The influence of anthropogenic activities on cheetah space use and hunting success across a landscape of coexistence

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Abstract

Cheetahs (*Acinonyx jubatus*) occupy vast landscapes shaped by natural ecological processes and increasing anthropogenic pressures. Understanding how cheetahs navigate these environments is critical for their conservation, particularly in ecosystems like the Serengeti, where human activities and infrastructure continually expand. This synthesis integrates findings from three key studies conducted within the Serengeti ecosystem, investigating habitat selection, movement patterns, and hunting success in response to human and environmental factors. Using GPS collar data collected from ten cheetahs between 2022 and 2024, along with over 24,300 recorded locations and 110 hours of behavioural observations, we explore how cheetahs adapt to dynamic landscapes while balancing resource acquisition with risk avoidance.

Cheetahs demonstrated selective use of habitats influenced by both natural and anthropogenic factors. Generalized Linear Mixed Models (GLMMs) revealed that proximity to bomas, roads, and lodges, as well as environmental features like woody cover, slope, elevation, NDVI, and distance to rivers, significantly affected their habitat selection. During the wet season, cheetahs avoided areas near tourist lodges and roads, likely due to increased human activity, while in the dry season, they avoided occupied Maasai bomas, highlighting seasonal variations in space use. Environmental preferences showed the selection for areas with higher woody cover, flatter terrains, lower elevations, less green vegetation, and proximity to rivers, which may provide critical resources while avoiding other large carnivores.

Cheetahs' movement patterns further underscored their adaptability and individual variation in how they responded to anthropogenic and environmental pressures at the local scale. Using Integrated Step Selection Functions (iSSFs), we assessed how proximity to human infrastructure influenced step lengths and turn angles of each collared cheetah, revealing complex responses. While bomas and roads generally deterred selection and changed the tortuosity of movement, some variability emerged, with cheetahs occasionally selecting areas near lodges during the dry season, potentially due to decreased human disturbance during this period of low tourism. Proximity to rivers was a consistent driver of movement across seasons, emphasizing the role of water availability in shaping cheetah movement decisions. These strategies illustrate how cheetahs navigate fragmented landscapes while mitigating risks from human activities.

Tourism, a cornerstone of Serengeti conservation, presents dual challenges and opportunities for wildlife. Our observational study of cheetah hunting behaviour revealed significant disruptions caused by tourist vehicles. Generalized Linear Mixed Models (GLMMs) indicated a strong negative relationship between vehicle presence and hunting decisions, with hunting probabilities dropping from 20% in vehicle-free conditions to nearly 0% in the presence of vehicles. Engine noise and the number of running engines further exacerbated these disturbances, prompting cheetahs to adopt passive behaviours such as lying down or sitting up, reminiscent of risk-avoidance strategies employed around dominant predators. These behavioural shifts have cascading demographic consequences, including reduced hunting opportunities and potential impacts on cub recruitment, threatening cheetah population viability.

This integrated understanding of cheetah space use, movement, and behaviour highlights critical areas for conservation focus. To mitigate the impacts of human activities, strategies should prioritize reducing human densities as well as activities that may directly and indirectly affect cheetahs' survival, maintaining habitat connectivity, and managing tourism practices to minimize disturbances. Specific measures include establishing buffer zones around bomas and lodges, enforcing regulations on tourist vehicle numbers and engine noise near cheetahs, and implementing robust reporting systems for wildlife harassment. Collaborative approaches that engage local communities, park authorities, and stakeholders are essential to balancing conservation goals with human land-use needs.

Cheetahs exemplify the resilience required to navigate increasingly anthropogenic landscapes. However, their survival depends on proactive conservation strategies that address the dual pressures of habitat loss and human-wildlife interactions. By integrating insights from habitat selection, movement patterns, and hunting behaviour, this research provides actionable recommendations to safeguard cheetah populations in the Serengeti ecosystem especially those individuals that live along the park borderlands.

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Preface

Pursuing this PhD has been a deeply personal and transformative journey, shaped by my passion for wildlife majoring in large carnivore conservation and my connection to the Serengeti ecosystem, home to the most beautiful large wild cat in the world - the cheetah. Growing up in Arusha, I was captivated by the wonders of nature through weekly TV show episodes of the Toyota world of wildlife documentaries. These documentaries, brought into our home by neighbourhood friends whose parents worked with Tanzania National Parks, sparked my fascination with wildlife and planted the seeds of my lifelong passion for conservation.

