beings (Darwin 1872).

In the early twentieth century, these interactions between the populations of predators and prey were given more quantitative analysis. The works of Lotka (1925) and Volterra (1926) ushered in a new period in theoretical population ecology and provided models for characterizing how the populations of two species (one preying on the other) influence one another and achieve an equilibrium with both species' populations oscillating at different phases over time. This relationship was also examined in the context of human manipulation - Volterra compared the populations of predatory and non-predatory fish during and after World War One (i.e., in the absence of commercial fishing and after its resumption) to argue that when both species' populations are reduced evenly (such as when being harvested by fishermen), the population of the predator species will decrease while the prey species' population increases (Volterra 1926). These Lotka-Volterra models influence our understanding of predator-prey dynamics to this day, although they require important adjustments to more accurately depict observed population trends (Ayala *et al.* 1973).

Emphasis on the myriad interactions between organisms within a community continued to grow. Lindeman (1942) called for using ecosystems as the basic unit in ecology and defined relationships within those ecosystems by trophic levels, with each level depending on those below it for the energy to survive, extending from the solar radiation which sustains us all to those fiercest consumers which use excessive amounts of energy to efficiently transform the food they do catch into organic materials like teeth and claws and bones. He even applied the variations in productivity seen across an Eltonian pyramid to describe the stages of succession entire ecosystems undergo (Lindeman 1942).

Attention shifted to the mechanisms of how a diverse array of species can exist in one place, influence one another, and coexist. Herbivores can coexist because they are limited by predation, whereas carnivores, decomposers, and producers compete with one another for the resources they depend on and are limited by (Hairston *et al.* 1960). When one species is capable of monopolizing the available resources, predators are needed to keep that species under control and thus increase local species diversity (Paine 1966). Paine (1980) later refined this idea to emphasize that key interactions between certain species across trophic levels have the potential to change the structure of entire food webs, if their interaction is part of an impactful module of interactions in the larger system (such as the links between sea otters *Enhydra lutris*, urchins *Strongylocentrotus* sp., and kelp *Nereocystis-Pterygophora*; Estes and Palmisano 1974). Impactful modules frequently included predators and their prey, with the removal or addition of key predators causing cascading effects on entire ecological communities (Paine 1980).

The optimal foraging theory was first developed in the 1960s (MacArthur and Pianka 1966; Emlen 1966). In their introductory textbook for the field of behavioural ecology, first published in 1981, Davies *et al.* (2012) devote a chapter to the economics of individual animals' foraging decisions and how they

are optimized based on various currencies (e.g. time and energy). This theory prompted a surge in studies investigating the behavioural ecology of foraging (Perry and Pianka 1997), and many investigated foraging in the context of predation.

Werner *et al.* (1983) documented how the presence of predators (and thereby predation risk) altered the foraging behaviours of fish, resulting in several 'indirect effects' on the fish's population, including delayed growth rates and habitat partitioning. In the context of predation risk, the prey species was forced to balance foraging opportunities with behaviours that reduced their risk of being eaten (Werner *et al.* 1983). Abrams (1984) described how behavioural interactions across trophic levels - mainly the optimization of foraging by both predators and prey and the prey's simultaneous avoidance of predators - can have a myriad of effects on the community in terms of both local density and foraging behaviour. Another example of prey species calculating the risks and rewards of foraging in the context of predation was documented by Burt Kotler (Kotler 1984). Experimental variation in the risk and food abundance of microhabitats revealed that kangaroo rats (*Dipodomys deserti*), a species better equipped to evade attacking predators than their rodent competitors, were more likely to forage in microhabitats where nutrients and risk were both high (Kotler 1984). This foraging strategy, seemingly a result of optimizing foraging and microhabitat selection under threat of predation, influenced how various rodents partitioned space and reduced interspecific competition (Kotler 1984).

Lima and Dill (1990) reviewed the decisions prey make to avoid predation, wrote theoretical equations illustrating the many components of predation events (leading from the initial encounter to the prey's death or other outcomes), and examined how prey animals can detect and respond to any of those components to reduce their overall likelihood of death by predation. The term 'ecology of fear' was coined by Brown *et al.* (1999) as a summarization of the interactions

between predators and their prey, with both optimizing their behaviour and thus responding to fluctuations in the populations and behaviours of other species in the ecological community. They proposed developing models of both population-driven and fear-driven systems, with the latter being measured in terms of prey's fear levels and resulting catchability (Brown *et al.* 1999).

Applications for Conservation

The study of risk effects and the behavioural interactions between predators and prey has continued to grow, and the findings have important implications of the conservation of large carnivores. The reintroduction of grey wolves (*Canis lupus*) to Yellowstone National Park was a seminal case study for research studies on trophic cascades (Creel *et al.* 2005) and brought widespread attention to the idea that apex predators have crucial roles to play that impact entire ecosystems. Understanding a landscape of fear also means understanding the nuanced and complex habitat selection of predators and their prey. For example, predators might concentrate hunting efforts around prey's food and water sources (see Valeix *et al.* 2010) or reproductive activities (see Balmford and Turyaho 1992). When conservationists understand how habitat use is influenced by predator-prey dynamics, they can make better informed decisions about which habitats to protect. When conserving large carnivores, especially those sharing landscapes with human communities, understanding how they perceive and respond to humans is key. Preventing carnivores' habituation to human activities remains a crucial part of mitigating human-wildlife conflict, and efforts to carefully impose risk effects on predators via behavioural deterrents are in development to protect people and their livestock from attacks (Petracca *et al.* 2019; Petracca *et al.* 2021). Human-carnivore conflict is particularly important to address in areas like East Africa, where guilds of carnivore species are still intact (Ripple *et al.* 2014), local prey species have been depleted, and agropastoralists'

livelihoods depend on protecting their livestock from predation. Effective methods for coexistence with carnivores have already been used by some cultures for centuries, and they can help guide the strategies conservationists and pastoralists implement (or reintroduce) today (Ogada *et al.* 2003).

Overview

This thesis examines the behaviour of African lions (*Panthera leo*) and one of their primary local prey species, Uganda kob (*Kobus kob thomasi*), in the context of anthropogenic risk. Lions are an apex predator throughout their remaining range, although that range has decreased to 17% of its historic size (Ripple *et al.* 2014). Over a 21 year period (1993-2014), the global lion population also decreased by 43% (Bauer *et al.* 2016). As lions in fragmented habitats travel between protected areas and human communities, conflict with humans must be mitigated to keep people safe and to prevent the retaliatory killing of lions following livestock depredation events. Understanding lions' behaviours in the context of a human-dominated landscape is essential for their conservation. As lions also depend on their wild prey, it is equally important to understand how their preferred ungulate prey are affected by human activity.

The aim of my thesis work is to develop a better understanding of how animals' behavioural decisions are influenced by their habitat and anthropogenic risk. In Chapter Two, I measure antipredator behaviours in Uganda kob in response to both poaching activity and vehicular activity in Murchison Falls National Park in Uganda. In Chapter Three, I build a model of female lions' energy expenditure over time and space based on habitat covariates and movement data in Hwange National Park, Zimbabwe. I then examine the outputs in the context of anthropogenic risk.

Chapter Two

Flight distance of Uganda kob in response to a vehicle relative to road networks and poaching activity

Introduction

When humans and wildlife share a landscape, humans' activities can influence other animals' behaviour in a myriad of ways. The presence of human communities can cause changes in resource availability and mortality risk, to which species must adapt (Oriol-Cotterill *et al.* 2015a; Blecha *et al.* 2018). These changes can be far-reaching both geographically and ecologically, as they impact wildlife in even remote areas (Griffiths and Van Schaik 1993) and at all levels of the food web (Clinchy *et al.* 2016; Suraci *et al.* 2019). Our capacity to disrupt members of species at all trophic levels means humans can act as ecological super-predators, and there is evidence of wild species responding to that risk (Darimont *et al.* 2015; Clinchy *et al.* 2016). Even non-lethal human activities can act as sources of disturbance for wildlife that impact behaviour and thus interactions between species (Smith *et al.* 2017; Zbyryt *et al.* 2018; Shamoon *et al.* 2018; Suraci *et al.* 2019).

As interactions between wildlife and human communities increase worldwide, particularly in situations where remote habitat has been lost or degraded (Kshettry *et al.* 2017; Shamoon *et al.* 2018), it is important to understand the ways in which different human activities impact ecosystems by altering animals' behaviour, and therefore their interactions with the environment and other species. This information could inform planning and policy, for example of eco-tourism, and enable mitigation of undesirable impacts (Parsons *et al.* 2016; Kays *et al.* 2017).

This study examines the effects of a lethal human activity (poaching via wire snare traps) and a non-lethal human activity (disturbance from vehicles) in

Murchison Falls National Park, Uganda (hereafter referred to as MFNP). Both these activities can be spatially predicted in the park, with certain areas experiencing much higher snaring pressure and tourism traffic than others, which provides a natural experiment to test how each of these activities impacts behaviour in a model species that lives throughout the park. We chose to study the responses of Uganda kob (*Kobus kob thomasi*) to poaching pressure and vehicle disturbance as this species is abundant and widespread throughout the study area and serves a critical role in the ecosystem as the main source of food for the park's lion (*Panthera leo*) population (Mudumba and Jingo 2014). Many studies have examined ungulates' behavioural responses to potential threats (Stankowich 2008; Kuijper *et al.* 2014; Moll *et al.* 2017; Zbyryt *et al.* 2018), meaning a well-established set of tools exist to quantify kob's responses to our chosen stimuli. We decided to use flight distance as a metric of the amount of risk a kob was willing to tolerate in a given situation before fleeing, which has been used in multiple studies to investigate antipredator responses in ungulates (Stankowich 2008; Malo *et al.* 2011; Muposhi *et al.* 2016).

By measuring the flight distance of many individual kob and contextualizing those observations spatially, one can discern underlying variation in the risk kob have associated with certain landscape features. Assessing those variations in perceived risk may also reveal the answers to questions about which human activities alter kob behaviour, how kob respond to those activities, and therefore to which human activities kob may be able to adapt. While flight distance is an intuitive measurement in response to a vehicle's approach, the mechanism linking snaring activity to flight distance is less direct. In the case of snaring, flight distance is less of a direct response and more indicative of a general, 'baseline' wariness of the animal in that particular location. The assumption is if snares impact the wariness of kobs, kobs will be generally more wary in those locations with many snares, and thus will have longer flight

distances than they would in areas where they feel lower ambient risk levels. That increase in flight distance from any stimulus could be similar to increases in routine vigilance associated with proactive antipredator behaviours (Creel 2018).

We used an observational approach to investigate the behavioural response of kob to two human activities; vehicle use and poaching. Vehicle use was represented by varying distances to the nearest road and poaching was quantified by large-scale differences in snaring pressure in different areas of the park. In the following section we describe the methods we used to obtain our results, which suggest biologically meaningful differences in kob behaviour between the sexes. To conclude, we discuss these findings in light of human-wildlife interactions worldwide and how these findings may be used to guide future studies and inform plans regarding the infrastructure and policy within protected areas.

Methods

Study Area and Establishment of Landscape Poaching and Tourism Metrics

Our primary study area within MFNP, located in Northwest Uganda, covered approximately 880 km^2 in the park's northern bank (the northern half of the park bordered to the south by the Victoria Nile, Fig. 1). The climate is predominantly arid with a dry season from July to March, a wet season from April to June, and a less intense wet season from September to October. The study area features open savanna with woodlands consisting of whistling acacia (*Acacia drepanolobium*) and borassus palm (*Borassus aethiopum*) trees.

Most of the illegal activity of deploying snares in MFNP comes from communities to the west of the park (Pakwach and bordering villages), and occurs predominantly in the western region of the northern bank (Fig. 1) (Mudumba 2019, Chapter 4). This distribution coincides with findings that snaring mostly occurs within a day's travel of the hunters' communities, acts as an edge effect within national parks, and is most intense where wildlife is abundant (Loveridge *et al.* 2017). While many snare deployers enter the park via the White and Victoria Nile Rivers (Fig. 1) and walk to check traps from the river's edge, the location of a 200-foot waterfall (i.e., Murchison Falls) restricts travel by boat into the eastern half of the park. The terrain becomes steeper and more densely vegetated along ravines north of the waterfall, and the frequency of wire snaring drops precipitously east from this natural barrier (Fig. 1). For these reasons, we have divided our study area into a western intense (high snaring pressure) site and an eastern infrequent (low snaring pressure) site (Fig. 1). This is not to suggest that there is no snaring or poaching activity in the eastern half of the northern bank, but the spatial density of those traps and the frequency of poaching is much lower due to restrictions in access and the relative distance from towns and villages (Mudumba 2019, Chapter 4). While this division is useful,

there may also be a confounding effect with poaching pressure and geography, including terrain steepness and vegetation.

As off-road tourism is strictly prohibited and that policy is enforced in MFNP, roads can be used as an indirect measure of vehicular activity in an area. For this reason, distance to the nearest road was used as a surrogate metric for vehicular activity that kob would be experiencing at the landscape scale.

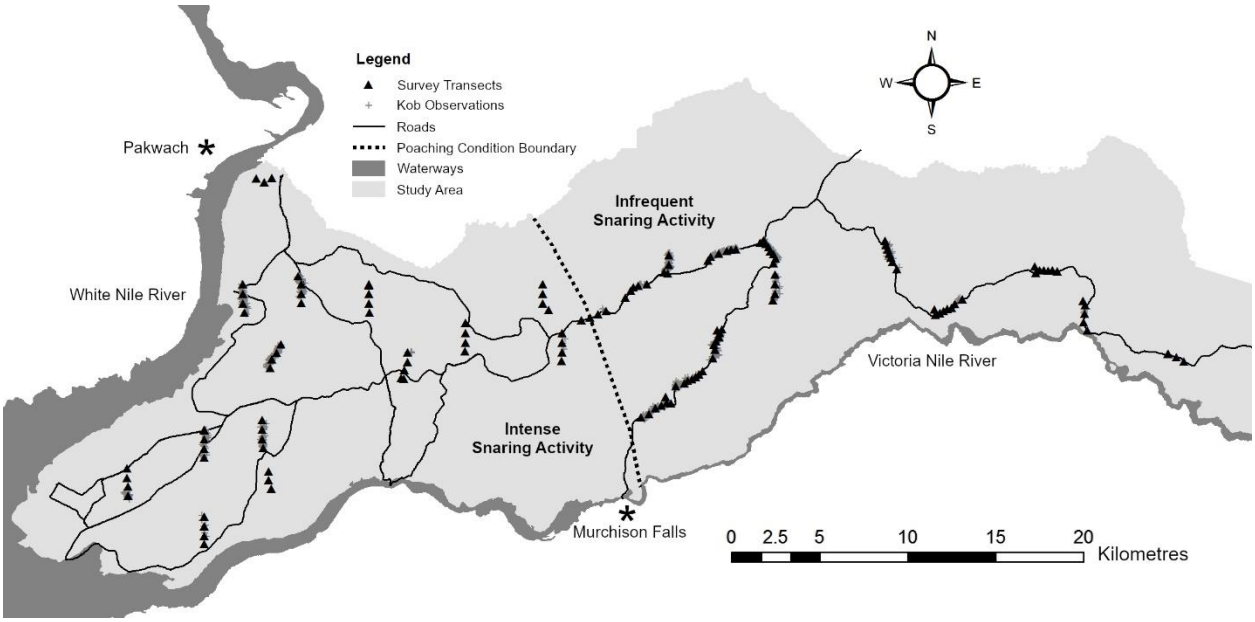


Figure 1. A map of our study area on the northern bank of Murchison Falls National Park in Uganda. The southern border of the study area is the Victoria Nile, and the Western border is the White Nile. Black lines indicate the roads in the park, which were unpaved during the time of the study. Black triangles indicate set markers along transects used to observe the flight distances of Uganda kob. Grey crosses represent individual kob behavioural observations. The study area was bisected (marked by a dashed line) into two poaching conditions: the western site with intense snaring activity, and the eastern site with infrequent snaring activity. Pakwach, the largest town close to the study area, is marked by a star.

Data Collection

We collected observational data between 2018 and 2019. We decided to limit our observations to kob within grasslands because kob and their behaviours are most readily observed in those areas and grassland covers most of the northern bank (Mudumba and Jingo 2014). To randomize our observations of individual kob, we used ArcGIS software to generate randomly located transects

along which to drive our vehicle throughout the study area. An equal number of transects were generated in both the Intense and Infrequent poaching sites. All transects were 1.5km long and ran in a north-south orientation where possible. The detectability of kob within MFNP grasslands had been determined as close to 1 within 250m for a previous study (Mudumba 2019, Chapter 3) and using those results we set the radial width of our transects at 250m which resulted in transects 500m wide.

Data were collected in 2018 and 2019, and in both years, efforts were made to drive along the transect in a direction that prevented us from disturbing wildlife on the transect prior to data collection. Each transect was sampled once in 2018, but in 2019 transects were sampled multiple times throughout the field season, with each round of sampling referred to as a replicate. As kob are very mobile, form dynamic herds, and frequently change ownership of territories (Balmford 1992; Deutsch and Weeks 1992), sampling one transect repeatedly on separate days was unlikely to result in repeatedly sampling the same individuals. Even when kobs moved away from our vehicle during observations, the speed and distance involved as we moved on to the next transect reasonably prevented the same groups of kobs being sampled twice at adjacent transects. While there may be some chance that kobs were repeatedly sampled across the entire study season, the number of kobs sampled compared to the number of kobs present in the park is a tiny proportion, and the odds of repeatedly sampling the same kob would thus be quite low as they moved around the landscape. Across replicates in 2019, we ensured all transects (but one) were sampled at various times of day to avoid collinearities between time of day and location. We also only included transects where kob had been observed in 2019 for the second and third replicates to avoid wasting resources sampling areas devoid of kob that season.

We recorded kob flight distances via vehicle-based surveys. We collected all data through July and August across consecutive years to achieve consistent

climatic conditions. We did not collect data in the rain. By limiting our data collection between the hours of 10:00 and 16:00, we targeted the warmest times of day when predation risk is lowest from nocturnal predators and kob were less likely to be responding to the risk of lion predation (Sirot *et al.* 2016).

We drove a Toyota Landcruiser along each transect at a speed at or below 10km/h. While driving along the transect, two to three observers in the vehicle scanned for kob through the open roof while another recorded data and navigated the driver along the transect. Once a kob was seen anywhere ahead of the vehicle, it was watched continuously by an observer until it fled (defined as a clear deviation in previous behaviours to move away from the vehicle) or until the moving vehicle passed it. When a kob fled, the observer would state “flight” and the vehicle stopped so the observer could obtain an accurate reading with a rangefinder, directed to where the kob was when it fled. We approximated each kob’s GPS location on a Garmin GPS (GPSMAP 78sc) by collecting the coordinates of the vehicle at the time of observation, the distance to the kob, and the direction toward the kob from the vehicle using an azimuth compass. Individual GPS locations were not recorded in 2018 and so those kobs’ locations were approximated as the midpoint of the transect section in which they were observed. We recorded the sex of the kob and whether it was an adult or a subadult. Juveniles were included in group size counts but not used as focal animals.

Group size was also recorded; a group was defined as animals within 10m of each other at the moment of flight. We measured group size in this way, understanding that the groups were parts of larger herds, as we wanted to focus on sub-groups of kob that might share more fine-scale environmental conditions that could influence flight distance, such as location relative to vegetative cover and the moment the vehicle became visible to the animals. When observing groups of kob, the first individual to flee in each group was taken as the focal

animal. This consistently biased our collection to focus on the flightiest individuals.

When kob did not flee from the vehicle, we recorded the shortest distance reached between them and the vehicle (typically the location of the kob when at a 90 degree angle from the transect and the vehicle's trajectory, before being passed by the vehicle). These distances were not used in the analysis because they were not purely determined by the animal's behaviour and were, instead, circumstantial reflections of how close the vehicle got to an animal that had not yet reached its flight distance. There was no way of knowing what those kobs' true flight distances were, or even if they would have fled from the vehicle at all.

Oribis (*Ourebia ourebi*) are small antelope that vocalize with a loud whistle to indicate the presence of predators, which may influence kob antipredator behaviours (since ungulates have been documented relying on the cues of other species to mitigate risk, Schmitt *et al.* 2016) and were thus recorded as present for an observation if they were observed within 50m of the focal kob.

Data Analysis

Using the lme4 (Bates *et al.* 2015) and lmerTest (Kuznetsova *et al.* 2017) packages in RStudio (R Core Team 2015; RStudio Team 2015), we created linear mixed-effects models to answer a set of specific research questions. Those questions and their corresponding models are listed in Table 1.

Table 1. A summary of the models created to analyse the flight distances of Uganda kob in response to distance to nearest road and poaching conditions.

Model	Purpose
Model One **(M1)**	Tests if kob differ in their flight distances between poaching conditions.
Model Two **(M2)**	Tests if male and female kob have different flight distances on average.
Model Three **(M3)**	Tests if male and female kob respond differently to poaching conditions.
Model Four **(M4)**	Tests if flight distances in all kob change with distance to the nearest road.
Model Five A **(M5a)**	Tests if male and female kob have different flight distances but respond in the same way to distance to the nearest road.
Model Five B **(M5b)**	Tests if the flight distances of male and female kob respond differently to distance to the nearest road.
Model Six A **(M6a)**	Tests if kob in different poaching conditions have different flight distances but respond in the same way to distance to the nearest road.
Model Six B **(M6b)**	Tests if the poaching condition alters how flight distance changes with distance to the nearest road.

While the randomly generated transects originally occurred at a variety of distances from the nearest road throughout the study area, some transects had to be moved onto roads in areas where off-road travel was impossible. As the infrequent poaching condition overlapped spatially with almost all of the transects that had to be conducted on the road, 12 of its 14 transects were relocated and it was not possible to distinguish the effects of poaching condition from distance to the nearest road (since so many data were clustered at very short distances from the nearest road in the combined dataset and those data were colinear with the infrequent poaching condition, Fig. 2).

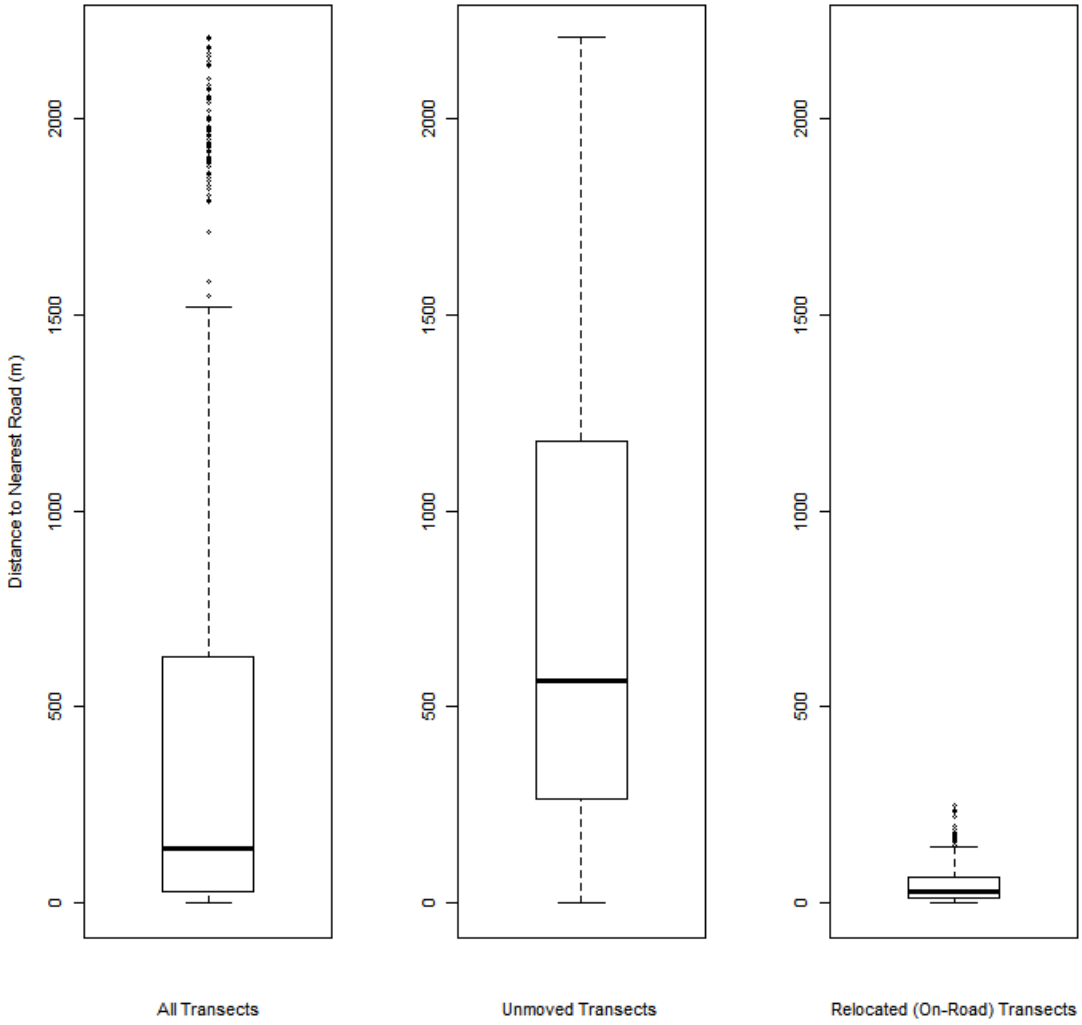


Figure 2a. Box and whisker plots comparing distances to the nearest road recorded within the full dataset and subsets including only observations from off-road transects and only observations from transects that were conducted entirely on roads. The centre lines indicate the median of each dataset.

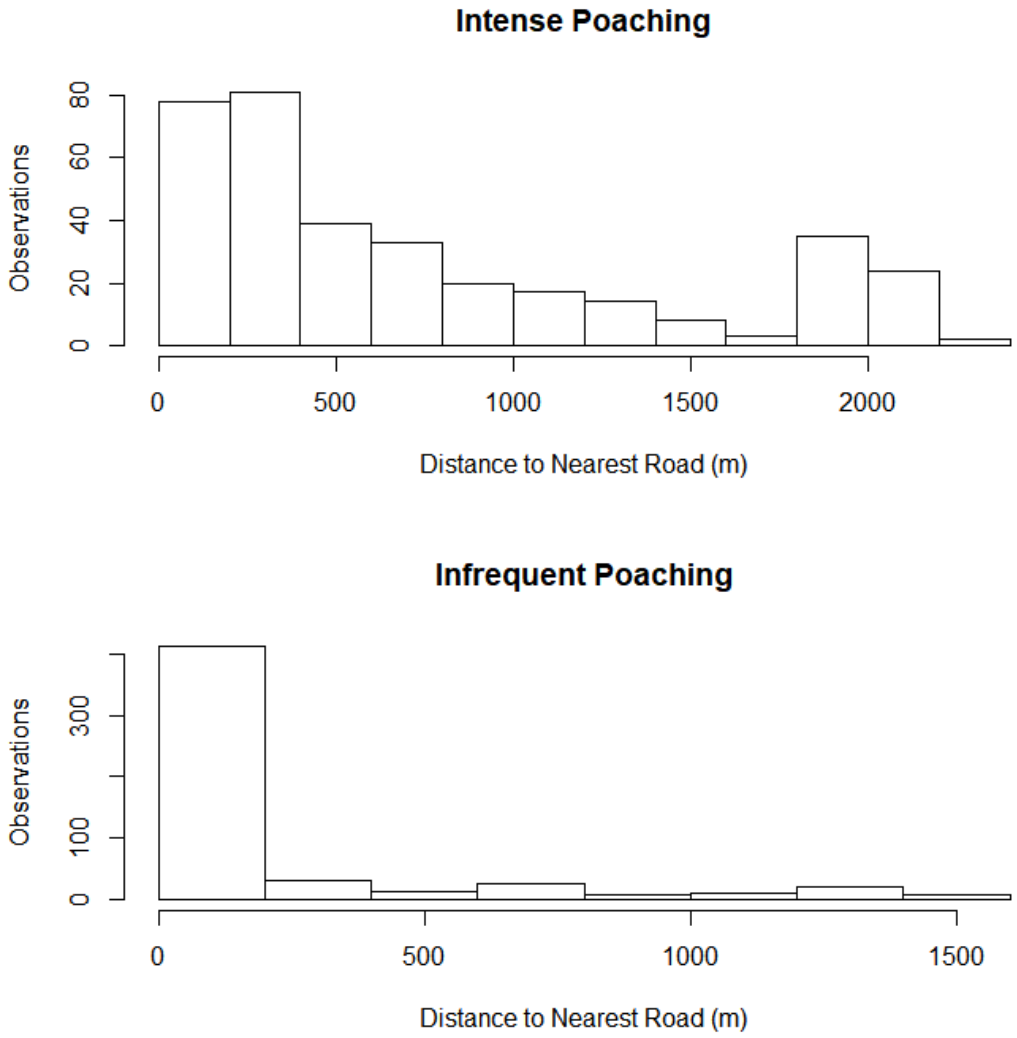


Figure 2b. Histograms comparing the counts of kob behavioural observations made at various distances from the nearest road (m) within both poaching conditions (Intense and Infrequent). While observations within the intense poaching condition were made at a variety of distances from the nearest road, almost all of the observations from the infrequent poaching condition were collected within 250m of the road. This resulted in collinearity between the infrequent poaching condition and distance to the nearest road.

To deal with this, where possible, statistical analyses were undertaken using a subset of the data with on-road transects removed (M2, M4, M5a, and M5b).

We used a box-cox transformation to find the most appropriate transformation for flight distance based on each model's assumptions of normality. For models M1-M3, Levene's Tests revealed p-values greater than 0.05, indicating homogeneity of variance for the groups being compared. For each model, random effects were included or not included based on AIC level. Once models were completed, an assortment of other tests and visual checks were used to ensure each model met its statistical assumptions and was appropriate for the data and the question being addressed, including Q-Q plots, histograms of the residuals, plots of residuals vs fitted values, and comparisons of residuals across categorical variables validated by Bartlett tests and tests of variance. Marginal and conditional R^2 values were calculated using the piecewiseSEM package (Lefcheck 2016).

Appendix S1 contains the construction for each model in R and their outputs.

Results

Flight distances were not different across poaching conditions (M1, Fig. 3, t = 0.997, p = 0.328, df = 25).

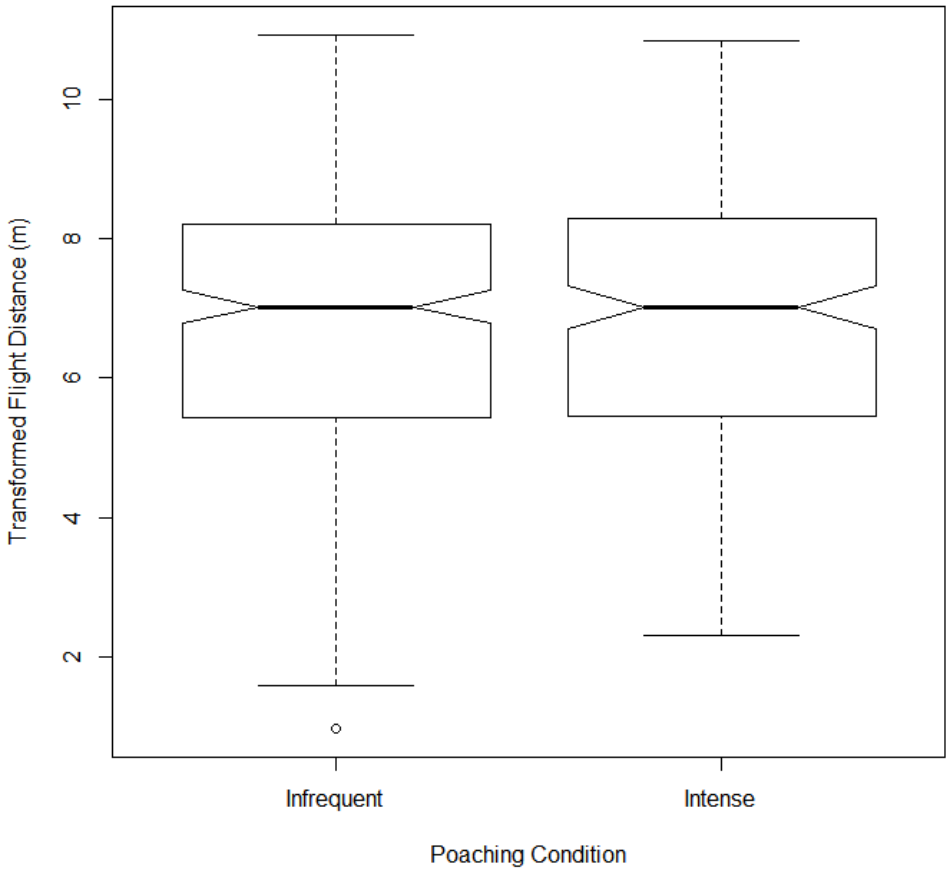


Figure 3. Notched box and whisker plots of the (transformed) flight distances of Uganda kob compared across poaching conditions in Murchison Falls National Park. The center lines indicate the median for each condition. There was no significant difference between flight distances in the Test and Control poaching conditions (t = 0.997, p = 0.328, df = 25).

A linear mixed-effects regression model showed that there was some evidence of a significant relationship between flight distance and the distance to the nearest road in the full dataset (M4, M4.O; p = 0.0518 and p = 0.164 for all transects and the subset respectively). When accounting for poaching conditions, a weak significant relationship was found between flight distance and distance to

the nearest road in the infrequent poaching condition only (M6b, Table 2). A simpler interaction model showed no significant relationship between flight distance and distance to the nearest road as well as no significant difference in the intercepts between poaching conditions (M6a).

When accounting for sex, a weak relationship between flight distance and distance to the nearest road was found that applied for both sexes (M5a, Table 2). A model allowing each sex to have its own slope found a relationship between only females' flight distances and the distance to the nearest road (M5b, Table 2), but no relationships between flight distance and distance to the nearest road were found in an identical model with on-road transects removed (M5b.O). Similarly, removing the on-road transects from the simpler model resulted in no statistically significant relationship between flight distance and distance to the nearest road in either sex (M5a.O). However, this model indicated that at the same distance from the nearest road, the (back-transformed) flight distances of males were on average 1.8m shorter than those of females (M5a.O, $p = 0.00165$).

Table 2. Table showing all the significant relationships found between flight distance and distance to the nearest road (Flight distance (m) ~ Distance to nearest road (m)) in linear mixed-effects models. Estimates are equivalent to the increase in flight distance in (transformed) metres associated with every additional meter from the nearest road. Categorical variables (poaching condition and sex) were included as additional fixed effects and estimates are displayed beneath their corresponding categories below. The marginal R^2 indicates the proportion of the variance explained by the fixed effects.

Model	**Estimate by Category**			**P value**	**Marginal R^2**
	Intense Poaching		*Infrequent Poaching*		
M6b	---		0.0011765	0.0178	0.0402
	Male		*Female*		
M5a	0.0005	=	0.0005	0.0457	0.0281
M5b	---		0.0006	0.0451	0.0284

A linear mixed-effects model comparing flight distance across the sexes resulted in no significant difference (M2), but once on-road transects were removed from the model there was a difference between the sexes, with males' average (back-transformed) flight distances being 1.7m shorter than females' (Fig. 4, M2.O; *t* = -3.019, p = 0.0028, df = 251). When comparing flight distances across both sex and poaching condition, a linear mixed-effects model highlighted a significant interaction term (M3, p = 0.0207) with a difference in the sexes' flight distances only observed in the intense poaching condition (Fig. 5).

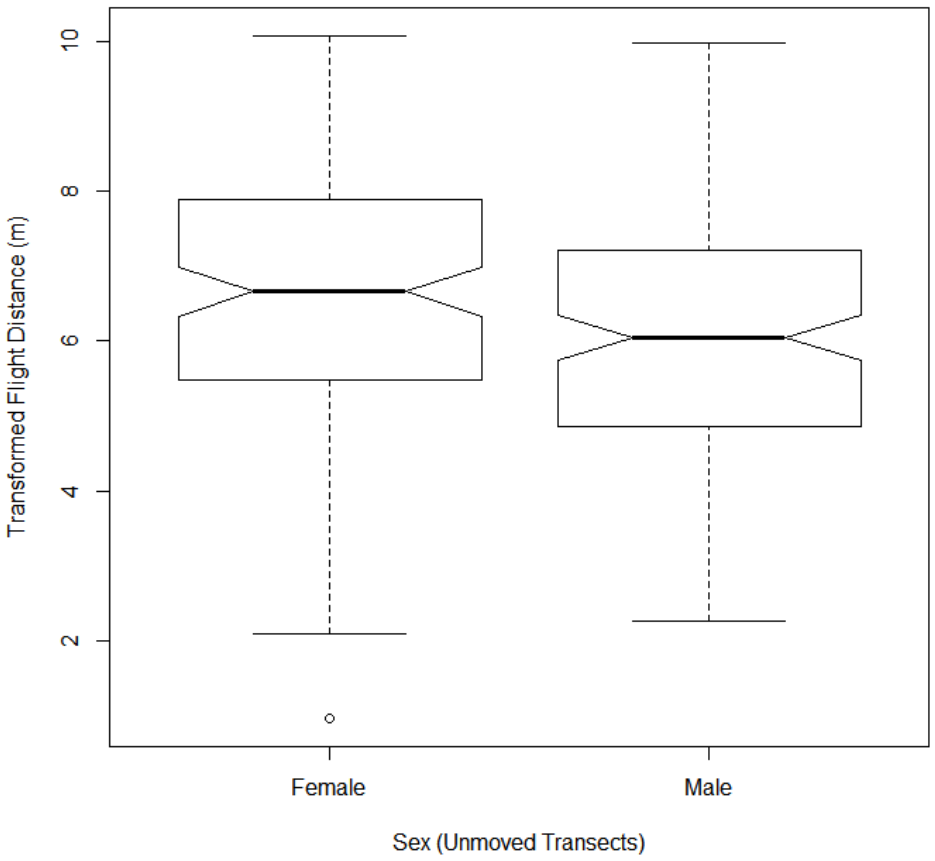


Figure 4. Notched box and whisker plots comparing the (transformed) flight distances of female and male Uganda kob in Murchison Falls National Park excluding data collected from transects moved onto roads. The center lines indicate the median for each sex. There was a significant difference between flight distances across the sexes ($t = -3.019$, $p = 0.0028$, $df = 251$).

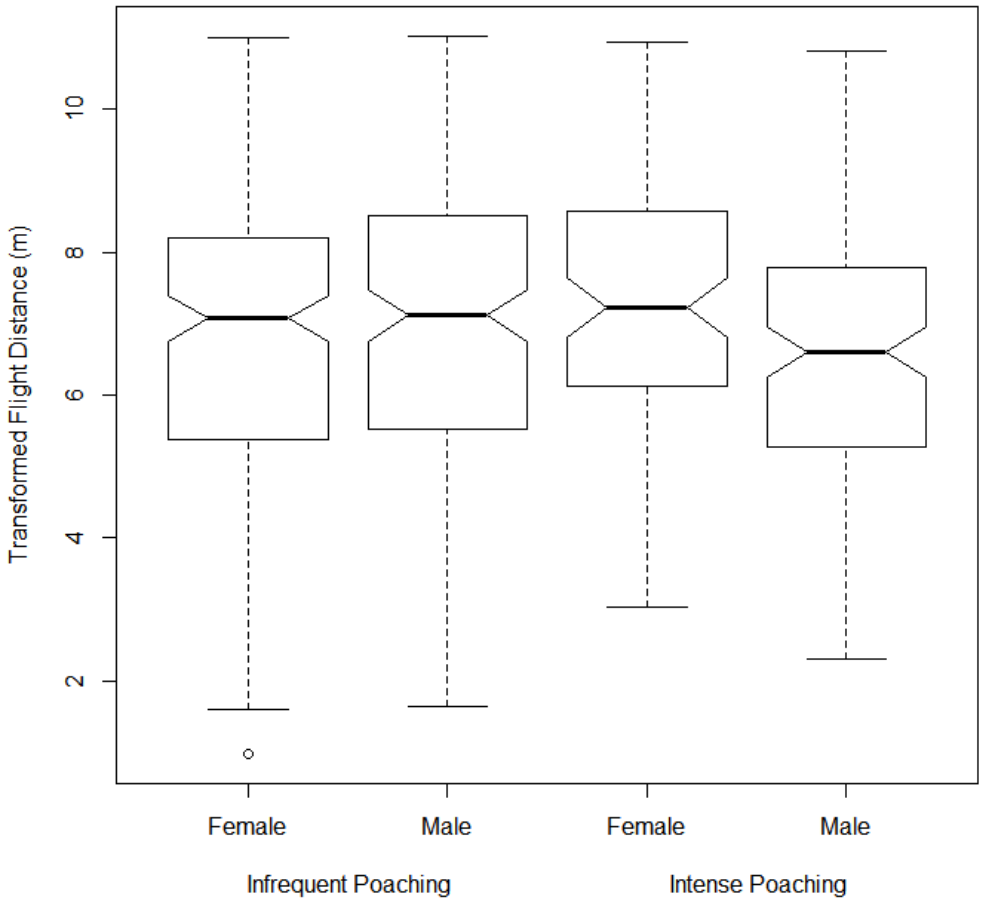


Figure 5. Notched box and whisker plots of the (transformed) flight distances of Uganda kob in Murchison Falls National Park compared across sexes and poaching conditions. The center lines indicate the median for each combination of sex and poaching condition. A linear mixed-effects regression model found a significant interaction term between sex and poaching condition ($p = 0.0207$).