One of the most profound influences on this journey has been the mentorship of Professor Sarah Durant, the world's most renowned cheetah researcher. Being mentored by someone of her stature has been an extraordinary privilege. Her guidance, expertise, and unwavering support have been instrumental in shaping my understanding of cheetah ecology and conservation. I am deeply grateful for the time and effort she has invested in grooming me as a researcher and for inspiring me to reach this milestone. Her impact on my academic and personal growth will remain with me for a lifetime.

Working in the Serengeti, I experienced the challenges and rewards of studying one of the world's most remarkable ecosystems. From navigating unpredictable weather to observing the intimate behaviours of cheetahs, for the past ten years - every moment reinforced my commitment to making the world a better place for the cheetahs. These experiences were not just academically enriching but also personally fulfilling, appreciating nature and glorify God the Almighty for his marvellous and perfected work of creation – "According to my Christian Faith".

It is my hope that the insights shared in this thesis will contribute to meaningful conservation efforts and inspire others to continue working toward sustainable solutions for humans and wildlife and thus fostering "Coexistence".

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I am profoundly grateful to my main supervisor, Dr. Thomas Morrison from the University of Glasgow, for his invaluable guidance and unwavering support. I first met Thomas in early 2014 when I had just begun working with the Serengeti Cheetah Project. I had the opportunity to give him a lift to Serengeti, though our journey was unexpectedly disrupted by a flooded river crossing, forcing us to turn back and drove again the following day. At the time, I had no idea that he would later become my main supervisor. During that period, I occasionally interacted with him at researcher gatherings, particularly during sundowners. He also introduced me to basketball, and we played a few times in the Serengeti. From the very start of my PhD, Thomas has played an instrumental role in guiding me through this journey. One thing I will always appreciate about him is his remarkable ability to offer solutions instantly whenever I encountered challenges especially in data analysis. It has been an absolute privilege to be mentored by you, words are not enough to express my sincere gratitude, and I truly look forward to collaborating again in the future.

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I first met Prof. Sarah Durant in 2008, shortly after completing my undergraduate degree, when she gave me the opportunity to work for her project Tanzania Carnivore Project (TCP) as a volunteer. Though our initial time working together was brief, she became an integral part of my career when I returned to work with her after completing my master's degree. Over the past decade, she has been an extraordinary mentor and leader, shaping my academic journey and personal growth. Sarah’s unwavering support and guidance have profoundly enhanced my fieldwork skills, deepened my understanding of large carnivores, and ignited my passion for the cheetahs. I owe much of my development and the opportunity to pursue a PhD to her dedication, for which I will forever remain grateful.

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To my dearest wife, Maria, I owe a debt of gratitude that words can hardly express. Your unwavering support, love, and patience have been the cornerstone of my journey. You stood by me through the highs and lows, offering strength when I needed it most, especially during the heartbreaking loss of my younger brother Giscar “may his soul continue to rest in eternal peace.” Your endless prayers, encouragement, sacrifices, and belief in me kept me moving forward even when the path felt impossible. You have been my greatest source of comfort and inspiration, and this achievement is as much yours as it is mine.

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“*And we know [with great confidence] that God [who is deeply concerned about us] causes all things to work together [as a plan] for good for those who love God, to those who are called according to His plan and purpose”* (Romans 8:28, AMP).

Author’s Declaration

I, Dennis G. Minja, declare that all the work presented in this thesis is my own work, written in my own words, and all the sources used are fully acknowledged and cited. Any collaborations, contributions, or assistance received during this research are clearly stated and appropriately acknowledged.

1 General introduction

1.1 Large carnivore conservation

Large carnivores as apex predators play essential roles in maintaining ecosystem services and functions through trophic cascades and habitat structuring (Abrams, 1992; Estes et al., 2011; Ripple et al., 2014). By regulating prey populations and influencing their distribution, these species help prevent overgrazing, promote vegetation recovery, and support biodiversity (Sinclair et al., 2000). Their wide-ranging behaviours also shape habitat connectivity and indirectly maintain habitat heterogeneity by affecting the spatial behaviour of herbivores (Fortin et al., 2005).

Despite their ecological importance, large carnivores face numerous anthropogenic threats that have led to significant declines in both their populations and geographic ranges (Wolf & Ripple, 2017). Chief among these threats is habitat loss and fragmentation driven by urbanization, agricultural expansion, and infrastructure development which disrupts ecological connectivity and isolates carnivore populations (Crooks et al., 2011; Cushman et al., 2018; Foley et al., 2005). In these fragmented landscapes, reduced genetic exchange heightens extinction risk, and carnivores are more likely to venture into human-dominated areas where conflict is prevalent (Inskip & Zimmermann, 2009). Outside core protected zones, such pressures are especially acute, as land-use changes intensify, and enforcement of wildlife-friendly practices may be weaker (Woodroffe, 2000).