Discussion

After investigating the variation in kob flight distance in relation to poaching pressure and vehicular activity along roads, our results indicated there was no difference in flight distance across the poaching conditions and insubstantial evidence of roads affecting flight distance. We did however observe that males had shorter flight distances than females in some areas (1.7m shorter, M2.O; 1.8m shorter, M5a.O), which may reflect an increased tolerance of risk in the presence of intrasexual competition. We discuss these findings and other considerations of the study in more detail below.

Poaching activity / Comparisons across the two conditions

While wire snaring is certainly a threat to wildlife in MFNP as it is in other protected areas (Mudumba and Jingo 2014; Loveridge *et al.* 2017), it does not appear to have had a discernible impact on the flight distances of kob. This lack of an effect could be due to how poaching activity was quantified in our study, which will be discussed in the methodological considerations later in the discussion. If we describe the threat of wire snares as akin to the threat of a lie-and-wait ambush predator, we might expect to see kob avoiding those threats in similar ways, such as avoiding the trees and brush where both predators might be lurking, altering their levels of vigilance while foraging, or adjusting group sizes to reflect the given risk of the situation (Valeix *et al.* 2009; Creel *et al.* 2014). Perhaps a study that investigated kob's various antipredator behaviours at a much finer scale could pick up more subtle changes in behaviour in response to snaring activity across microhabitats (Brown and Kotler 2004) within the park.

Vehicular Activity / The Response to Roads

While the results of our analysis indicate statistically significant relationships between flight distance and distance to the nearest road, the effect

was not large or consistent across models (Table 3). The low marginal R^2 values also indicated that only a small fraction of the variance in the data could be explained by the fixed effects (Table 2), as we address later in the discussion.

Table 3. Table showing all the significant relationships found between flight distance and distance to the nearest road (Flight distance (m) ~ Distance to nearest road (m)) in linear mixed-effects models, with estimates back-transformed to indicate actual changes in flight distance (m) at various distances from the nearest road. Estimates had to be back-transformed at specific distances from the nearest road because the transformation was non-linear.

	Change in flight distance (m) with each additional meter from road		
Model	10m from road	100m from road	1km from road
M6b	1.0118	1.1232	2.8471
M5a	1.0055	1.0557	1.67309
M5b	1.0063	1.06436	1.7993

Distance to the nearest road can be used as an indirect measurement of disturbance. It has been shown to directly correlate with anthropogenic disturbance in geese (*Anser brachyrhynchus*) and alter where flocks of geese forage, although that study did not examine spatiotemporal variation or quantify the risk geese perceive relative to road proximity to investigate habituation to that disturbance (Gill *et al.* 1996). The lack of a strong significant relationship between flight distance and distance to the nearest road indicates that kob in MFNP react to a slowly approaching vehicle similarly when they are very close to a road as they do when far away from one. This result does not suggest they have become habituated to vehicle traffic on roads. That being said, M6b showed there was only a relationship between distance to the nearest road and flight distance in the infrequent poaching site, which is also the site where roads are used much less frequently. That finding corresponds with a study on guanaco which revealed that

the ungulates were sensitive to traffic, with more traffic on roads resulting in faster habituation to vehicles and guanaco being more likely to flee from vehicles on less-used roads (Marino and Johnson 2012). In a review of ungulate flight responses to anthropogenic disturbance, all but one of the studies that used flight distance as a metric and compared areas of high and low human traffic found that flight distances were greater with lower human traffic (Stankowich 2008). The aforementioned guanaco study found that groups with young were more likely to flee and that mothers often fled first in a group (Marino and Johnson 2012), which could correspond with our results from M5b (indicating females' flight distances are affected by roads but not males'). Likelihood of flight and the presence of an effect from distance to road are not equatable, but these are interesting overlaps that may suggest traffic levels and sex are important factors influencing kob responses to vehicular disturbance. Other studies have shown similar species of ungulates becoming somewhat habituated to the presence of vehicles on roads, but did not examine flight behaviour farther away from them (Mulero-Pázmány *et al.* 2016).

We have anecdotally observed kob in MFNP moving in large herds that freely cross high-traffic roads and do not change direction or flee in response to vehicles even in very close proximity. While our study does not show strong evidence that kob are adjusting their antipredator behaviours relative to their distance from the nearest road, it could be that a study incorporating levels of traffic along those roads would provide more insights into kob's perceptions of risk from vehicular disturbance in the park. The speed and direction of vehicles relative to kob may also greatly influence their perception of risk, as faster and more direct approaches by potential threats have resulted in increased flight responses in multiple species of ungulate (Stankowich 2008).

Differences Between Sexes

Statistically significant differences in behaviour between males and females were found in the results of M3, which indicated that the difference in flight distance between the sexes was significantly different in the intense poaching site compared to the infrequent poaching site. M2.O, which is essentially an analysis done predominantly in the intense poaching site, showed a significant difference between male and female flight distance while the same analysis across the entirety of the park (M2) did not. This finding suggests that males and females diverge in their tolerance of risk in the intense site (with males being more tolerant/less willing to flee than females) while they respond more similarly to each other in the infrequent site. A difference of 1.7m or 1.8m may be small, but in a landscape with variable vegetative cover and microhabitats defined by dense thickets separated by a few metres of grass, that decrease in flight distance could be quite impactful for a kob fleeing from a true threat.

We may be able to explain these behaviours by considering the reproductive strategies of male kob. Multiple studies using flight (or 'fleeing behaviour') as a response variable have found that the cost of leaving a particular site will influence the animal's flight, as reviewed by Frid and Dill (2002). A male's chances of mating relate directly to his spatial location when guarding a territory, both on and off lek breeding arenas (Leuthold 1966; Estes 1991; Balmford 1992; Balmford and Turyaho 1992). Males' movements become smaller with proximity to a lek's centre, as territories tend to decrease in size as one approaches the centre of a lek and competition becomes more fierce for desirable patches (Estes 1991; Deutsch and Weeks 1992). Therefore a male kob holding a patch of territory on or near a lek faces potentially high costs for moving away from his patch in response to a potential threat, and may consequently be less willing to flee because of the incurred costs (Bonnot *et al.* 2017). Unfortunately we only have anecdotal observations of more leks being present in the intense poaching

site than in the infrequent poaching site, although the taller grass height and occurrence of woodlands and thickets in the infrequent site would render it a generally less desirable landscape for kob leks (Deutsch and Weeks 1992). If we assume the intense site is used for lekking more than the infrequent site, males' unwillingness to sacrifice territories may explain their shorter flight distances in the intense site.

Methodological Considerations: Poaching condition as an independent variable

It may be that halving the study area into two poaching conditions could not accurately capture varying degrees of poaching pressure experienced by kob in this landscape, and that poaching activity measured at a finer spatial scale would be more useful for assessing its impacts on kob behaviour. An alternative approach might be to calculate poaching pressure via retrieved snare density within an area of the park over some amount of time to provide more fine-scale information on poaching pressure. If we assume that poaching pressure was accurately represented by the two poaching conditions used in this analysis, we might still explain its lack of impact on flight distance in other methodological terms. As a vehicle is quite dissimilar from a typical ambush predator, kob might not express their perception of risk from snares in response to the vehicle, and therefore using a slow-moving vehicle as a stimulus may not accurately capture kob responses to poaching activity. Snaring is not the only form of poaching in the park, but other forms are predominantly done on foot, and again are unlikely to be conflated with vehicles by kob (particularly as numerous studies have indicated ungulates have higher flight responses to humans than to vehicles when directly compared, Stankowich 2008). Poaching activity in its various forms might induce a generally heightened sense of anxiety in ungulates, and perhaps that could lead to increased flight distances when stimulated by vehicles or

people, but such a generalized increase in anxiety at the landscape level would be difficult to attribute to any particular source.

Methodological Considerations: Significance and comparing subsets of data

The ecological relevance on our findings hinge on statistical significance. With this, it is important to acknowledge that even where statistically significant effects were detected, the marginal R^2 values (Nakagawa and Schielzeth 2013) for all of the models were low. The R^2 value is the proportion of the total variance in our response variable (flight distance) that was explained by the variance in our explanatory variable (distance to nearest road) (Crawley 2013). Low R^2 values indicate that extrapolating these results should be done with caution, but do not inherently mean that our models were poorly fitted for the data, especially for an observational ecological study. McCullagh and Nelder (1989, pages 118-119) argued a high residual deviance (a metric used as a goodness of fit measure for generalized linear models that is theoretically similar to the R^2 value inverted) does not inherently mean the model is a poor fit. Low R^2 values for significant relationships are also not uncommon in ecological studies (Møller and Jennions 2002). A low R^2 from a significant difference in flight distance in response to distance to nearest road would mean a small proportion of a kob's variation in flight distance was attributable to its distance to the nearest road, with the rest of the variance coming from an assortment of factors that are extremely complex and difficult to measure, as biological and ecological factors often are (Møller and Jennions 2002).

An interesting component of this study was the comparison of results between models using all of the data and a subset of the data with on-road transects removed. In some cases, this change resulted in no meaningful difference, but for models M2, M5a, and M5b, the removal of on-road transects either produced or removed a statistically significant result. We can potentially

credit the differing results of M2 and M2.O to the presence of leks in the Test site, as described above. The change in significance between the estimates of M5a and M5a.O is difficult to explain, but is not particularly striking because of the weak ecological implications, while the significance of the differences between sexes in models M5a and M5a.O behave very similarly to the results of models M2 and M2.O. Model M5b initially found a significant relationship between females' flight distances and the distance to the nearest road, but when repeated using the subset it was no longer significant. This result is also not easily explained, but again given the estimate's very small size and low marginal R^2 value, it is unlikely to be ecologically meaningful.

Methodological Considerations: Data collection

Practical methodological issues should also be considered when reviewing these results. The compass being used to determine each kob's azimuth (and therefore calculate its GPS location and distance to the nearest road) was known to be sporadically malfunctioning during one afternoon of data collection, but at this time the kob being observed were almost all within 100m of the vehicle and thus any potential miscalculations of their locations would be off by a maximum of 200m and are unlikely to have greatly altered our results. Despite our best efforts to be quiet, the sound of a car's engine is likely audible to kob from more than 250m away and there may have been flight behaviours we missed because they happened before we were within sight. There were also areas in the infrequent poaching site where large herds of kob seemed to flee from our vehicle when we were still much greater than 250m away and thus those flights were not recorded. If we regularly missed the initial flight responses of kob outside of 250m or otherwise obscured/out of sight, it would skew our flight distances to be lower than reality. We do not believe this to be a significant threat to the interpretation of our results because we worked predominantly in open

areas where most groups of kob could be seen continuously within 250m and noticed within 500m and the sound of the vehicle did not usually cause kob to flee from over 250m away.

Implications

It is important to understand the impacts on animal behaviour that may arise from changes to a protected area's infrastructure or policies. MFNP is currently undergoing large infrastructural renovations, including the construction of a multi-lane bridge and tarmac road which will bisect the study area and provide a route through the park that physically (if not legally) allows high-speed travel. If drivers increase their speeds, they may increase collisions with wildlife and it will be valuable to know if kob adjust their perceptions of risk from roads and vehicles in response to that change. This study can serve as an important baseline for future work investigating those behavioural adjustments. As kob attempt to cross the road to access the water of the Nile on the park's western boundary, high-speed vehicles could cause more collisions and become more of a threat to the population. Because these data were collected during the road's construction (before its frequent use or vehicles' ability to travel at great speed along it), this study can be the 'before' in a 'before and after' analysis of a multilane road's impacts on wildlife. Such a study would be immensely valuable, as it is important to understand how wildlife (particularly ungulates which are often struck by vehicles worldwide) will or will not adapt to the presence of and use of road networks, particularly those built through protected areas and habitats densely populated by wildlife.

Conclusions

While our study did not reveal a basic relationship between flight distance and vehicular disturbance (via distance to the nearest road) or poaching pressure, it did reveal some potential differences between males and females and possible interactions between sex, location, and distance to the nearest road. The most ecologically meaningful results are likely the observed differences in flight distance between males and females and how those differences may relate to reproductive behaviours, including male intrasexual competition and the protection of young by mothers. Regardless of the presence or absence of significant findings, these results provide an important baseline for future studies wishing to investigate the impact of massive infrastructural changes on the antipredator behaviours of ungulates in a protected area.

Chapter Three

Estimating the energy expenditure of lions over space and time using landscape covariates

Introduction

In the cost-benefit calculations underpinning all animals' behavioural decisions, energy can be used as a common currency (in addition to the probability of survival or offspring produced, depending on one's research question; Mangel and Clark 1988, Ch 2.3, 2.5). As such, energy expenditure and metabolic processes are key underlying components of all animals' behaviour. They inform the amount of food an animal needs, how frequently that food must be obtained, which activities the animal is capable of performing given the amount of food acquired, and whether the animal has enough reserves to reproduce and carry out other essential tasks. As such, understanding an animal's energy expenditure can be an important part of developing an effective conservation strategy (Rosen and Trites 2002; Miller *et al.* 2014). It is particularly important to understand large carnivores' energy expenditures due to the high amounts of energy required to pursue and capture prey and maintain their day-to-day functions (Muñoz-Garcia and Williams 2005).

Energy expenditure is difficult and expensive to monitor directly in large carnivores, and particularly so in the wild. Therefore researchers aiming to estimate energy expenditure generally depend on studies of captive animals (e.g. Chassin *et al.* 1976) and models with measurable proxy variables, such as habitat features and movement patterns (Miller *et al.* 2014; Williams *et al.* 2014). In many cases, it is more appropriate to model behaviour without including estimates of energy expenditure, especially when the research question can be answered with movement data or recorded decisions alone. Many studies have modelled patch selection in carnivores, often with a focus on identifying areas

where carnivores are most likely to predate livestock near human communities (Miller 2015; Miller *et al.* 2015).

A theoretical advantage of including energetic measurements in a behavioural model is the ability to solve for other parameters which are difficult or impossible to measure directly. This chapter is a first step toward my interest: the possibility of measuring risk perceived by carnivores, a variable that is almost impossible to measure directly in the field. Previous studies have examined how predators respond to human-induced risk by ecologically relevant but indirect means, with researchers defining levels of risk based on relevant landscape features (Smith *et al.* 2015; Sazatornil *et al.* 2016). Other studies have calculated risk based on mortality events (Loveridge *et al.* 2017). The first step in producing a behavioural model that could solve for perceived risk as a parameter is to build a model capable of estimating energy expenditure itself. Doing so would highlight the parameters that are important to include in a lion's decision-making process as well as improve understanding of lions' behaviour in general. Once a model has been made that can predict energy expenditure with some accuracy, using measurable parameters, one could construct a dynamic programming model using those parameters with energy as the currency and compare the modelled decisions against reality. If the lion's perceived risk is included as a variable, one could solve for it at each time step based on the values of the other parameters and the lion's decisions (assuming the lion is behaving optimally).

The lion (*Panthera leo*) population of Hwange National Park in Zimbabwe has been monitored for more than three decades. Dating back to 1990, a substantial database of global positioning system (GPS) records from collared lions can track individual lions from various prides. The population's interactions with nearby communities and livestock (Kuiper *et al.* 2015; Loveridge *et al.* 2017; Petracca *et al.* 2019) makes it an ideal study system when testing and developing models to examine lions' behaviour in the context of human activity.

In this chapter I will use GPS records to construct a model of female lions' changing energy levels as a result of landscape features and estimated metabolic parameters. I will determine if there a relationship between lions' energy levels and their position relative to their home ranges, with the prediction that a lion's energy levels will be higher on average within its home range. That result could indicate if our estimated energy levels have some grounding in reality, assuming lions are choosing to spend most of their time in locations where they can conserve or replenish their energetic reserves. I also investigate if the estimated energy levels have any relationship with observed anthropogenic risk, and if so, what that relationship is. If high anthropogenic risk is correlated with higher average energy levels, that would support the notion that some of these risky areas surrounding the park may act as 'attractive sinks' (Loveridge *et al.* 2017).

Methods

Study Area

Hwange National Park (hereafter HNP, 19°0' S, 27°3' E) is located in north-western Zimbabwe and covers 14,600km^2 of semi-arid savanna (Loveridge *et al.* 2009). The altitude ranges from 800 to 1,100m (Loveridge *et al.* 2009) and the mean annual rainfall is 600mm (Loveridge *et al.* 2017). Seasonality has a strong effect on rainfall and water availability throughout the year, and prey congregate to drink at artificially supplied waterholes in the dry months (May-October, Davidson *et al.* 2013). The vegetation is predominantly woodland and bushland savanna on both soil and sandy terrains (Arraut *et al.* 2018).

This chapter uses data on lions which moved beyond HNP and into the surrounding protected areas and community lands in Zimbabwe and Botswana. Residents in the neighbouring communal lands are mostly subsistence agropastoral farmers (Loveridge *et al.* 2017). Cattle, donkeys, goats, and sheep (*Bos indicus*, *Equus asinus*, *Capra hircus*, *Ovis aries*) are the most popular livestock tended in the area and are typically left untended during the day and brought into protective bomas at night (Kuiper *et al.* 2015).

Lions in HNP are opportunistic and predominantly feed on medium to large prey, with an observed 83% of all kills being buffalo *Syncerus caffer*, wildebeest *Connochaetes taurinus*, giraffe *Giraffa camelopardalis*, zebra *Equus quagga*, and elephant *Loxodonta africana* calves (Loveridge *et al.* 2006; Loveridge *et al.* 2009).

Designing the Model: Overview

As this model is designed to work with GPS data, spatially varying variables are denoted as varying over time, as a lion will be in a different location with different covariate values at each time *t.* I have denoted all non-constant variables in the equation by time, with an understanding that the nature of GPS

data makes changes in space commensurate with changes in time. The denotation is in units of time because of the potential to have a lion in the same location over multiple time points, and because spatial variables (such as habitat type) are relative to each lion as it is being observed over time.

This model is not intended to be fitted to a dataset in a way that accurately describes a lion's actual energy level at any given time. There are too many unknown variables without corresponding data to use the model in that way. As such, using biologically reasonable parameter estimates, the model is used to provide relative changes in energy levels at each point in time/space.

Energy Level of a Lion

The approach developed to describe an individual lion's change in energy (kcal) over time is a linear differential equation of the form:

$$\frac{\Delta E_{(kcal)}}{\Delta t_{(min)}} = -B_{(kcal/min)}\Delta t_{(min)} - S_{t\ (metres)}J_{(kcal/metre)} - G_t C_{(kcal)} + \sum_{i=1}^{n} \frac{D_{it}V_t A_i}{1+N_t} W_{i\ (kcal)}$$

Change in energy (*ΔE*) is affected by ten covariates. This includes five covariates defined or informed by datasets (*S,G,D,V,N*), two covariates estimated using metabolic principles (*J,B*), and two unknown constants (*C,A*). Here *B* represents a constant energy expenditure over time, *S* is the step length between observations, *J* is the energetic cost of traveling, *G* is pride size, *C* is a scaling factor defining pride size's influence on energy expenditure, D_i is the local population density of prey, *V* is the advantageousness of the local vegetation type for hunting lions, A_i is the intrinsic availability of prey *i*, *N* is the local human population density, and W_i is the caloric value of prey *i*. Each of these terms is explained more fully (see below). In general, this equation can be understood in terms of actions that cost energy and actions that replenish energy through the

consumption of food. Each component of this equation will be explained below to recreate the reasoning behind its construction.

First, it is acknowledged that energy (*E*) decreases over time due to the continuous energy needs to keep a lion's body alive and functioning, even while resting. This basal metabolic rate (BMR) will be a negative constant rate representing an amount of energy lost over each time interval *t* in kcal/min. BMR is also defined as the energetic cost of resting. For most mammals, it can be calculated based on the animal's body weight with an allometric function (White and Seymour 2003), but it can also be calculated by measuring the volume of oxygen consumed by an animal over time. Here I used values calculated using oxygen levels as some studies have indicated lions have less efficient metabolisms than expected given the trends observed in other mammals (Chassin *et al.* 1976; McNab 2000). McNab (2000) measured a female adult lion's relative volume of oxygen (V O2) levels as 0.173 ± 0.0048 cm3 O2 / (g*h) at night, and the daytime rate of metabolism (in thermoneutrality) was 0.267 ± 0.0099 cm3 O2/(g*h*°C). Muñoz-Garcia and Williams (2005) used those values to find an average BMR for lions: 8,137.92 kJ/day, which converts to 1,945.00956 kcal/day and 1.3507 kcal/minute.

Schaller (1972, pg 276) summarized findings by Lamprey (1964) that estimated a lioness weighing 113kg would require an average of 7,272 kcal/day. Lamprey (1964) also estimated that a lion weighing 145kg would require 389 kcal/hour, based on a rough average of the lion's BMR and a more strenuous working rate. That average was approximately three times the BMR over the course of the day (Lamprey 1964). As it was not possible to account for all the activities that a lion would spend energy doing in a day, I adapted the constant *B* to represent a combined rate of energy expenditure including BMR and any other expected activity besides travel (estimated cost of traveling is described separately below). Thus, the assigned value for the constant *B* was

4.861kcal/min. This value, which is just above three times the BMR (4.05kcal/min), was calculated by subtracting the average daily travel costs from the daily energetic cost predicted by Lamprey (1964) for a lion weighing 145kg. This was relevant for the subjects in this study, as the mean weight (± SD) for adult female lions in HNP is 143 ± 11kg (Loveridge *et al.* 2009). As noted above, *B* is negative as it represents an energetic cost.

$$-B$$

Now I assume that energy is increased when the lion successfully hunts and eats prey. Energy gained from a successful hunt is represented by *H*.

$$-B + H$$

The probability of a successful hunt is the probability of encountering prey *i* (e_i) multiplied by the probability of catching that prey *i* (c_i). This is adapted from Lima and Dill (1990), where predation equations define the probability of a prey's death given various elements of risk, including the probability of death given an encounter with the predator (d), the encounter rate (α), and time spent vulnerable to encounter (T). I have replaced α and T with e_i, and d with c_i. Additionally, this model is formulated from the predator's perspective rather than the prey's.

$$H = e_i c_i$$

$$-B + e_i c_i$$

At each time *t,* the multiplied encounter rates and capture rates pertaining to the several prey species a lion may encounter (*i – n*) are added together to represent the overall likelihood of hunting success at time *t*.

$$-B + \sum_{i=1}^{n} e_i c_i$$

I replace e_i with a proxy for encounter rate, D_{it}. D_{it} is the estimated population density of prey *i* at time *t*, and can be thought of as the availability of prey. The probability of catching prey *i* (c_i) is represented as a combination of factors that influence hunting success, including the advantageousness of

vegetation and the prey's intrinsic availability. In summary, $e_i = D_{it}$ and $c_i = V_t A_i$.

V_t changes with the advantageousness of the vegetation type the lion is in at time *t,* and will be treated as the lion's likelihood of hunting success in each type of vegetation described in the study area. Terrain features and vegetation types have been noted as important factors influencing lions' hunting success, especially where they provide cover (see Macdonald and Loveridge 2010, pg 143). Van Orsdol (1984) found that lions in Uganda had overall capture efficiencies (defined as average hunts per hour multiplied by hunting success rate) of 0.021 and 0.015 during daytime and night time hours, respectively. I will use the mean of those values, 0.018, as a baseline for lions' hourly capture efficiency. For this model, 0.018 will be the baseline likelihood of successfully hunting prey over any given time interval. The vegetation types in HNP were described and mapped by Arraut *et al.* (2018).

In Kruger National Park, the density of shrubs had no impact on hunting success alone, while hunting success increased linearly with grass height (Funston *et al.* 2001). The same positive relationship between grass height and hunting success was observed in Queen Elizabeth National Park (Van Orsdol 1984). Interestingly, the effect of grass height was more extreme in areas with more bush cover, with hunting success ranging from 0% to 100% along with increasing grass height (Funston *et al.* 2001). That benefit of bushed grassland is observed in a previous study of the lions in HNP, where a preference for bushed grassland was observed in all seasons (Davidson *et al.* 2012). However, denser thicketed areas were preferred as kill sites, either because of increased hunting success or because kills were dragged to thickets near bushed grassland for feeding (Davidson *et al.* 2012). Using 0.018 as a midrange value, and referencing the depictions provided by (Arraut *et al.* 2018), I set the hunting success probability *V* for each habitat type as follows: moderately advantageous habitat

types (grassland and mopane-dominated woodland on grassy soil) were set to 0.018, disadvantageous vegetation types (deciduous woodland on sand, scrubland, and evergreen woodland) were set to 0.009, and highly advantageous vegetation types (bushed grassland and bushland) were set to 0.027. V_t is therefore the *V* value assigned to whatever vegetation type the lion is in at time *t*.

A_i is the intrinsic availability of prey type *i*. Intrinsic availability refers to the relative ease with which a lion can capture and consume this type of prey. Prey species that are more difficult to catch or that pose a threat to lions will have lower intrinsic availability than species that are easier to catch. Our prey population estimates were divided into wild prey and domestic prey (livestock). For simplicity, intrinsic availability was set to one for wild prey and two for domestic prey. These values reflect the relative ease with which a lion can subdue a domestic animal of similar size to a wild one, such as a cow versus a buffalo, and effectively increases the energetic gains from hunting domestic prey in our model.

To summarize the above, I replace the encounter rate e_i with prey population density D_{it}. The probability of capture c_i is replaced by a product of vegetation type advantageousness V_t and the prey's intrinsic availability A_i.

$$-B + \sum_{i=1}^{n} e_i c_i$$

$$e_i c_i = D_{it} V_t A_i$$

$$-B + \sum_{i=1}^{n} D_{it} V_t A_i$$

The above terms increase both the probability of a successful hunt and the consumption of prey. Now I need to account for variables that would have an adverse effect on hunting success. When considering factors that would impede a lion's ability to hunt, one must account for the impact of human populations. Lions will typically avoid interactions with people (Oriol-Cotterill *et al.* 2015a), so I

have assumed hunting will be interrupted when in areas with higher human populations. People will also take action to prevent lions from hunting their livestock. I will divide the hunting success term by N_t., where N_t is the human population density at time *t* within 100m^2. The denominator is added to one to avoid dividing by zero. A higher human population density at time *t* will decrease a lion's probability of hunting successfully. This results in the following term.

$$-B + \sum_{i=1}^{n} \frac{D_{it} V_t A_i}{1 + N_t}$$

So far, I have accounted for the likelihood of acquiring food, but in order to apply that to a change in energy levels, the probability must be multiplied with the energetic value of the food acquired. W_i is the amount of energy in kcal a lion should gain from successfully capturing prey *i*. Schaller (1972, pg. 276) suggested that an average kilogram of meat would contain 1500 kcal, a female lion can eat up to 22kg in a sitting, and that a female lion requires approximately 5kg per day to sustain moderate activity. The amount of meat consumed at a kill will vary and depend on a number of factors I could not measure, including the group size sharing the kill, how recently the lion last ate, and interactions with scavengers and other competing carnivores. I set *W* to 5,000 kcal for both wild and domestic prey. 5,000 kcal initially seems like a low amount for an adult lion to eat from a kill, equivalent to roughly 3.3kg. However, this is a constant that is not time-dependent, and the average time interval was 152.6 min (slightly less than three hours) in the dataset, that equates to roughly 40,000 kcal per day, or 26.7kg of meat potentially consumed. It is important to consider that this value is multiplied with V_t, but it still is likely much higher than a lion's true food consumption.

By making the value of *W* the same for wild and domestic prey, I remove some variation and can accommodate this inaccuracy as I am more interested in relative changes across lions and landscapes than predicting actual energy levels.

$$-B + \sum_{i=1}^{n} \frac{D_{it} V_t A_i}{1 + N_t} W_i$$

Next, I incorporate some of lions' social structure into the model. If a female lion is in a larger pride, it may need to hunt more to help provide for the pride (and perhaps more importantly, it may receive less food per meal). I can represent this social element in an individual lion's model by multiplying group size G_t by a scaling factor *C*. G_t is the number of subadults and adult females in the subject's pride at time *t*. *C* is a scaling factor that shows how group size G_t impacts *ΔE*. *C* has been arbitrarily set to 100kcal, as the total amount of calories is not as important as the relative impact of pride size for this study.

$$-B - G_t C + \sum_{i=1}^{n} \frac{D_{it} V_t A_i}{1 + N_t} W_i$$

When considering an animal's energy expenditure, many factors are important to consider, including the energy spent reproducing, rearing young, acclimatising to weather conditions, and the energetic costs of certain crucial activities like traveling, hunting, and resting. As the dataset includes only positional data every few hours, I can feasibly include only the cost of travel over each time interval *t*. *S* is the step length, or minimum distance travelled from the lion's position at *t* to the lion's position at *t*+1. Step length will be multiplied by *J*, a constant representing the energetic cost of traveling.

$$-B - SJ - G_t C + \sum_{i=1}^{n} \frac{D_{it} V_t A_i}{1 + N_t} W_i$$

Chassin *et al.* (1976) measured the energy expenditure of two adolescent lions on treadmills, and reported 0.36 mL $O_2(g * km)^{-1}$ as "the observed slope

for the relationship between oxygen consumption and speed" (Chassin *et al.* 1976). The observed maximum aerobic capacity for the lions was 3 mL O_2 $(g * h)^{-1}$ (Chassin *et al.* 1976). White *et al.* (2016) summarized those findings by defining their minimum cost of transportation (COTmin) as 0.36 $mL\ O_2/kg$/m. The energetic cost of an animal's movement typically increases linearly with the rate of that movement (Taylor *et al.* 1974). It also increases with the animal's weight. In HNP, the mean weights of adult lions (±SD) were 199±10 kg and 143±11 kg for males and females, respectively (Loveridge *et al.* 2009). That results in a cost of transportation for females of 51.48 mL O_2/m. One litre of oxygen is typically equated to 4.8kcal in heat (Schmidt-Nielsen 1997), so the final energetic cost of transportation by distance is 0.247kcal/m or 247kcal/km. The average rate of travel across all the lions observed was 9.4km/day, or 2,322kcal/day spent traveling.

If a lion weighing 145kg has a daily energy requirement of 9,336kcal (based on Lamprey (1964)), this means roughly a quarter of the lion's daily energy expenditure is spent moving. Previous calculations for BMR account for 1,945kcal/day, leaving a little more than half of a lion's expected daily energy expenditure unaccounted for. It is likely to be a combination of many unmeasured factors, including increased energy expenditure in hot temperatures, the gestation and feeding of offspring, and the highly demanding activities of hunting and subduing prey. As calculating precise breakdowns of energy expenditure for each of those activities is beyond the scope of this chapter, I adjusted the value of *B* to represent all the average energy expenditure not captured by the lion's movements.

The final equation is as follows.

$$\frac{\Delta E_{(kcal)}}{\Delta t_{(min)}} = -B_{(kcal/min)}\Delta t_{(min)} - S_{t\ (metres)}J_{(kcal/metre)} - G_t C_{(kcal)} + \sum_{i=1}^{n} \frac{D_{it} V_t A_i}{1 + N_t} W_{i\ (kcal)}$$

Data Sourcing and Processing

All data processing and analysis was done using ArcGIS, R, and RStudio (RStudio Team 2015; R Core Team 2015).

GPS Collar Data

A database of GPS-collared lions in HNP with records dating back to 1990 was available for this study. Data from 29 female lions were used for this chapter. The total number of observations for each lion ranged from 372 to 18580 (mean = 6303, median = 5815) and the total number of observed days ranged from 32 to 1279 (mean = 532.5, median = 467).

Lions were immobilized in the field following established protocols for the species (Fahlman *et al.* 2005). GPS collars were fitted and equipped with either ultra-high frequency (UHF) or satellite remote downloads (Televilt Positioning, Lindesberg, Sweden; Sirtrack, Hawkes Bay, New Zealand; Africa Wildlife Tracking, Pretoria, South Africa). Appendix S2 contains more information on animal handling and ethical considerations.

Lion Demographics: Pride Size and Mortality

Pride size at time *t* as the number of subadults plus the number of adult females alive in the pride at time *t*. Adults were defined as greater than or equal to four years old (Petracca *et al.* 2021) and subadults were defined as between 30 and 48 months old. Subadults were included because they will impact the amount of food needed to support the pride. Adult males were not included

because the database only tracked natal pride membership, and males typically disperse from their natal prides before reaching adulthood.

I was also able to view records of lion mortalities in the same park dating back to 2002 (see Loveridge *et al.* 2017). I categorized recorded causes of death as 'Unknown', 'Natural', 'Conflict', 'Snare', 'Poached', or 'Collision', with the latter four being classified as anthropogenic causes of death.

Prey Population Estimates

The prey population estimates used in this chapter were produced using camera trap data (Loveridge, unpublished). Generalized additive models (GAMs) modelled the abundance of lions' preferred prey species in relation to various landscape features (Loveridge, unpublished). Preferred prey species were organized into three groups based on body size (small, medium, and large), and a GAM was created for each group to investigate the covariates' effects on the total number of independent records. The most parsimonious model for each group was then validated against remaining data not used in the model's construction and used to estimate prey abundance across the study area. The final spatial raster used in this chapter was a projection of the summed abundances of small, medium, and large preferred wild prey species per square kilometre. These prey population estimates are part of a separate study, and the outputs were shared as geospatial rasters that I was permitted to use for this chapter (Loveridge, unpublished).

The population estimate for domestic prey was defined as 60 individual livestock animals (shoats, donkeys, or cattle) per square kilometre for all locations within 2km of a village.

Human population density data:

The human population datasets used in this chapter were obtained from WorldPop (www.worldpop.org, Linard *et al.* 2012). Spatial files for the estimated total number of people per 100 square metres in Zimbabwe and Botswana from

2000-2020 were obtained from WorldPop. These unconstrained “top-down” models do not account for actual buildings or settlements, so population estimates are based on census data spread across areas according to various covariates. This method produces nonzero population estimates everywhere, which ignores the reality of uninhabited areas in HNP and lowers predicted population densities in settlements. Despite the limitations of these datasets, they are still useful for comparing relative changes in human population density for the purposes of this chapter. These estimates were created using a mapping approach called Random Forest-based dasymetric redistribution (Stevens *et al.* 2015).

Locations of Households

Locations of villages and households were mapped by a previous study (Loveridge *et al.* 2017) and those spatial rasters were used for this analysis.

Coding the Model

By integrating the model and setting an initial value for *E* (with an arbitrarily defined *E*(0) = 10), *E* can be solved iteratively using Euler’s Method. Euler’s Method truncates a nonlinear problem into a linear problem to find an approximate solution. By scaling time for each lion so that the total time observed is equal to one, time steps become small fractions and sources of computational errors can be reduced.

I divided Δt in minutes by the sum of all observed minutes in each lion’s record, so that each time interval was just a small fraction of the total observation time. Those values were then multiplied by 1000 to make the number of digits smaller for each value. Changing the units of Δt from minutes to a proportion meant that I needed to convert the units of B from kcal/min to kcal so the result would be in kcal. This conversion was done by multiplying B by m. m is the unscaled time interval in minutes ($t - (t - 1)$). The integrated model is shown

below, with Δt having been scaled and the units of B having been adjusted. See Appendix S3 for details of the integration.

The equation was coded in R within a 'for' loop to perform this iterative solution. The code also required strict definitions for which time step each value was pulled from when solving this equation. If we consider this equation as representing all of the changes in energy that occur between time steps, it makes sense to say that E_t will be the result of conditions at $t - \Delta t$ and the journey occurring over Δt. Thus, we defined each parameter as indicated. *S* was kept at time *t* because S_t is equal to the distance traveled from $t - \Delta t$ to t, so this arrangement ensures all the variables and their biological implications are referring to the same period of time. An assumption was built into the code that a lion's energy level should resume from its most recent point after a gap in the data (more than 72 hours) rather than returning to the starting value of *E*(0).

The model created in R is shown below as an equation.

$$E_t = E_{t-\Delta t} + \Delta t \left(-B_{(kcal/min)} \mathrm{m}_{(min)} - S_{t\ (metres)} J_{(kcal/metre)} - G_{t-\Delta t} C_{(kcal)} + \sum_{i=1}^{n} \frac{D_{it-\Delta t} V_{t-\Delta t} A_i}{1 + N_{t-\Delta t}} W_{i\ (kcal)} \right)$$

Rather than coding a separate equation to model *ΔE*, *ΔE* was calculated by subtracting $E_{t-\Delta t}$ from E_t and dividing the result by Δt in minutes. Thus, each value for *ΔE* in this chapter is in units of kcal/min.

Sensitivity Analysis

Sensitivity analysis was conducted by creating a large 'for' loop in R that solved the energy model as described above and stored the absolute value of the coefficient of variation for the resulting *E* values. This process was repeated for each lion while adjusting one covariate from its default value at a time. Each covariate was multiplied by 0.8 and 1.2 to create minimum and maximum values,

respectively. I generated a table populated with these coefficients of variation to compare the effects of different covariates on the model's output. See Appendix S4 for the full table.

Question 1: Does average change in energy level vary in relation to home range?

Home range status for each observation was assigned by measuring the home range and core home range for each lion and then categorizing each observation as being either within the core (Core), within the home range (but outside of the core; In), or outside of the home range altogether (Out). Home ranges were measured using a kernel density estimator in the adehabitatHR package (Calenge 2006) in R. I defined the home range with 90% contour lines, meaning 90% of the lion's estimated distribution is within that contour. 50% contour lines were used to measure the core home range area. These contour values were based on a previous study of lions' home ranges within HNP (Loveridge *et al.* 2009). Within the estimate, the smoothing factor h was set as the reference bandwidth, as a slight overestimation of home range should not be an issue with our research questions and wide-ranging subject species.

A one-way ANOVA output table was generated from a linear mixed-effects model using R packages lme4 (Bates *et al.* 2015) and lmerTest (Kuznetsova *et al.* 2017). The model was built with each lion's average ΔE (aggregated by individual lion and home range status) as the response variable, with home range status as a fixed effect and including random effects of pride and individual lion (nested within pride). The data were heteroscedastic, so the average ΔE values were transformed using a boxcox transformation coefficient of 0.175.

Question 2: Is there a relationship between anthropogenic risk and change in energy level?

A map of anthropogenic risk faced by female lions over HNP and the surrounding areas was produced by Loveridge *et al.* (2017). Using this anthropogenic risk at each location for all lions' observations, a linear mixed-effects model (Bates *et al.* 2015) was used to investigate changes in energy levels as a function of this anthropogenic risk. All of the lions' observations were compiled into one data frame, and the model was built using ΔE as the response variable, anthropogenic risk as the fixed effect, and pride and individual lion as random effects. Negative outliers skewed the residuals strongly to the left, so outlying values of ΔE were removed. Outliers were defined as lying more than 1.5 times the interquartile range above the third quartile or below the first quartile. The 14,599 outliers removed (9.3% of the observations) were mostly extreme highs or lows following breaks in the data and were likely produced by errors in the model's code. A transformation of ΔE was necessary to reduce heteroscedasticity, so a boxcox transformation was used with a coefficient of 0.84. Removing outliers and transforming the response variable successfully produced homoscedasticity and normally-distributed residuals. Marginal and conditional R^2 values were calculated using the MuMIn package (https://CRAN.R-project.org/package=MuMIn).

Results

The 29 female lions included in this study belonged to 15 different prides. 10 prides were represented by only one lion each, while two prides had two, one pride had three, and two prides had six lions represented in these data. The average travel speed across all lions' observations was 0.39 km/h. Only three lions travelled within 2km of villages in this dataset, totalling 76 entries within those boundaries (0.2% of all observations).

Appendix S5 contains this chapter's regression models and their R outputs.

Energy Model Outputs

Across all lions' observations, Energy (*E*) ranged from -1,339,829 kcal to 1,382,805 kcal, with a mean of 100,511 kcal and a median of 88,399 kcal (Fig. 7). Change in Energy (ΔE) ranged from -133.258 kcal/min to 46.765 kcal/min, with a mean of 1.454 kcal/min and a median of 0.888 kcal/min (Fig. 8).