Moreover, large carnivores are further impacted by pressures such as prey depletion and competition with humans for shared resources (Ripple et al., 2014). Many species also require extensive home ranges to fulfil their energy demands, leaving them particularly vulnerable to fragmentation and conflict (Ripple et al., 2014). Understanding the ecological and behavioural adaptations of these apex predators is thus essential for developing conservation strategies that address direct threats such as retaliatory killings, harassment and indirect pressures, including habitat degradation and prey reduction.

This section establishes the ecological significance of large carnivores while introducing the anthropogenic challenges they face. It sets the stage for exploring their ecological roles, the impacts of human activities, and how such challenges influence their space use and behavioural responses.

1.2 The role of large carnivores in ecosystems

Large carnivores are key indicators of ecosystem health, exerting influence not only through predation but also by shaping the behaviour of prey and other carnivores (Ritchie & Johnson, 2009). For instance, wolves (*Canis lupus*) help regulate elk populations in North America, thereby allowing riparian vegetation such as willows and aspens to recover (Ripple & Beschta, 2004). In African savannas, apex predators create a “landscape of fear”, causing herbivores like gazelles and wildebeest to shift grazing patterns to avoid predation, fostering biodiversity across multiple trophic levels (Sinclair et al., 2009). Additionally, large carnivores provide critical resources for scavengers: their kills and carcasses supply food to species such as hyenas and vultures, supporting scavenger populations and playing a significant role in nutrient recycling and redistribution within ecosystems (DeVault et al., 2003; Wilson & Wolkovich, 2011). Apex predators also suppress mesopredator populations through processes such as competition, predation and kleptoparasitism, this contributes to the complexity of biological processes underpinning biodiversity (Prugh et al., 2009). However, while ecological and behavioural research has advanced our understanding of these dynamics, gaps remain in linking such knowledge to effective conservation action. In many cases, conservation challenges stem less from an absence of ecological insight than from socio-political and economic pressures, limited enforcement capacity, and conflicting land-use priorities (Dickman, 2010; Lindsey et al., 2018; Redpath et al., 2013; Treves et al., 2006). Nonetheless, detailed knowledge of species’ behavioural ecology such as their movement patterns, habitat use, and responses to human disturbance remains essential for designing context-specific interventions, predicting species’ resilience to environmental change, and informing strategies that can realistically be implemented within political and economic constraints (Berger-Tal et al., 2011; Caro, 2007).

1.3 Anthropogenic impacts on large carnivore populations

These apex predators face a range of anthropogenic pressures that threaten their survival, which can be broadly categorized into direct and indirect impacts. Direct impacts, such as habitat loss, fragmentation, and human-wildlife conflict, are among the most pervasive challenges, resulting from urbanization, agriculture, and infrastructure development (Foley et al., 2005). These processes isolate populations, reduce genetic diversity, and restrict access to resources, ultimately raising extinction risks (Cushman et al., 2018). Habitat fragmentation often leads to declines in prey abundance, forcing carnivores into human-dominated areas in search of food, thereby increasing the likelihood of conflict with humans (Carter & Linnell, 2016; Wolf & Ripple, 2017). In borderland areas adjacent to core protected areas, these threats converge. Growing human populations, expanding agriculture, and road networks further degrade habitats, intensifying resource competition and raising mortality risks due to wildlife-vehicle collisions (Laurance et al., 2009).

In addition to these direct threats, indirect impacts also profoundly influence large carnivore behaviour and movement patterns. Unlike direct impacts, which involve immediate physical changes to the landscape, indirect pressures subtly reshape how animals perceive and interact with their environment over time. These pressures may alter resource availability, increase perceived risks, and necessitate behavioural adjustments that influence survival and fitness. For example, anthropogenic structures such as roads and lodges fragment habitats and disrupt natural behaviours (Hovick et al., 2014). Human presence often leads to spatial and temporal shifts in activity patterns, as seen in lions (*Panthera leo*) and brown bears (*Ursus arctos*), which have been observed to adopt more nocturnal behaviours to avoid humans during the day (Coltrane & Sinnott, 2015; Oriol-Cotterill et al., 2015).