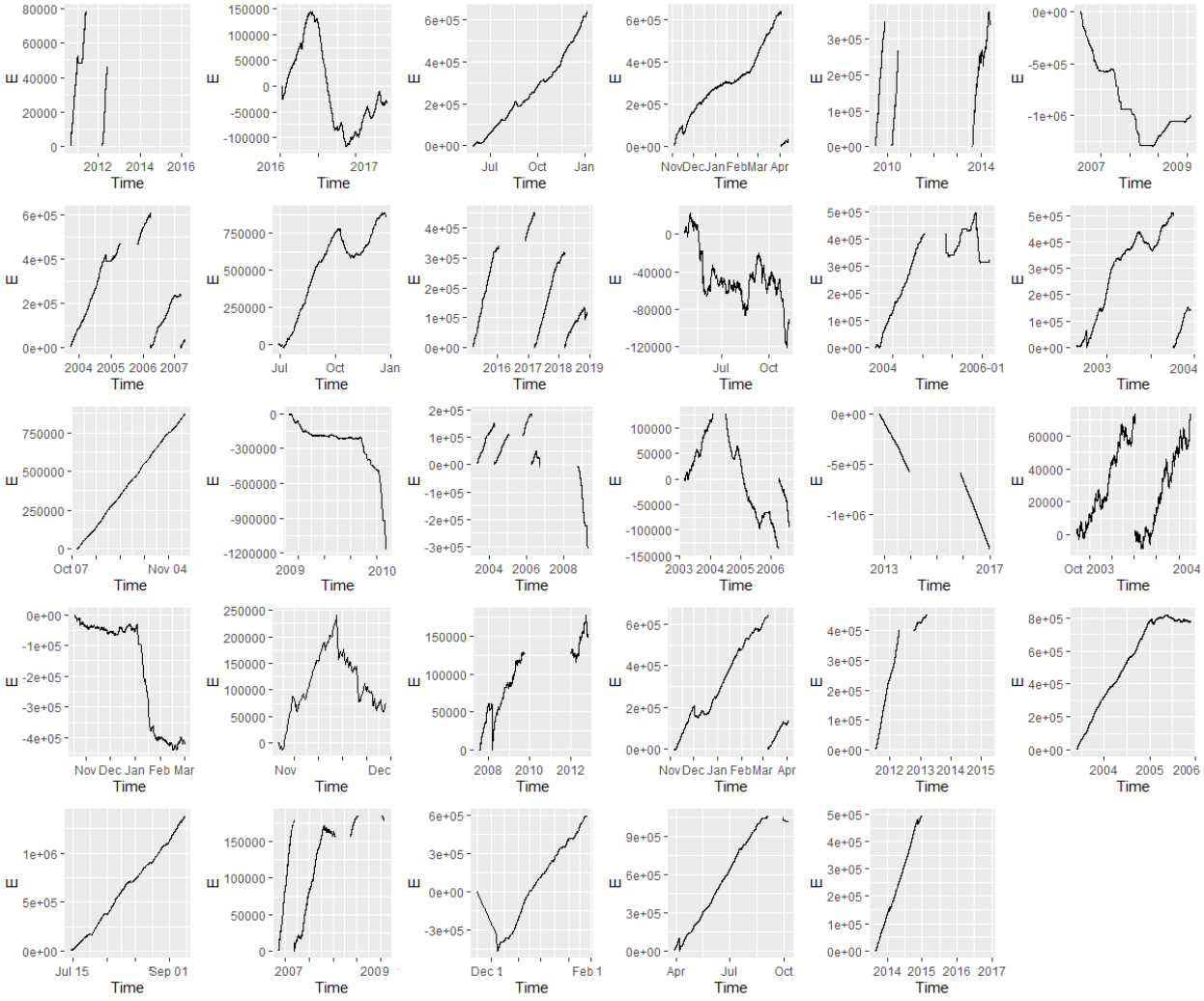


Figure 7: Energy (*E*) over time as projected by a model of African lions' (*Panthera leo*) energy expenditure based on landscape covariates. Each line chart represents the results of an individual female lion and time scales vary depending on the range of time for which each lion was observed with a GPS collar. Gaps in the data were created when lions did not have GPS observations for over three days.

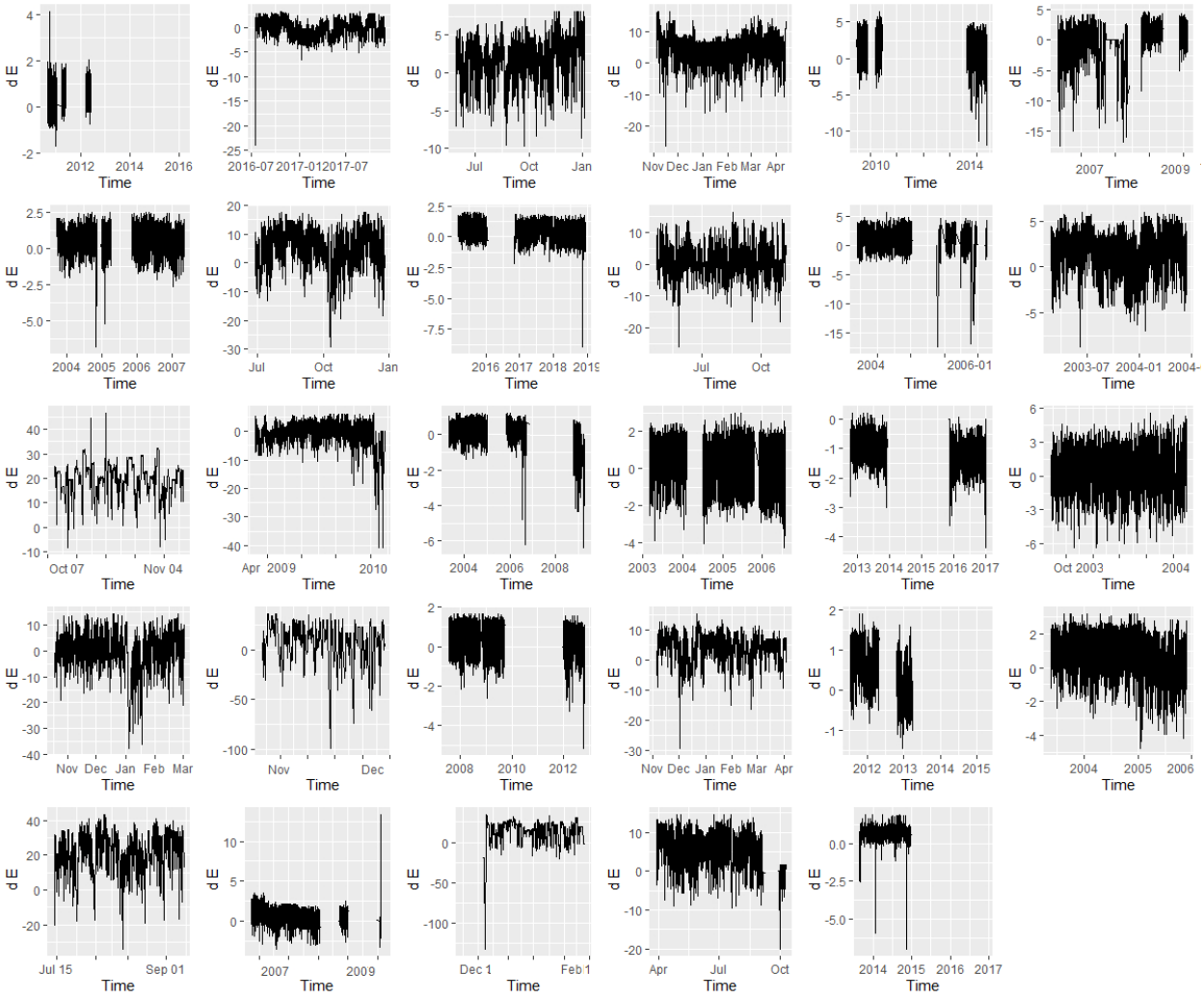


Figure 8: Change in energy (*ΔE*) over time as projected by a model of African lions' (*Panthera leo*) energy expenditure based on landscape covariates. Each line chart represents the results of an individual female lion and time scales vary depending on the range of time for which each lion was observed with a GPS collar. Gaps in the data were created when lions did not have GPS observations for over three days.

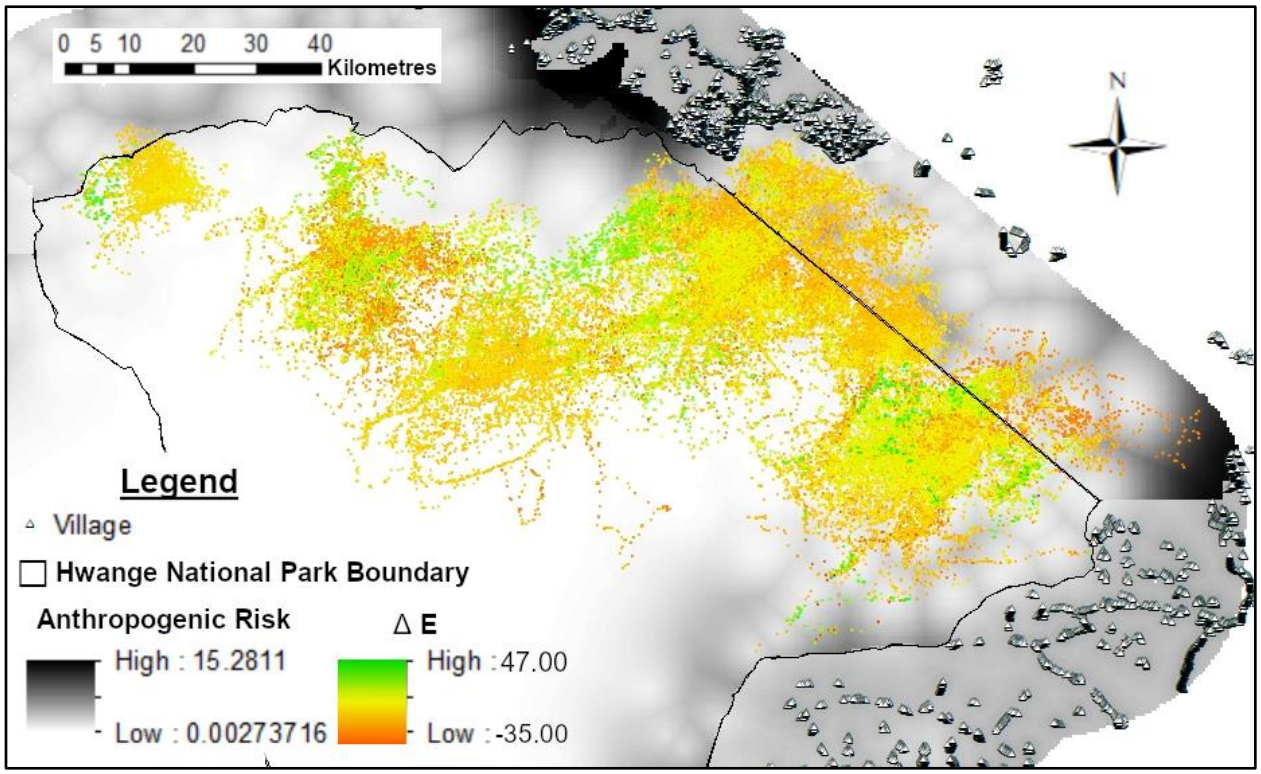


Figure 9: A map of Hwange National Park and surrounding areas, with the park boundary outlined and villages marked by triangles. A raster is displayed showing the anthropogenic risk of mortality for female lions (Loveridge *et al.* 2017), with higher risk indicated by darker shading. GPS collar observations from 29 female lions are displayed, color-coded by the corresponding change in energy (*ΔE*) modelled by an energy expenditure equation for each observation.

Sensitivity Analysis

I identified the variables that caused the largest coefficients of variation in *E* when altered, and they varied across individual lions. For 13 lions, the intrinsic availability and caloric value of wild prey (A_{wild}, W_{wild}) were equally impactful more than any other variables. Of those, eight lions were most impacted by the minimum values, and five lions were most impacted by the maximum values. Two lions' *E* values were most impacted by the minimum and maximum values of *B*, respectively. The remainder of the lions for which coefficients of variation could be calculated were most impacted by vegetation advantageousness values.

Research Questions

Question 1: Does average change in energy level vary in relation to home range?

From the ANOVA table associated with the analysis on the three levels of home range, there were two degrees of freedom associated with this treatment effect and 48.102 error degrees of freedom. The sum of squares associated with the effects of home range was 3.5669, the mean sum of squares was 1.7835, and the F value was 11.08. The P value was 0.0001, indicating a highly significant difference in the (transformed) mean change in energy level in at least one of the home range statuses.

The parameter estimates/mean ΔE values for this linear model were as follows: within the core home range the mean transformed ΔE was 1.1513 (P = 0.000446), the mean transformed ΔE within the rest of the home range was 0.8422 (P = 0.009351), and the mean transformed ΔE outside of the home range was 0.6071 (P = 0.0000219). This indicated that both the 'In' and 'Out' home range statuses had significantly different mean transformed ΔE values than the 'Core' home range.

The 95% confidence interval was -0.53 to -0.09 for the expected value of the difference between transformed ΔE in the Core home range and the rest of the home range. The 95% confidence interval for the expected value of the difference between transformed ΔE in the Core home range and outside of the home range was -0.77 to -0.32.

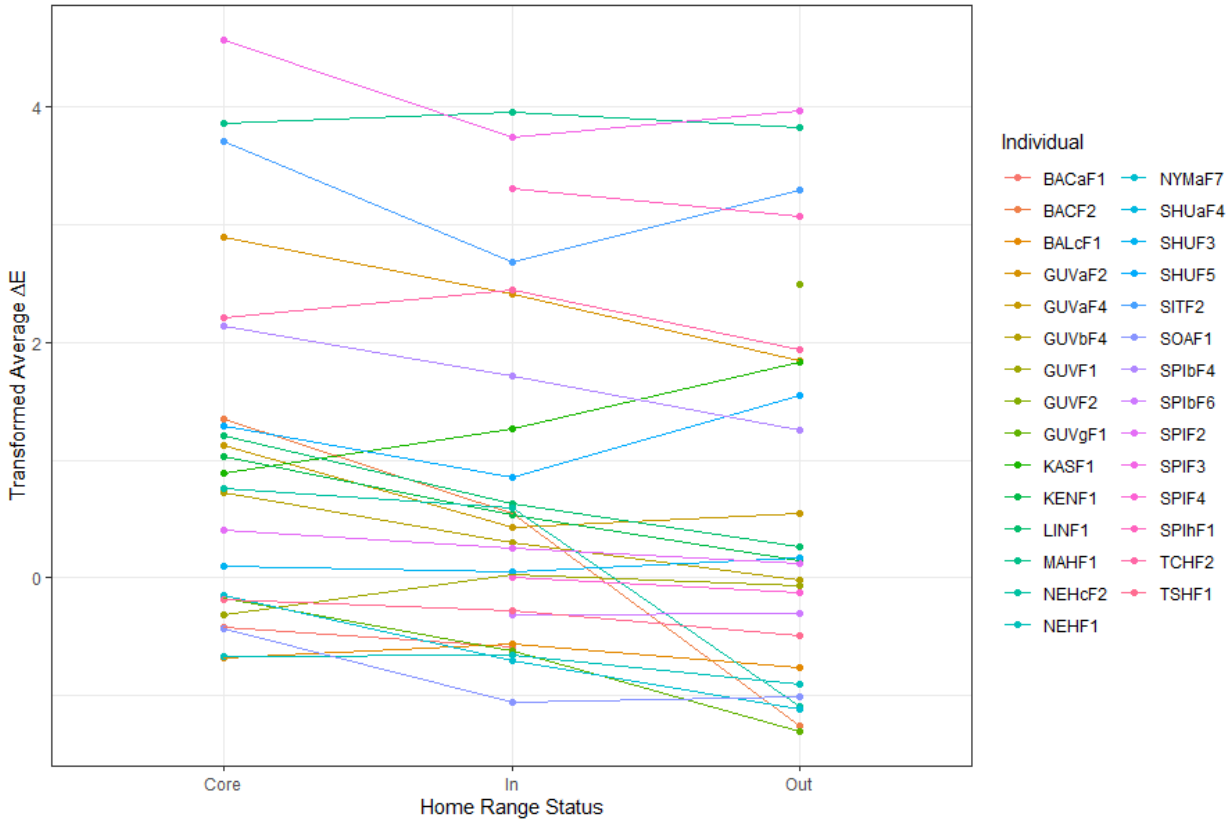


Figure 10: Transformed values of change in energy (*ΔE*, kcal/min) calculated by a model of energy expenditure in lions (*Panthera leo*) were averaged within each Home Range Status for each Individual lion. Using a record of GPS locations, each observation was categorized as being in the Core of the lion's home range, Inside the home range (but not in the core), or Outside of the home range entirely. Home ranges were created with 90% contour lines and cores were created with 50% contour lines. Lines correspond with individual lions to highlight the overall trends between *ΔE* and home range status.

Question 2: Is there a relationship between anthropogenic risk and change in energy level?

A highly significant (P < 2e-16) negative correlation (fixed effect = -0.2965) was observed between transformed *ΔE* and anthropogenic risk. The conditional R^2 value was 0.43, and the marginal R^2 value was 0.04. The x-intercept, or the value of anthropogenic risk above which energy should decrease over time, was 8.13.

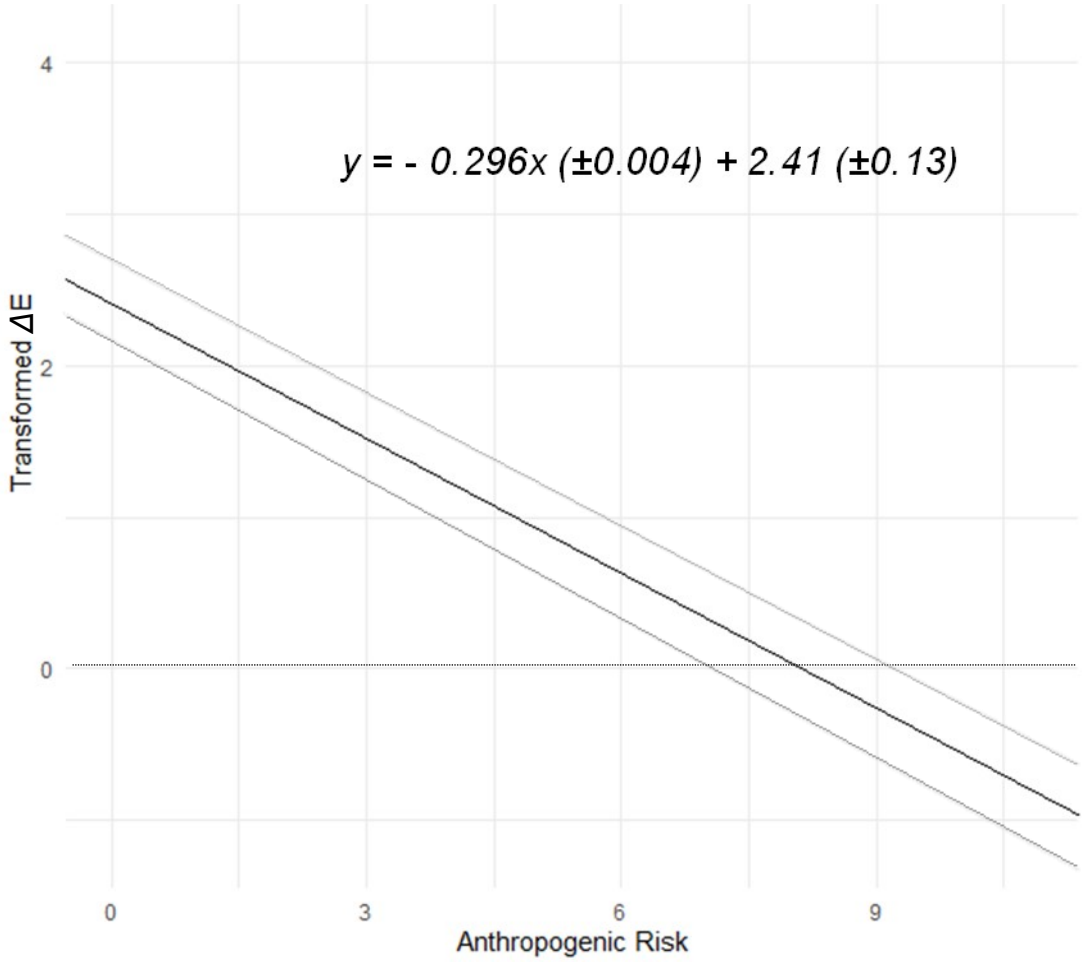


Figure 11: A regression line from a linear mixed effects regression model, with transformed values of change in energy (*ΔE*, kcal/min) as an effect of a numerical measure of anthropogenic risk (Loveridge *et al.* 2017). *ΔE* was calculated using a model of energy expenditure in lions (*Panthera leo*) based on landscape covariates, and outliers were removed prior to building the mixed-effects model. The regression line (intercept = 2.410, slope = -0.2965) is in black, and the equation (± standard error) is displayed. 95% confidence intervals are displayed as grey lines.

Discussion

Overview

Here I have developed a model of female lions' energy expenditure over space and time based on landscape covariates. The model projected both positive and negative trends in energy levels over time across individual lions, with some lions' energy levels decreasing steadily, some lions' energy levels rising steadily, and some lions' energy levels fluctuating between the two over the observation period (Fig. 7). This discussion will briefly examine the key results of this model's outputs and describe how the development of this model can inform models of lions' hunting behaviour with more detailed parameters in the future.

Interpreting the Sensitivity Analysis

For most of the lions for which sensitivity figures could be calculated (13 of 24), the most influential variables in the model related to the energetic worth and catchability (intrinsic availability) of wild prey. This result makes sense, given this equates to almost all of the energy the lions would gain over time (as so few lions in this study entered community areas where livestock would be more available). The second most frequent type of variable influencing energy change (found to be most influential in 9 of 24 lions) related to the advantageousness associated with vegetation types. This finding is also reasonable, as lions that spend most of their time in particular vegetation types would be heavily impacted by that vegetation's influence on hunting success. Overall, both of these findings are encouraging as this suggests the model's predictions accord well with expected trends in reality.

Interpreting Question 1: Does average ΔE vary in relation to home range?

The significant differences observed between the Core home range and the other home range statuses indicates that average transformed *ΔE* decreased with increasing distance from each lion's central (core) home range. This suggests lions were progressively gaining less energy or spending more energy as they moved farther from their central home ranges.

This result is interesting as it provides some credibility to the model framework, as one would expect lions to become less efficient outside of their core home ranges. When controlled for pride biomass, female lions' home ranges in HNP decrease in size when prey biomass increases (Loveridge *et al.* 2009), which could maximize energy efficiency within the home range by increasing food availability and decreasing the costs of traveling a larger area (Kelt and Van Vuren 2001). Lions moving outside of their core home ranges may also incur increased costs from travel and unfamiliarity of the area (similar to the energetic problems lions and other large carnivores would face if their home ranges were too large; Kelt and Van Vuren 2001). As described by Loveridge *et al.* (2009), lions' home ranges are likely shaped by intraspecific relations with other prides, and any lioness moving outside her home range may have to move less efficiently to avoid confrontations.

Interpreting Question 2: Is there a relationship between anthropogenic risk and ΔE?

The results reveal a potential relationship between anthropogenic risk and *ΔE*, where areas with higher risk had a negative effect on *ΔE*. The low marginal R^2 value (0.04) means only a small proportion of the variance could be explained by the fixed effect (anthropogenic risk). This result is likely because all of the observations at risk levels over 7.5 (while risk levels ranged from 0.01 to 10.84) belonged to one individual lion (Appendix S6). Conditional R^2 was 0.43, meaning

that the random effects of individual and pride explained a bit less than half of the variance.

The lion with these influential observations was not removed from the analysis because it was the only eligible individual that spent time in high-risk areas. Other lions that had high-risk observations frequently left the study area, which was limited by the size of the rasters for estimated prey populations and anthropogenic risk used to model energy (*E*). Although the negative correlation between ΔE and anthropogenic risk was statistically significant, its accuracy cannot be further substantiated without adding more lions with high-risk movements to the analysis. A negative correlation between ΔE and anthropogenic risk could indicate that these areas are less likely to be 'attractive sinks' (Loveridge *et al.* 2017) for female lions, as they would be less tempted to wander into high-risk areas if they had fewer energetic benefits to offer. A positive correlation between ΔE and anthropogenic risk would suggest those areas are 'attractive sinks' (Loveridge *et al.* 2017) and thus pose a greater danger to the local lion population.

Strengths and Limitations

Dataset limitations were particularly important in determining the structure of the model because so many variables had to be estimated rather than measured. The differential equation is simpler and more appropriate for such a theoretical study compared to a patch selection function or dynamic programming model (Mangel and Clark 1988), as either alternative would require more detailed records on hunting events and other energetic parameters. That simplicity allows us to glean some meaning from the output despite the many variables for which no data exist. The results of Question One also indicate that this model, despite its simplicity, has some grounding in realistic lion behaviour (specifically the tendency for home ranges to benefit lions in terms of energy expenditure).

That said, this model has several key weaknesses. It could not be fit to a dataset to produce accurate outputs due to the limited covariates for which data existed. The results of this model are therefore only useful for examining relative differences across and within observations of lions, rather than quantifying the impacts of particular parameters on lions' behaviour. Reproductive status and its energetic requirements (particularly gestation and nursing) were not recorded, and time spent hunting or resting could not be discerned from the GPS records.

My estimate of travel cost was limited to linear step length and may have missed important behavioural details (such as path tortuosity and detailed records of speed that could reveal hunts). Williams *et al.* (2014) calculated the energy pumas (*Puma concolor*) expended traveling per meter by dividing VO2 by speed and performed a separate calculation for the cost of acceleration that was mass-dependent. Miller *et al.* (2014) defined the energetic cost of an amur tiger's (*Panthera tigris altaica*) travel as a function of the tiger's weight, time spent traveling, and distance travelled. Williams *et al.* (2014) also identified important pre-kill movements made by these large ambush carnivores, which were crucial in the overall understanding of pumas' energy expenditure. Unfortunately, lions do not exhibit the same predictable caching behaviours as pumas, and thus I could not account for pre-kill and feeding behaviours in the data. I also did not have each individual lion's weight.

Future Directions

Future directions for this work might include incorporating seasonality in home ranges, prey availability, and vegetation as this would almost certainly account for some unexplained variance in ΔE. Lions in HNP respond to seasonal changes in water availability and resulting prey densities, especially by targeting wild prey densely congregated at waterholes in the dry season (although lions show year-round attraction to these water sources; Valeix *et al.* 2010; Davidson *et al.* 2013). Female lions have also been shown to seasonally shift secondary food sources due to herbivores' interactions with water (Davidson *et al.* 2013). Livestock availability and communities' husbandry practices also vary seasonally (Kuiper *et al.* 2015).

As this model could not be fit to a dataset and contained multiple unknown variables, it was not possible to solve for any given variable's relative impact on the lions' behaviour. In future, a very thorough dataset (including information on hunts, feeding, reproductive status, and social statuses) could allow one to answer more detailed questions about factors influencing lions' movements, especially factors that cannot be directly measured. This model has demonstrated that even a formula created with many estimated values can produce plausible measurements of relative energy levels. It is worth attempting this again with more data to discern how many recorded parameters are needed to start solving for the impacts of those we cannot measure in the field.

Conclusion

This model used a combination of movement data, landscape features, and estimations of metabolic processes to estimate the energy expenditure and energy levels of female lions over space and time in HNP. The model produced energy level estimates that varied across individuals but showed some trends consistent with understandings of lions' energetic expenditures, particularly regarding the relationship between energy expenditure and home range. The model was also capable of highlighting an interesting relationship between anthropogenic risk and energy expenditure, although the accuracy was limited by the small number of lions included. Similar models of energy expenditure in this lion population, supplemented by more data, will help researchers understand how lions make decisions in an environment where the needs to hunt, defend territory, and reproduce must be balanced with avoiding anthropogenic risk and other costs.

Chapter Four

Discussion

My research has investigated the behavioural decisions of a prey species, Uganda kob, and an apex predator, the African lion. Prey species, particularly ungulates, have well-documented antipredator behaviours (e.g. vigilance, flight responses, alarm calls) that can be used as reliable indicators of how much risk they perceive at a given time and place (Brown 1999; Bonnot *et al.* 2017). These antipredator cues supplement other behavioural data like movement, group dynamics, patch use, and habitat selection (Brown 1999; Prugh *et al.* 2019). The study of risk effects in carnivore-ungulate systems has documented ungulates' antipredator behaviours in ecosystems across the globe and contributed to many recent studies within this field of research (e.g. Brown *et al.* 1999; Creel *et al.* 2008; Basille *et al.* 2015; Moll *et al.* 2017; Prugh *et al.* 2019)

Usually, studies of carnivores' responses to risk (whether imposed by larger carnivores or humans) utilize movement and habitat selection data (Wang *et al.* 2015; Smith *et al.* 2015; Oriol-Cotterill *et al.* 2015b; Blecha *et al.* 2018; Suraci *et al.* 2019). Many studies have also documented the partitioning of habitats, diets, and daily activity patterns as responses to risk (Harihar *et al.* 2011; Wang *et al.* 2015; Oriol-Cotterill *et al.* 2015b). As movement and habitat selection are fundamental to carnivore foraging and reproduction success, it can be complicated to quantify how much of movement behaviour is attributable to risk avoidance. In one study, cheetahs' (*Acinonyx jubatus*) movements were influenced by tiered needs: resource availability was higher in the hierarchy than avoiding larger predators (Broekhuis *et al.* 2013).

It is likely that predators, like prey, are capable of dynamic decision-making to optimize their overall fitness depending on their state and environmental conditions. The construction of behavioural models might allow researchers to identify just how much of an effect risk has on carnivore decision-

making in relation to other factors. In a model where decisions are optimized to maximize some variable (e.g. reproductive fitness or energy reserves), when datasets exist for key behavioural ecological variables, and decisions are recorded, one may be able to solve for remaining variables that cannot be directly measured in the field (such as perceived risk).

The ability to quantify the risk perceived by carnivores would provide valuable insight into the effects of various conflict mitigation tools, such as non-lethal carnivore-deterring technologies or changes in local hunting policies or livestock management practices (McManus *et al.* 2015; Petracca *et al.* 2019). If particular features are linked to increased perceived risk, it might be possible to reproduce those features in communities experiencing intense predation events to mitigate that conflict by deterring carnivores. As such mitigation strategies are put into place, the ability to solve for perceived risk could be increasingly important in monitoring how carnivores respond to these strategies over time and may or may not become habituated to them (McManus *et al.* 2015).

Several types of models could be candidates to solve for the risk of death perceived by large carnivores. Dynamic patch selection models (Mangel and Clark 1988) and utility functions based in economic theory offer means to isolate and understand variables that influence an agent's decisions. Doing so would require extensive data for the model to be fitted and validated. To attempt to solve for the risk perceived by a lion, as a variable influencing its optimal decision-making strategy, one would also require data on lion decisions made over time (e.g. GPS records, interpreted as patch selections), the availability of food and mates at every patch, the lion's energetic state over time, its reproductive and social statuses, and a common currency for all of these variables' impacts on fitness. Such data could be logistically challenging and expensive to obtain, but it could reveal nuances in lions' behaviour that may be invaluable for the development of effective conservation strategies.

In my thesis I have made a first step toward developing the kind of behavioural model that could be capable of solving for lions' perceived anthropogenic risk. Developing an energy expenditure model gave me experience translating biological and environmental conditions into variables to be fit into an equation. It bolstered my understanding that answering any scientific question is entirely dependent on the data one has access to. I hope to continue this line of inquiry in future and continue to explore the capabilities of mathematical models in behavioural ecology, especially concerning how large carnivores respond to anthropogenic risk.

I also investigated how kobs in Murchison Falls National Park (MFNP) respond to vehicular activity in relation to road networks. Although this particular alteration to their environment did not seem to affect their perception of vehicles, gathering this data provides a crucial baseline for future studies to investigate how the construction of road infrastructure will change that perception of risk.

Humans have fundamentally altered ecosystems across the globe. For any future where humans and non-human animals coexist, it is crucial that we examine all of the impacts we have on wildlife – not just on their habitats and populations, but on their behaviours. We must also recognize that our direct impacts do not exist in a vacuum. In ecological communities containing complex webs of behavioural interactions, our influence on one species may have cascading effects on others. The study of risk effects and predator-prey interactions allows us to understand more thoroughly the ecosystems that we want to protect and restore, and how we fit into them.

Conclusion

I have conducted two studies investigating the behavioural ecology of a predator, the African lion, and the Uganda kob, one of its locally preferred prey species.

By measuring antipredator responses in the kobs in response to a vehicle in relation to road networks and poaching activity, I observed that kobs do not seem to adjust their responses to vehicles based on proximity to road. They do however show a difference between sexes that may be indicative of their intraspecific competition and how it impacts their responses to potentially threatening stimuli. As road networks in the area continue to be developed, this study can serve as a useful baseline for investigating whether kobs' behaviours around roads change over time.

I developed a model of lions' energy expenditure over space and time based on landscape covariates. The construction of the model drew on the literature around energy expenditure in carnivores and compiled several large datasets from Hwange National Park. The model indicated that female lions' average change in energy was lower when not in their core home range, and that there may be a negative relationship between change in energy and spatial anthropogenic risk. While data limitations made the outputs of the model uncertain, the development of detailed behavioural models like this may be applicable in future studies hoping to solve for variables influencing lions' decisions that cannot be directly measured otherwise.

Both of these studies demonstrate how the study of risk effects can be used to better understand the ways in which human activities influence wildlife.

Appendices

Appendix S1: Chapter Two Models and Outputs, as Displayed in RStudio

M1

```
require(lmerTest)
M1 <- lmer(
  noNAdata1$Flight_Dist ~
    noNAdata1$Poaching_Pressure
  + (1|noNAdata1$Distance_to_nearest_road)
  + (1|noNAdata1$Group_Size)
  + (1|noNAdata1$Transect_Number)
  + (1|noNAdata1$Observers)
)
```

```
> summary(M1)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: noNAdata1$Flight_Dist ~ noNAdata1$Poaching_Pressure + (1 | noNAdata1$Distance_to_nearest_road) +
    (1 | noNAdata1$Group_Size) + (1 | noNAdata1$Transect_Number) +      (1 | noNAdata1$Observers)

REML criterion at convergence: 2308.9

Scaled residuals:
     Min       1Q   Median       3Q      Max
-1.72767 -0.43853 -0.01419  0.39202  1.54630

Random effects:
 Groups                            Name        Variance Std.Dev.
 noNAdata1$Distance_to_nearest_road (Intercept) 1.8718   1.3681
 noNAdata1$Group_Size               (Intercept) 0.1832   0.4280
 noNAdata1$Transect_Number          (Intercept) 0.4102   0.6405
 noNAdata1$Observers                (Intercept) 0.3869   0.6220
 Residual                                       1.0877   1.0429
Number of obs: 582, groups:
noNAdata1$Distance_to_nearest_road, 545; noNAdata1$Group_Size, 46; noNAdata1$Transect_Number, 22; noNAdata1$Obse
rvers, 5

Fixed effects:
                             Estimate Std. Error      df t value Pr(>|t|)
(Intercept)                    6.8968     0.3871  8.2589  17.816    7e-08 ***
noNAdata1$Poaching_PressureTest   0.3705     0.3717 24.9884   0.997    0.328
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr)
nNAdt1$P_PT -0.328
```

M2

```
require(lmerTest)
M2 <- lmer(
  noNAdata2$Flight_Dist ~
    noNAdata2$Sex
  + (1|noNAdata2$Distance_to_nearest_road)
  + (1|noNAdata2$Group_Size)
  + (1|noNAdata2$Transect_Number)
  + (1|noNAdata2$Observers)
)
```

```
> summary(M2)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: noNAdata2$Flight_Dist ~ noNAdata2$Sex + (1 | noNAdata2$Distance_to_nearest_road) +
    (1 | noNAdata2$Group_Size) + (1 | noNAdata2$Transect_Number) +      (1 | noNAdata2$Observers)

REML criterion at convergence: 2305.1

Scaled residuals:
     Min       1Q   Median       3Q      Max
-1.80674 -0.44432 -0.00393  0.38434  1.54714

Random effects:
 Groups                              Name        Variance Std.Dev.
 noNAdata2$Distance_to_nearest_road (Intercept) 1.8325   1.3537
 noNAdata2$Group_Size               (Intercept) 0.1683   0.4102
 noNAdata2$Transect_Number          (Intercept) 0.4049   0.6363
 noNAdata2$Observers                (Intercept) 0.3756   0.6128
 Residual                                       1.1003   1.0490
Number of obs: 582, groups:
noNAdata2$Distance_to_nearest_road, 545; noNAdata2$Group_Size, 46; noNAdata2$Transect_Number, 22; noNAdata2$Obse
rvers, 5

Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)    7.0899     0.3673   7.1458  19.301 1.99e-07 ***
noNAdata2$SexM -0.2117     0.1560 552.0313  -1.357    0.175
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr)
noNAdt2$SxM -0.188
```

M2.O

```
require(lmerTest)
M2.O <- lmer(
  noNAdata2.O$Flight_Dist ~
    noNAdata2.O$Sex
  + (1|noNAdata2.O$Distance_to_nearest_road)
  + (1|noNAdata2.O$Transect_Number)
  + (1|noNAdata2.O$Observers)
)
```

```
> summary(M2.O)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: noNAdata2.O$Flight_Dist ~ noNAdata2.O$Sex + (1 | noNAdata2.O$Distance_to_nearest_road) +
    (1 | noNAdata2.O$Transect_Number) + (1 | noNAdata2.O$Observers)

REML criterion at convergence: 1103.4

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.20429 -0.45202  0.01197  0.44692  1.61537

Random effects:
 Groups                                Name        Variance Std.Dev.
 noNAdata2.O$Distance_to_nearest_road (Intercept) 1.4050   1.1853
 noNAdata2.O$Transect_Number          (Intercept) 0.2965   0.5445
 noNAdata2.O$Observers                (Intercept) 0.1865   0.4318
 Residual                                         1.0264   1.0131
Number of obs: 296, groups:
noNAdata2.O$Distance_to_nearest_road, 267; noNAdata2.O$Transect_Number, 12; noNAdata2.O$Observers, 4

Fixed effects:
                Estimate Std. Error       df t value Pr(>|t|)
(Intercept)       6.5202     0.3425   5.1350  19.040 5.83e-06 ***
noNAdata2.O$SexM -0.5571     0.1845 250.7071  -3.019   0.0028 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr)
nNAdt2.O$SM -0.293
```

M3

```
require(lmerTest)
M3 <- lmer(
  noNAdata3$Flight_Dist ~
    noNAdata3$Poaching_Pressure * noNAdata3$Sex
  + (1|noNAdata3$Distance_to_nearest_road)
  + (1|noNAdata3$Group_Size)
  + (1|noNAdata3$Transect_Number)
  + (1|noNAdata3$Observers)
)
```

```
> summary(M3)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: noNAdata3$Flight_Dist ~ noNAdata3$Poaching_Pressure * noNAdata3$Sex +
    (1 | noNAdata3$Distance_to_nearest_road) + (1 | noNAdata3$Group_Size) +
    (1 | noNAdata3$Transect_Number) + (1 | noNAdata3$Observers)

REML criterion at convergence: 2318.2

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.7800 -0.4508  0.0010  0.4092  1.5465

Random effects:
 Groups                              Name        Variance Std.Dev.
 noNAdata3$Distance_to_nearest_road (Intercept) 1.8719   1.3682
 noNAdata3$Group_Size               (Intercept) 0.1752   0.4185
 noNAdata3$Transect_Number          (Intercept) 0.3923   0.6264
 noNAdata3$Observers                (Intercept) 0.3982   0.6310
 Residual                                       1.1363   1.0660
Number of obs: 582, groups:
noNAdata3$Distance_to_nearest_road, 545; noNAdata3$Group_Size, 46; noNAdata3$Transect_Number, 22; noNAdata3$Obse
rvers, 5

Fixed effects:
                                          Estimate Std. Error        df t value Pr(>|t|)
(Intercept)                                6.88871    0.39798   8.81937  17.309 4.12e-08 ***
noNAdata3$Poaching_PressureTest            0.74804    0.39807  34.81322   1.879   0.0686 .
noNAdata3$SexM                             0.05377    0.19849 571.13631   0.271   0.7866
noNAdata3$Poaching_PressureTest:noNAdata3$SexM -0.72288    0.31149 478.70857  -2.321   0.0207 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) nNAd3$P_PT nNA3$S
nNAdt3$P_PT -0.339
noNAdt3$SxM -0.219  0.181
nNA3$P_PT:N  0.157 -0.378     -0.604
```

M4

```
M4 <- lmer(
  noNAdata4$Flight_Dist ~
    noNAdata4$Distance_to_nearest_road
  + (1|noNAdata4$Group_Size)
  + (1|noNAdata4$Transect_Number)
  + (1|noNAdata4$Observers)
)
```

```
> summary(M4)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: noNAdata4$Flight_Dist ~ noNAdata4$Distance_to_nearest_road +
    (1 | noNAdata4$Group_Size) + (1 | noNAdata4$Transect_Number) +      (1 | noNAdata4$Observers)

REML criterion at convergence: 2335

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.85346 -0.69254 -0.00366  0.62969  2.66082

Random effects:
 Groups                 Name        Variance Std.Dev.
 noNAdata4$Group_Size   (Intercept) 0.1704   0.4127
 noNAdata4$Transect_Number (Intercept) 0.5017   0.7083
 noNAdata4$Observers    (Intercept) 0.3846   0.6201
 Residual                           2.8786   1.6966
Number of obs: 582, groups:  noNAdata4$Group_Size, 46; noNAdata4$Transect_Number, 22; noNAdata4$Observers, 5

Fixed effects:
                                Estimate Std. Error        df t value Pr(>|t|)
(Intercept)                    6.800e+00  3.801e-01 8.681e+00  17.889 3.75e-08 ***
noNAdata4$Distance_to_nearest_road 5.236e-04  2.638e-04 5.961e+01   1.985   0.0518 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr)
nNAdt4$D___ -0.246
```