Cheetahs (*Acinonyx jubatus*), as members of the large carnivore guild, exhibit sensitivity to anthropogenic disturbances similar to that observed in other large carnivores such as lions, leopards, and hyenas. Their behavioural plasticity allows them to adapt by avoiding areas with high densities of larger predators or human activity. To navigate these fragmented and human-dominated landscapes, cheetahs rely on their mobility and vast, interconnected, and heterogeneous habitats (Durant et al., 2017). However, such adaptations come with costs. Increased energy expenditure and reduced access to optimal resources are common consequences, which may independently or collectively affect an individual's fitness, reproductive success, and survival (Ripple et al., 2014). These indirect impacts emphasize how human activities shape the fine-scale behaviours of large carnivores, which cumulatively contribute to broader ecological patterns. Together, the direct and indirect impacts of anthropogenic activities create complex challenges for large carnivores, requiring them to navigate fragmented habitats, adjust their behaviours, and adapt to human-dominated landscapes. The dual challenges faced by large carnivores explored here lay the groundwork for understanding how these pressures affect their space use and ranging patterns.

1.4 Habitat selection and adaptation

Habitat, including biotic and abiotic components, provide critical resources including food and shelter for an organism's survival and reproductive success (Kearney, 2006). Organisms typically select habitats that maximize access to resources critical for fitness, including food, mates, and refuges from predation or competition (Klaassen & Broekhuis, 2018). This process of habitat selection not only shapes species distribution and population dynamics but also drives evolutionary processes, influencing speciation and adaptive divergence (Morris, 2003). However, contemporary land-use practices encompassing agriculture, urban expansion, and deforestation are driving rapid and large-scale changes to habitat quality and connectivity, posing substantial threats to wildlife populations worldwide at rates rarely observed in previous ecological history outside of mass extinction events (Carlson et al., 2022; Mcdonald et al., 2008). Large carnivores are especially susceptible to habitat degradation because they typically require extensive areas and abundant prey to sustain viable populations (Nisi et al., 2023). Fragmented landscapes and the conversion of natural areas for agriculture, for instance, can disrupt predator prey interactions and precipitate declines in critical prey species (Treves & Karanth, 2003). In addition, habitat fragmentation leads to increased “edge effects,” where encounters with human settlements and livestock become more frequent, exacerbating human - wildlife conflict and increasing the likelihood of retaliatory killing (Woodroffe & Ginsberg, 1998). Furthermore, habitat fragmentation can disrupt population dynamics by creating a mosaic of habitat patches that function as sources, where populations thrive, and sinks, where mortality exceeds reproduction, as described by (Durant et al., 2017). This section bridges the concepts of habitat selection and fragmentation, linking broader ecological challenges to the specific vulnerabilities of large carnivores and establishes a foundation for focusing on cheetah ecology as my focal species.

1.5 Cheetah ecology and conservation

Cheetahs possess distinct characteristics that set them apart from other carnivores. Notably, they require extraordinarily large home ranges, often exceeding 3,000 km² which is exceptional among carnivores of comparable size (Marker et al., 2003; Van Der Weyde et al., 2017). Cheetahs occur at low densities in the wild, a pattern largely driven by their high mobility and the extensive home ranges they require to meet their ecological needs. These include access to widely dispersed prey, avoidance of dominant competitors such as lions and hyenas, and the need for open habitats suitable for their hunting strategy, which relies on speed and visibility. (Broekhuis & Gopalaswamy, 2016; Durant, 2000a). However, most protected areas in Africa are smaller than an individual cheetah's home range, meaning only a limited number of reserves can support viable cheetah populations in isolation (Durant et al., 2017). Consequently, cheetahs often roam beyond protected area boundaries, increasing their vulnerability to habitat fragmentation, human-wildlife conflict, and localized prey depletion. Although cheetahs are capable of occupying a diverse array of habitats ranging from dry forest and thick scrub to hyper-arid deserts such as the Sahara (Durant et al., 2017) their movements and densities are tightly linked to prey availability and competitive pressures (Laurenson, 1995).

Cheetahs avoid direct conflict by seeking "competition refuges" with fewer dominant predators (e.g., lions and spotted hyenas), thus reducing agonistic encounters (Durant, 1998, 2000a). This strategy requires high mobility, often resulting in dynamic space use patterns that shift as predators and prey move (Caro, 1994; Durant et al., 2017). Within multi-predator ecosystems like the Serengeti, cheetahs occur at notably lower densities than sympatric carnivores, with abundances reaching just 10% of lion numbers and 5% of spotted hyena numbers (Caro, 1994). In desert environments such as the Sahara, cheetah densities are even lower due to the scarcity of reliable prey and harsh climatic conditions (Belbachir et al., 2015; Durant et al., 2017). Estimates suggest densities as low as 0.21 - 0.55 individuals per 1,000km², in contrast to approximately 10 individuals per 1,000km² in savannah ecosystems (Belbachir et al., 2015). These small, often isolated populations suffer heightened extinction risks when they lose access to interconnected landscapes. Indeed, around two-thirds (67%) of cheetahs' range outside core protected areas, exposing them to threats like persecution in response to livestock depredation and ongoing habitat conversion (Durant et al., 2017).