M4.O

```
M4.O <- lmer(
  noNAdata4.O$Flight_Dist ~
    noNAdata4.O$Distance_to_nearest_road
  + (1|noNAdata4.O$Sex)
  + (1|noNAdata4.O$Transect_Number)
  + (1|noNAdata4.O$Observers)
)
```

```
> summary(M4.O)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: noNAdata4.O$Flight_Dist ~ noNAdata4.O$Distance_to_nearest_road +
    (1 | noNAdata4.O$Sex) + (1 | noNAdata4.O$Transect_Number) +      (1 | noNAdata4.O$Observers)

REML criterion at convergence: 1110

Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.3511 -0.6795  0.0233  0.6780  2.3864

Random effects:
 Groups                     Name        Variance Std.Dev.
 noNAdata4.O$Transect_Number (Intercept) 0.3340   0.5779
 noNAdata4.O$Observers      (Intercept) 0.2301   0.4797
 noNAdata4.O$Sex            (Intercept) 0.1555   0.3944
 Residual                               2.2031   1.4843
Number of obs: 296, groups:  noNAdata4.O$Transect_Number, 12; noNAdata4.O$Observers, 4; noNAdata4.O$Sex, 2

Fixed effects:
                                  Estimate Std. Error        df t value Pr(>|t|)
(Intercept)                      5.849e+00  4.751e-01 5.160e+00  12.310 5.07e-05 ***
noNAdata4.O$Distance_to_nearest_road 3.679e-04  2.594e-04 4.086e+01   1.418    0.164
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr)
nNA4.O$D___ -0.370
```

M5a

```
M5a <- lmer(
  noNAdata5a$Flight_Dist ~
    noNAdata5a$Sex +
    noNAdata5a$Distance_to_nearest_road
  + (1|noNAdata5a$Group_Size)
  + (1|noNAdata5a$Transect_Number)
  + (1|noNAdata5a$Observers)
)
```

```
> summary(M5a)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: noNAdata5a$Flight_Dist ~ noNAdata5a$Sex + noNAdata5a$Distance_to_nearest_road +
    (1 | noNAdata5a$Group_Size) + (1 | noNAdata5a$Transect_Number) +      (1 | noNAdata5a$Observers)

REML criterion at convergence: 2338.6

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.9271 -0.7011 -0.0234  0.6520  2.6246

Random effects:
 Groups                    Name        Variance Std.Dev.
 noNAdata5a$Group_Size     (Intercept) 0.1628   0.4035
 noNAdata5a$Transect_Number (Intercept) 0.5374   0.7331
 noNAdata5a$Observers      (Intercept) 0.3809   0.6172
 Residual                              2.8904   1.7001
Number of obs: 582, groups:
noNAdata5a$Group_Size, 46; noNAdata5a$Transect_Number, 22; noNAdata5a$Observers, 5

Fixed effects:
                                  Estimate Std. Error         df t value Pr(>|t|)
(Intercept)                      6.927e+00  3.883e-01  9.521e+00  17.842 1.23e-08 ***
noNAdata5a$SexM                 -2.765e-01  1.589e-01  5.740e+02  -1.740   0.0824 .
noNAdata5a$Distance_to_nearest_road  5.457e-04  2.677e-04  6.317e+01   2.038   0.0457 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) nNA5$S
noNAdt5$SxM -0.183
nNAdt5$D___ -0.245 -0.007
```

M5a.O

```
M5a.O <- lmer(
  noNAdata5a.O$Flight_Dist ~
    noNAdata5a.O$Sex +
    noNAdata5a.O$Distance_to_nearest_road
  + (1|noNAdata5a.O$Transect_Number)
  + (1|noNAdata5a.O$Observers)
)
```

```
> summary(M5a.O)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: noNAdata5a.O$Flight_Dist ~ noNAdata5a.O$Sex + noNAdata5a.O$Distance_to_nearest_road +
    (1 | noNAdata5a.O$Transect_Number) + (1 | noNAdata5a.O$Observers)

REML criterion at convergence: 1132.8

Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.3188 -0.6851  0.0072  0.6819  2.4195

Random effects:
 Groups                       Name        Variance Std.Dev.
 noNAdata5a.O$Transect_Number (Intercept) 0.3654   0.6045
 noNAdata5a.O$Observers       (Intercept) 0.2493   0.4993
 Residual                                 2.3957   1.5478
Number of obs: 296, groups:  noNAdata5a.O$Transect_Number, 12; noNAdata5a.O$Observers, 4

Fixed effects:
                                    Estimate Std. Error         df t value Pr(>|t|)
(Intercept)                        6.299e+00  4.135e-01  1.003e+01  15.233 2.93e-08 ***
noNAdata5a.O$SexM                 -6.141e-01  1.933e-01  2.892e+02  -3.177  0.00165 **
noNAdata5a.O$Distance_to_nearest_road  3.874e-04  2.707e-04  4.124e+01   1.431  0.15998
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) nNA5.O$S
nNAdt5.O$SM -0.242
nNA5.O$D___ -0.441 -0.010
```

M5b

```
M5b <- lmer(
  noNAdata5b$Flight_Dist ~
    noNAdata5b$Sex *
    noNAdata5b$Distance_to_nearest_road
  + (1|noNAdata5b$Group_Size)
  + (1|noNAdata5b$Transect_Number)
  + (1|noNAdata5b$Observers)
)
```

```
> summary(M5b)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: noNAdata5b$Flight_Dist ~ noNAdata5b$Sex * noNAdata5b$Distance_to_nearest_road +
    (1 | noNAdata5b$Group_Size) + (1 | noNAdata5b$Transect_Number) +      (1 | noNAdata5b$Observers)

REML criterion at convergence: 2352.9

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.91616 -0.69935 -0.00714  0.64904  2.62572

Random effects:
 Groups                   Name        Variance Std.Dev.
 noNAdata5b$Group_Size    (Intercept) 0.1611   0.4014
 noNAdata5b$Transect_Number (Intercept) 0.5437   0.7373
 noNAdata5b$Observers     (Intercept) 0.3788   0.6154
 Residual                             2.8940   1.7012
Number of obs: 582, groups:
noNAdata5b$Group_Size, 46; noNAdata5b$Transect_Number, 22; noNAdata5b$Observers, 5

Fixed effects:
                                                 Estimate Std. Error         df t value Pr(>|t|)
(Intercept)                                     6.892e+00  3.934e-01  1.006e+01  17.519 7.17e-09 ***
noNAdata5b$SexM                                -2.209e-01  1.924e-01  5.752e+02  -1.148   0.2515
noNAdata5b$Distance_to_nearest_road             6.283e-04  3.096e-04  9.920e+01   2.029   0.0451 *
noNAdata5b$SexM:noNAdata5b$Distance_to_nearest_road -1.382e-04  2.672e-04  5.708e+02  -0.517   0.6052
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
Correlation of Fixed Effects:
            (Intr) nNAd5$SM nNA5$D
nNAdt5b$SxM -0.241
nNAdt5$D___ -0.291  0.276
nNA5$SM:NA5  0.163 -0.563   -0.498
```

M5b.O

```
M5b.O <- lmer(
  noNAdata5b.O$Flight_Dist ~
    noNAdata5b.O$Sex *
    noNAdata5b.O$Distance_to_nearest_road
  + (1|noNAdata5b.O$Transect_Number)
  + (1|noNAdata5b.O$Observers)
)
```

```
> summary(M5b.O)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: noNAdata5b.O$Flight_Dist ~ noNAdata5b.O$Sex * noNAdata5b.O$Distance_to_nearest_road +
    (1 | noNAdata5b.O$Transect_Number) + (1 | noNAdata5b.O$Observers)

REML criterion at convergence: 1141.1

Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.3437 -0.6789  0.0138  0.6549  2.3947

Random effects:
 Groups                      Name        Variance Std.Dev.
 noNAdata5b.O$Transect_Number (Intercept) 0.3450   0.5874
 noNAdata5b.O$Observers       (Intercept) 0.2434   0.4934
 Residual                                 2.3573   1.5353
Number of obs: 296, groups:  noNAdata5b.O$Transect_Number, 12; noNAdata5b.O$Observers, 4

Fixed effects:
                                                    Estimate Std. Error         df t value Pr(>|t|)
(Intercept)                                        6.318e+00  4.298e-01  1.188e+01  14.700 5.52e-09
noNAdata5b.O$SexM                                 -6.996e-01  2.955e-01  2.913e+02  -2.368   0.0185
noNAdata5b.O$Distance_to_nearest_road              3.060e-04  3.207e-04  6.865e+01   0.954   0.3434
noNAdata5b.O$SexM:noNAdata5b.O$Distance_to_nearest_road  1.233e-04  3.009e-04  2.887e+02   0.410   0.6823

(Intercept)                                       ***
noNAdata5b.O$SexM                                 *
noNAdata5b.O$Distance_to_nearest_road
noNAdata5b.O$SexM:noNAdata5b.O$Distance_to_nearest_road
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) nNAd5.O$SM nNA5.O$D
nNAdt5.O$SM -0.393
nNA5.O$D___ -0.525  0.417
nNA5.O$SM:N  0.320 -0.761     -0.555
```

M6a

```
M6a <- lmer(
  noNAdata6a$Flight_Dist ~
    noNAdata6a$Poaching_Pressure +
    noNAdata6a$Distance_to_nearest_road
  + (1|noNAdata6a$Group_Size)
  + (1|noNAdata6a$Transect_Number)
  + (1|noNAdata6a$Observers)
)
```

```
> summary(M6a)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: noNAdata6a$Flight_Dist ~ noNAdata6a$Poaching_Pressure + noNAdata6a$Distance_to_nearest_road +
    (1 | noNAdata6a$Group_Size) + (1 | noNAdata6a$Transect_Number) +      (1 | noNAdata6a$Observers)

REML criterion at convergence: 2339.5

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.84432 -0.69071 -0.01091  0.63146  2.67943

Random effects:
 Groups                   Name        Variance Std.Dev.
 noNAdata6a$Group_Size    (Intercept) 0.1754   0.4188
 noNAdata6a$Transect_Number (Intercept) 0.5291   0.7274
 noNAdata6a$Observers     (Intercept) 0.3954   0.6288
 Residual                             2.9020   1.7035
Number of obs: 582, groups:
noNAdata6a$Group_Size, 46; noNAdata6a$Transect_Number, 22; noNAdata6a$Observers, 5

Fixed effects:
                                 Estimate Std. Error        df t value Pr(>|t|)
(Intercept)                     6.767e+00  4.031e-01 1.009e+01  16.788 1.05e-08 ***
noNAdata6a$Poaching_PressureTest    1.710e-01  4.230e-01 2.270e+01   0.404   0.6898
noNAdata6a$Distance_to_nearest_road 4.965e-04  2.852e-04 6.974e+01   1.741   0.0862 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) nNA6$P
nNAdt6$P_PT -0.289
nNAdt6$D___ -0.121 -0.349
```

M6b

```
M6b <- lmer(
  noNAdata6b$Flight_Dist ~
    noNAdata6b$Poaching_Pressure *
    noNAdata6b$Distance_to_nearest_road
  + (1|noNAdata6b$Group_Size)
  + (1|noNAdata6b$Transect_Number)
  + (1|noNAdata6b$Observers)
)
```

```
> summary(M6b)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: noNAdata6b$Flight_Dist ~ noNAdata6b$Poaching_Pressure * noNAdata6b$Distance_to_nearest_road +
    (1 | noNAdata6b$Group_Size) + (1 | noNAdata6b$Transect_Number) +      (1 | noNAdata6b$Observers)

REML criterion at convergence: 2322

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.85453 -0.70731 -0.01166  0.62773  2.83601

Random effects:
 Groups                    Name        Variance Std.Dev.
 noNAdata6b$Group_Size     (Intercept) 0.1634   0.4042
 noNAdata6b$Transect_Number (Intercept) 0.6843   0.8272
 noNAdata6b$Observers      (Intercept) 0.3770   0.6140
 Residual                              2.7382   1.6548
Number of obs: 582, groups:
noNAdata6b$Group_Size, 46; noNAdata6b$Transect_Number, 22; noNAdata6b$Observers, 5

Fixed effects:
                                                                        Estimate Std. Error         df
(Intercept)                                                            6.5306434  0.4184023 12.0730114
noNAdata6b$Poaching_PressureTest                                       0.5147095  0.5126625 24.9237524
noNAdata6b$Distance_to_nearest_road                                    0.0011765  0.0004874 90.5240618
noNAdata6b$Poaching_PressureTest:noNAdata6b$Distance_to_nearest_road -0.0009511  0.0006081 88.2921853
                                                                       t value Pr(>|t|)
(Intercept)                                                             15.609 2.28e-09 ***
noNAdata6b$Poaching_PressureTest                                         1.004   0.3250
noNAdata6b$Distance_to_nearest_road                                      2.414   0.0178 *
noNAdata6b$Poaching_PressureTest:noNAdata6b$Distance_to_nearest_road  -1.564   0.1214
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) nNAd6$P_PT nNA6$D
nNAdt6$P_PT -0.360
nNAdt6$D___ -0.196  0.185
nNA6$P_PT:N  0.156 -0.454     -0.800
```

Appendix S2: Animal Handling and Ethical Statement

My field work was approved by the Department of Zoology's Local AWERB under Ref. No. APA/1/5/ZOO/NASPA/WildCRU/CarnivorUngulateUganda.

The data used for Chapter Three were obtained as part of a larger network of projects based in Hwange National Park, Zimbabwe, and previous papers have compiled the relevant ethical approvals and veterinary protocols used during animal handling.

The following ethical statement is a compilation of the appropriate veterinary protocols and ethical approvals used while collecting the data used in Chapter Three of this thesis. It is presented verbatim from Appendix S1, Petracca *et al.* (2021).

“Animal handling and care protocols were consistent with guidelines provided in the ‘Code of Practice for Biologists using Animals’, Department of Zoology, University of Oxford and approved by University of Oxford, Biomedical Sciences, Animal Welfare and Ethical Review Body (AWERB). Animal handling procedures were carried out by project staff trained and certified by the Zimbabwe Veterinary Association, Wildlife Group (Certificate numbers: Davidson: 09/03; Elliot: 9/10; Hunt: A11/04, 005/09, 5/14; Loveridge: 6/2000, 20/36 (2007), 6/14; Stapelkamp: 34/2008) in accordance with Statutory Instrument 409 of 1999 (Clause 21A to 21J) amending the Regulations of 1975 to the Dangerous Drugs Act, Zimbabwe. Initial training and refresher training (every five years) was undertaken through attendance at the Chemical and Physical Restraint of Wild Animals Course (run by Zimbabwe Veterinary Association, Wildlife Group and Government Veterinary Services Wildlife Unit, see http://wildlifecaptureafrica.com/the-course/about-the-course/). All procedures were undertaken with the permission of the Zimbabwe Parks and Wildlife Management Authority (Permit numbers: REF:DM/Gen/(T) 23(1)(c)(ii):713/12/01, 03/2002, 07/2003, 20/2004, 01/2005, 01/2007, 03/2008, 03/2009, 25/2010, 06/2011, 12/2012, 08/2013, 51/2014, 10/2015) and under license from the Zimbabwe Veterinary Association, Wildlife Group (Veterinary Committee) and Medicines Control Authority, Zimbabwe (license numbers: Davidson: 2005/046, 2006/033, 2007/04, 2008/07; Elliot: 2010/18, 2011/04, 2012/24, 2013/13, 2014/25; Hunt: 2004/053, 2005/032, 2006/032, 2007/06, 2008/06, 2009/19, 2010/03, 2011/02, 2012/23, 2013/11, 2014/26, 2015/03, 2016/24; Loveridge: 2000/75, 2001/037,2002/47, B/279/21/16/2003, 2007/08, 2008/08, 2009/20, 2010/04, 2011/03, 2012/22, 2013/10, 2014/24, 2015/02, 2016/23; Stapelkamp: 2008/34, 2009/21, 2010/05, 2011/01, 2012/01, 2013/12. 2014/27, 2015/04).” – **Petracca *et al.* (2021)**

Full Citation for this Quote:

Petracca, Lisanne S., Jacqueline L. Frair, Guillaume Bastille-Rousseau, David W. Macdonald, and Andrew J. Loveridge. 2021. “Harassment-Induced Changes in Lion Space Use as a Conflict Mitigation Tool.” *Conservation Science and Practice* 3 (5): e373.

Appendix S3: Integrating the Model

The integration from $\frac{\Delta E}{\Delta t}$ to *E(t)* is demonstrated below. Note that Δt has been scaled, and *B* has been converted from kcal/min to kcal.

$$\frac{\Delta E}{\Delta t} = -B - S_t J - G_t C + \sum_{i=1}^{n} \frac{D_{it} V_t A_i}{1 + N_t} W_i$$

Re-write the first term, then cancel out *t*.

$$\frac{\Delta E}{\Delta t} = \frac{E_{t+\Delta t} - E_t}{t + \Delta t - t} = -B - S_t J - G_t C + \sum_{i=1}^{n} \frac{D_{it} V_t A_i}{1 + N_t} W_i$$

Multiply both sides by Δt, then cancel out Δt on the first term.

$$\frac{E_{t+\Delta t} - E_t}{\Delta t} \Delta t = \left(-B - S_t J - G_t C + \sum_{i=1}^{n} \frac{D_{it} V_t A_i}{1 + N_t} W_i \right) \Delta t$$

This results in the following equation.

$$E_{t+\Delta t} - E_t = \left(-B - S_t J - G_t C + \sum_{i=1}^{n} \frac{D_{it} V_t A_i}{1 + N_t} W_i \right) \Delta t$$

Isolate $E_{t+\Delta t}$.

$$E_{t+\Delta t} = \left(-B - S_t J - G_t C + \sum_{i=1}^{n} \frac{D_{it} V_t A_i}{1 + N_t} W_i \right) \Delta t + E_t$$

Appendix S4: Sensitivity Analysis Coefficients of Variation

Table S4: Absolute values of the coefficients of variance produced by altering each covariate in a model of African lions' energy levels over space and time. The covariates' minimums and maximums are the default values multiplied by 0.8 and 1.2 respectively. Due to the size of the table, it has been presented in three parts in Landscape orientation to assist with legibility. The 'lion' column has been repeated to keep coefficients labelled by individual in each picture.

Lion	Default	B.max	B.min	J.max	J.min	C.max	C.min	A.wild.max	A.wild.min	A.dom.max	A.dom.min	W.wild.max	W.wild.min	W.dom.max	W.dom.min
BACF2	67.75657784	70.70375616	66.09195656	68.9651044	66.70806815	77.97816197	64.59711051	63.87020336	305.6262101	67.75657784	67.75657784	63.87020336	305.6262101	67.75657784	67.75657784
BACaF1	1112.783884	139.7707268	96.72129385	368.0549623	888.7525879	93.07518571	49.6516552	47.36204554	75.54031325	1112.783884	1112.783884	47.36204554	75.54031325	1112.783884	1112.783884
BALcF1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
GUVF1	72.21588031	71.42754657	72.78067664	72.21591732	72.21640769	73.89178099	70.99275429	71.75989799	74.26213405	72.21588031	72.21588031	71.75989799	74.26213405	72.21588031	72.21588031
GUVF2	58.26683784	58.99222887	59.66616536	58.43497331	58.13718367	58.54327537	58.25641006	59.49433257	73.66038231	58.26683784	58.26683784	59.49433257	73.66038231	58.26683784	58.26683784
GUVaF2	57.48648684	54.73959901	59.15801144	56.87050345	58.0614054	55.95317995	58.62263863	59.89155473	71.14663254	57.48648684	57.48648684	59.89155473	71.14663254	57.48648684	57.48648684
GUVaF4	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
GUVbF4	35.76110488	36.32799481	35.64313484	35.39985077	36.17116616	35.64679313	35.97506955	37.04247276	36.14174104	35.76110488	35.76110488	37.04247276	36.14174104	35.76110488	35.76110488
GUVgF1	65.1522862	68.96866989	62.91250224	65.78215768	64.58143925	66.23646451	64.40594529	62.61761985	76.5817719	65.1522862	65.1522862	62.61761985	76.5817719	65.1522862	65.1522862
KASF1	59.68598832	53.56305163	69.52229772	54.11575067	74.15389651	53.3296866	75.56551687	62.46629196	54.76951268	59.68598832	59.68598832	62.46629196	54.76951268	59.68598832	59.68598832
KENF1	56.11399053	53.96468404	58.40203372	55.83451785	56.39289449	55.99728248	56.22834689	58.32017618	53.92160479	56.11399053	56.11399053	58.32017618	53.92160479	56.11399053	56.11399053
LINF1	63.09035852	60.65751001	65.50025837	62.98215784	63.20977064	62.38600118	63.76498757	65.67336079	64.44879211	63.09035852	63.09035852	65.67336079	64.44879211	63.09035852	63.09035852
MAHF1	58.43647104	58.57680043	58.33025792	58.37972888	58.49009038	58.48189148	58.39702063	58.36228025	58.63288032	58.43647104	58.43647104	58.36228025	58.63288032	58.43647104	58.43647104
NEHF1	93.4385499	124.7561718	79.39130446	95.62625066	91.4416799	103.5861526	86.13756769	76.96827069	199.082171	93.4385499	93.4385499	76.96827069	199.082171	93.4385499	93.4385499
NEHcF2	58.58914426	62.09980637	73.43738051	59.03295916	58.27761466	57.0178862	78.51699627	977.20034	61.88057389	58.58914426	58.58914426	977.20034	61.88057389	58.58914426	58.58914426
NYMaF7	2215.096344	119.9787671	54.61078419	759.7814578	397.2958462	161.4874706	77.73272899	53.65928978	91.26248417	2215.096344	2215.096344	53.65928978	91.26248417	2215.096344	2215.096344
SHUF3	81.34941699	44.64891806	65.8670311	88.19489961	77.35805786	44.13404109	64.11702956	62.34055428	52.64179345	81.34941699	81.34941699	62.34055428	52.64179345	81.34941699	81.34941699
SHUF5	102.808475	88.46196062	244.9531556	100.7054609	105.3241822	83.69098198	217.7794291	128.5609366	77.99815654	102.808475	102.808475	128.5609366	77.99815654	102.808475	102.808475
SHUaF4	65.04001262	64.79951837	65.31163569	65.00605595	65.07477813	64.3893709	66.39860156	66.54593441	64.08462386	65.04001262	65.04001262	66.54593441	64.08462386	65.04001262	65.04001262
SITF2	50.95597319	1015.013176	42.27164297	61.49534215	45.57795956	95.51840677	42.28034178	43.41575681	130.4900787	50.95597319	50.95597319	43.41575681	130.4900787	50.95597319	50.95597319
SOAF1	55.96073325	36.87960143	66.91998465	53.49289695	58.24342084	51.74317014	59.21005272	67.93040938	435.5316645	55.96073325	55.96073325	67.93040938	435.5316645	55.96073325	55.96073325
SPIF2	51.93539342	48.2494546	54.77381314	51.38404523	52.46711802	50.92598315	52.90466629	55.34561672	45.93352815	51.93539342	51.93539342	55.34561672	45.93352815	51.93539342	51.93539342
SPIF3	60.14947796	60.87589054	59.62356006	60.21812875	60.08418288	60.35223576	59.97077805	59.55019183	61.71461788	60.14947796	60.14947796	59.55019183	61.71461788	60.14947796	60.14947796
SPIF4	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
SPIbF4	69.42450085	69.57745939	69.39938083	69.30668902	69.53842124	69.4314637	69.53925073	69.59221133	72.70761217	69.42450085	69.42450085	69.59221133	72.70761217	69.42450085	69.42450085
SPIbF6	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
SPIhF1	394.0061993	436.0360809	157.7179628	592.9996658	298.7925436	2398.700209	233.0496979	135.2740241	102.552102	394.0061993	394.0061993	135.2740241	102.552102	394.0061993	394.0061993
TCHF2	60.44367102	60.26512502	60.59394707	60.33388264	60.54911748	60.39224728	60.49272778	60.68165152	59.95159497	60.44367102	60.44367102	60.68165152	59.95159497	60.44367102	60.44367102
TSHF1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Lion	grassland.max	grassland.min	bushed_grassland.max	bushed_grassland.min	bushland.max	bushland.min	woodland_deciduous.max	woodland_deciduous.min	mopane_scrub_stunted_bushed.max	mopane_scrub_stunted_bushed.min	mopane_woodland.max	mopane_woodland.min
BACF2	67.0776477	68.93236972	65.64125016	73.34593662	64.99457743	73.65811351	67.41126956	68.12138978	67.76477904	67.74838519	67.71193146	67.80131015
BACaF1	108.663892	132.0901163	61.72406838	102.0101343	148.1635111	171.5640518	1896.715263	463.340783	1116.69517	1108.901967	1146.9472	1080.702771
BALcF1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
GUVF1	70.95338239	73.63571716	72.50338758	71.81334152	72.74263413	71.4153467	71.9039329	72.55605797	72.20883032	72.22293495	72.21332746	72.21843372
GUVF2	58.34099687	58.23266355	58.65525058	58.94098675	58.897665	58.14881332	58.23351912	58.33510487	58.26683784	58.26683784	58.26683784	58.26683784
GUVaF2	56.79115367	58.22900802	58.37617698	55.90606729	60.23604497	53.50316988	57.50706864	57.46760603	57.48648684	57.48648684	57.48648684	57.48648684
GUVaF4	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
GUVbF4	35.51076831	36.00837011	36.50629165	35.41763333	35.56335167	36.10579935	35.7615367	35.76486986	35.76043259	35.76177756	35.76110488	35.76110488
GUVgF1	64.73754697	65.85296363	63.80678943	67.48068286	63.44690248	67.86100714	65.0397216	65.29041664	65.15298635	65.15158646	65.1522862	65.1522862
KASF1	74.38665296	56.26762553	145.7368097	49.13230665	188.5658983	52.88364569	65.27604943	55.83939917	130.2333406	53.28403853	84.54165229	55.08686254
KENF1	56.15836971	56.07866519	56.82949115	55.31143251	57.50878602	54.51636339	56.6483967	55.54286304	56.12785519	56.10010355	56.06736301	56.16083488
LINF1	63.60420089	62.87279009	64.88165468	60.61035803	62.93333724	63.43898358	63.76235116	62.41718598	63.10105551	63.07965676	63.19116071	62.98903451
MAHF1	59.60042805	56.46544448	58.45821232	58.41540891	58.43647104	58.43647104	58.43647104	58.43647104	58.43647104	58.43647104	57.07563934	60.35662588
NEHF1	91.58240151	95.5467389	83.54314154	114.8606622	83.78417473	111.3935013	92.26114032	94.70162066	93.23364093	93.648633	92.66863043	94.2744972
NEHcF2	56.30695997	60.9499731	68.6690734	58.14931114	65.29568438	60.07942673	59.2567461	57.98836148	58.58486921	58.59350315	58.69325879	58.4975296
NYMaF7	273.9856139	446.9990895	113.3998921	200.1418482	63.91133757	115.0161801	331.903117	664.3842587	2163.345508	2269.293057	2097.92225	2345.676187
SHUF3	79.62395742	84.05030874	74.42609195	119.0826424	69.19626591	102.677471	77.15251059	87.84278138	74.80647023	97.54847962	64.09673972	44.99831963
SHUF5	105.7255306	100.1803636	107.695275	99.12740936	109.2938022	98.78906881	103.3473134	102.2854442	116.3994356	93.21056564	355.5693142	82.55785205
SHUaF4	65.1501503	64.93183168	65.20356386	64.88573461	65.1639683	64.92326132	65.05302966	65.02718694	65.42968258	64.6745103	65.48651289	64.69239714
SITF2	44.17891172	66.13114387	40.51646683	851.6317176	44.901705	92.97675321	50.4659963	51.46631452	50.95597319	50.95597319	50.95597319	50.95597319
SOAF1	59.53870209	51.68912283	62.87714636	43.16149845	60.08240549	50.04452071	58.70042837	52.17946625	55.996202	55.92584397	56.01492594	55.90642553
SPIF2	52.18824793	51.64993065	53.57193741	49.81208633	54.10934656	49.0153726	52.0638311	51.8059871	51.93539824	51.9353886	51.93539342	51.93539342
SPIF3	58.68510388	62.09461392	60.39735612	59.78361898	60.61031742	59.62524317	60.13952405	60.16015678	60.14947796	60.14947796	60.14947796	60.14947796
SPIF4	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
SPIbF4	68.81315666	70.34879874	69.65894669	69.27769282	69.79365628	69.13324623	69.68672597	69.15579291	69.42450085	69.42450085	69.42450085	69.42450085
SPIbF6	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
SPIhF1	318.7930565	530.8673125	221.8140349	5054.111102	221.5571357	2609.793981	247.0443804	1063.036517	394.0061993	394.0061993	394.0061993	394.0061993
TCHF2	60.42751036	60.46025178	60.74571755	60.11526615	60.47155059	60.40622483	60.58393093	60.29736591	60.29078284	60.59802403	60.44461173	60.4427311
TSHF1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Lion	woodland_evergreen.max	woodland_evergreen.min	village_boundary_cattle.max	village_boundary_cattle.min	village_boundary_shoats.max	village_boundary_shoats.min	village_boundary_donkeys.max	village_boundary_donkeys.min	D_cattle.max	D_cattle.min	D_shoats.max	D_shoats.min	D_donkeys.max	D_donkeys.min
BACF2	67.76303007	67.75018177	67.75657784	67.75657784	67.75657784	67.75657784	67.75657784	67.75657784	67.75657784	67.75657784	67.75657784	67.75657784	67.75657784	67.75657784
BACaF1	3381.186735	685.4620748	1112.783884	1112.783884	1112.783884	1112.783884	1112.783884	1112.783884	1112.783884	1112.783884	1112.783884	1112.783884	1112.783884	1112.783884
BALcF1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
GUVF1	72.1585899	72.27369866	72.21588031	72.21588031	72.21588031	72.21588031	72.21588031	72.21588031	72.21588031	72.21588031	72.21588031	72.21588031	72.21588031	72.21588031
GUVF2	58.28936225	58.24430992	58.26683784	58.26683784	58.26683784	58.26683784	58.26683784	58.26683784	58.26683784	58.26683784	58.26683784	58.26683784	58.26683784	58.26683784
GUVaF2	57.48818922	57.48478487	57.48648684	57.48648684	57.48648684	57.48648684	57.48648684	57.48648684	57.48648684	57.48648684	57.48648684	57.48648684	57.48648684	57.48648684
GUVaF4	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
GUVbF4	35.78426506	35.73807864	35.76110488	35.76110488	35.76110488	35.76110488	35.76110488	35.76110488	35.76110488	35.76110488	35.76110488	35.76110488	35.76110488	35.76110488
GUVgF1	65.26038667	65.043985	65.1522862	65.1522862	65.1522862	65.1522862	65.1522862	65.1522862	65.1522862	65.1522862	65.1522862	65.1522862	65.1522862	65.1522862
KASF1	59.68598832	59.68598832	59.68598832	59.68598832	59.68598832	59.68598832	59.68598832	59.68598832	59.68598832	59.68598832	59.68598832	59.68598832	59.68598832	59.68598832
KENF1	56.10114155	56.12874084	56.11399053	56.11399053	56.11399053	56.11399053	56.11399053	56.11399053	56.11399053	56.11399053	56.11399053	56.11399053	56.11399053	56.11399053
LINF1	63.49474008	62.69136197	63.09035852	63.09035852	63.09035852	63.09035852	63.09035852	63.09035852	63.09035852	63.09035852	63.09035852	63.09035852	63.09035852	63.09035852
MAHF1	58.43647104	58.43647104	58.43647104	58.43647104	58.43647104	58.43647104	58.43647104	58.43647104	58.43647104	58.43647104	58.43647104	58.43647104	58.43647104	58.43647104
NEHF1	93.43759228	93.43950768	93.4385499	93.4385499	93.4385499	93.4385499	93.4385499	93.4385499	93.4385499	93.4385499	93.4385499	93.4385499	93.4385499	93.4385499
NEHcF2	58.58182907	58.5965053	58.58914426	58.58914426	58.58914426	58.58914426	58.58914426	58.58914426	58.58914426	58.58914426	58.58914426	58.58914426	58.58914426	58.58914426
NYMaF7	310.5433059	640.0096879	2203.686991	2215.096344	2198.023934	2215.096344	2209.377726	2215.096344	2215.096344	2215.096344	2215.096344	2215.096344	2215.096344	2215.096344
SHUF3	81.34941699	81.34941699	81.34941699	81.34941699	81.34941699	81.34941699	81.34941699	81.34941699	81.34941699	81.34941699	81.34941699	81.34941699	81.34941699	81.34941699
SHUF5	102.808475	102.808475	102.808475	102.808475	102.808475	102.808475	102.808475	102.808475	102.808475	102.808475	102.808475	102.808475	102.808475	102.808475
SHUaF4	65.04001262	65.04001262	65.04001262	65.04001262	65.04001262	65.04001262	65.04001262	65.04001262	65.04001262	65.04001262	65.04001262	65.04001262	65.04001262	65.04001262
SITF2	50.95597319	50.95597319	50.95597319	50.95597319	50.95597319	50.95597319	50.95597319	50.95597319	50.95597319	50.95597319	50.95597319	50.95597319	50.95597319	50.95597319
SOAF1	56.49093101	55.41775474	55.96073325	55.96073325	55.96073325	55.96073325	55.96073325	55.96073325	55.96073325	55.96073325	55.96073325	55.96073325	55.96073325	55.96073325
SPIF2	51.95232973	51.91844575	51.93539342	51.93539342	51.93539342	51.93539342	51.93539342	51.93539342	51.93539342	51.93539342	51.93539342	51.93539342	51.93539342	51.93539342
SPIF3	60.1776444	60.12130813	60.14947796	60.14947796	60.14947796	60.14947796	60.14947796	60.14947796	60.14947796	60.14947796	60.14947796	60.14947796	60.14947796	60.14947796
SPIF4	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
SPIbF4	69.43050002	69.41850166	69.42450085	69.42450085	69.42450085	69.42450085	69.42450085	69.42450085	69.42450085	69.42450085	69.42450085	69.42450085	69.42450085	69.42450085
SPIbF6	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
SPIhF1	367.4666458	425.4901872	394.0061993	394.0061993	394.0061993	394.0061993	394.0061993	394.0061993	394.0061993	394.0061993	394.0061993	394.0061993	394.0061993	394.0061993
TCHF2	60.44367102	60.44367102	60.44367102	60.44367102	60.44367102	60.44367102	60.44367102	60.44367102	60.44367102	60.44367102	60.44367102	60.44367102	60.44367102	60.44367102
TSHF1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Appendix S5: Chapter Three Models and Outputs, as Displayed in RStudio

Question 1

```
modelaov3 <- lmer(dE ~ HR_Status
                  +  (1|pride)
                  +  (1|indiv_code), data = trans.lions.aov)
```

```
> summary(modelaov3)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: dE ~ HR_Status + (1 | pride) + (1 | indiv_code)
   Data: trans.lions.aov

REML criterion at convergence: 183.8

Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.0658 -0.4391  0.1184  0.4299  2.0851

Random effects:
 Groups     Name        Variance Std.Dev.
 indiv_code (Intercept) 2.19e+00 1.480e+00
 pride      (Intercept) 2.01e-09 4.483e-05
 Residual               1.61e-01 4.012e-01
Number of obs: 78, groups:  indiv_code, 28; pride, 15

Fixed effects:
            Estimate Std. Error      df t value Pr(>|t|)
(Intercept)    1.1513     0.2924 30.3598   3.938 0.000446 ***
HR_StatusIn   -0.3091     0.1141 48.0335  -2.708 0.009351 **
HR_StatusOut  -0.5442     0.1157 48.1870  -4.702 2.19e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) HR_StI
HR_StatusIn -0.212
HR_StatusOt -0.216  0.537
```

Question 2

```
modelreg4 <- lmer(dE ~ a_risk_f
                  +  (1|pride)
                  +  (1|indiv_code), data = trans.lions.reg2)
```

```
> summary(modelreg4)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: dE ~ a_risk_f + (1 | pride) + (1 | indiv_code)
   Data: trans.lions.reg2

REML criterion at convergence: 347839.8

Scaled residuals:
    Min      1Q  Median      3Q     Max
-5.2838 -0.4930  0.1012  0.5877  4.6928

Random effects:
 Groups     Name        Variance Std.Dev.
 indiv_code (Intercept) 0.4737   0.6883
 pride      (Intercept) 0.0000   0.0000
 Residual               0.6731   0.8205
Number of obs: 142346, groups:  indiv_code, 29; pride, 15

Fixed effects:
             Estimate Std. Error         df t value Pr(>|t|)
(Intercept)  2.410e+00  1.284e-01  2.812e+01   18.77   <2e-16 ***
a_risk_f    -2.965e-01  3.918e-03  1.423e+05  -75.67   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
         (Intr)
a_risk_f -0.025
optimizer (nloptwrap) convergence code: 0 (OK)
boundary (singular) fit: see ?isSingular
```

Appendix S6: Scatter plot of *ΔE* and anthropogenic risk

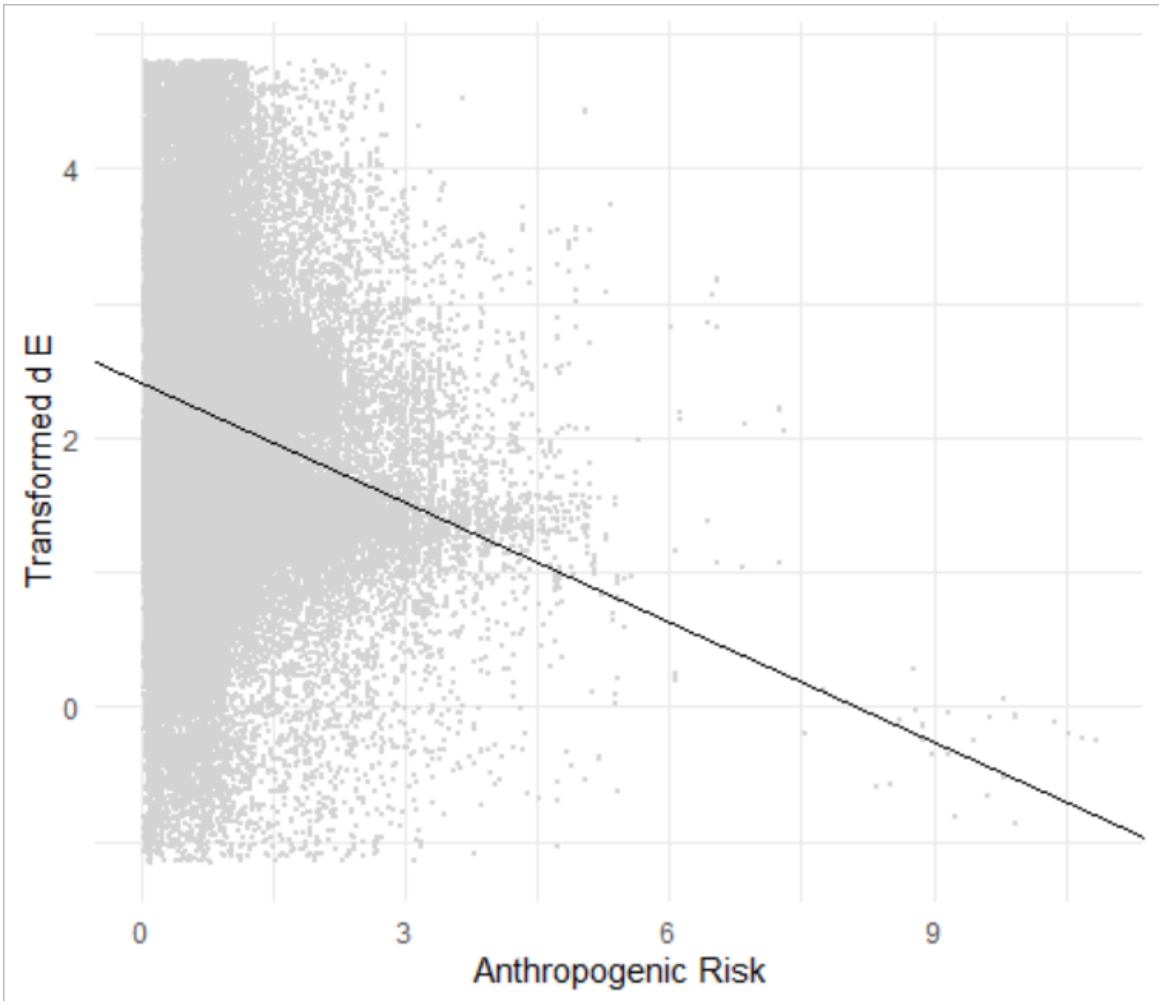


Figure S6: A scatter plot of GPS data records obtained from all the lions used in an energy expenditure model, with transformed change in energy *ΔE* on the y axis and a continuous scale of anthropogenic risk on the x axis. A cluster of points is visible in the lower right quadrant of the plot. These points almost exclusively belonged to one individual lion, and influenced the trend line.

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