In certain ecosystems, cheetahs exhibit migratory behaviour, particularly in response to seasonal prey movements. For example, in the Serengeti ecosystem, cheetahs often follow the migration of Thomson's gazelles (*Eudorcas thomsonii*), moving between short-grass plains during the wet season and adjacent woodland and scrub areas in the dry season (Durant et al., 1988, 2007). This seasonal movement enables cheetahs to access sufficient prey while avoiding areas dominated by other apex predators (Caro, 1994; Durant et al., 2007). Ultimately, this mobility increases their exposure to anthropogenic threats as they frequently venture outside of the core protected areas where they confront intensified human pressure (Durant et al., 2007). Understanding the interplay between cheetah mobility and their ecological requirements is critical, as such ecological and spatial dynamics underline the vulnerability of cheetahs to both natural and anthropogenic pressures, reflecting the complex challenges of maintaining their populations in multi-predator and human-dominated landscapes.

1.5.1 Study system and species context

The Serengeti ecosystem in northern Tanzania is one of the most iconic savanna systems globally, hosting one of the last remaining intact large-mammal assemblages, including cheetahs, lions and spotted hyenas (Sinclair et al., 2009). Cheetahs in this ecosystem exhibit a complex spatial ecology, shaped by both ecological dynamics and anthropogenic pressures. A key distinction in cheetah population structure is between resident individuals, which maintain stable home ranges year-round, and migrants, which move widely in response to prey availability and risk from dominant predators (Durant et al., 1988, 2007). This distinction has critical implications for space use, detectability, and vulnerability to human activities.

This study focuses on the borderlands of Serengeti National Park, a region characterised by a mosaic of land uses including tourism lodges, livestock bomas, roads and human settlements. These features vary in both spatial distribution and seasonal intensity of use. For example, certain roads are heavily used during the wet season, coinciding with peak tourism activity. Maasai bomas are more actively used during the dry season when livestock are moved closer to the park due to reduced pasture availability in village areas (Jansson et al., 2024).

Studying carnivore responses within this heterogeneous and seasonally dynamic landscape presents both logistical and methodological challenges. Cheetahs, in particular, are wide-ranging and occur at low densities (Durant et al., 2017), making them difficult to monitor using conventional survey methods. To overcome these limitations and obtain fine-scale data on movement and behaviour, GPS collars were deployed on individual cheetahs. However, deploying collars on cheetahs in Tanzania is subject to strict regulatory frameworks and depend on the availability of skilled personnel, veterinary support, and suitable individuals for collaring. These constraints, combined with the elusive nature of the species (Durant et al., 2017), mean that collaring is rare and sample sizes are necessarily small. Nevertheless, in this case, even small-sample data are scientifically valuable due to the cheetah's globally vulnerable status (Durant et al., 2022). Evidence of individual-level responses to human pressures from this study can still yield important insights into population-level vulnerabilities and inform conservation policy.

1.5.2 Analytical approach and conceptual scale

This thesis employs a multi-scale approach to assess cheetah responses to environmental and anthropogenic features. At the landscape scale (Chapter 2), I applied resource selection functions (RSFs) to examine how broad-scale habitat features influence cheetah distribution (Boyce et al., 2002). At the local scale (Chapter 3), I used integrated step selection analysis (iSSA) to investigate how movement decisions are shaped by localised features such as proximity to roads, bomas, and lodges (Avgar et al., 2016; Thurfjell et al., 2014). One conceptual distinction between these approaches lies in the definition of available habitat: RSFs typically sample availability across an animal's home range, while iSSA models generate available points based on movement constraints from observed steps, capturing more immediate decision contexts.

This difference in how availability is defined translates into different ecological inferences: RSFs infer habitat preferences over longer periods and broader areas, while iSSA captures fine-scale behavioural decisions during movement. These methodological differences helps to clarify the link between analytical method and ecological scale. For instance, pseudo-absence or available point generation strategies during analysis can substantially influence model outcomes and interpretation (VanDerWal et al., 2009; Barbet-Massin et al., 2012). Recognising these nuances enables stronger justification of the comparative framework employed in this thesis (Fieberg et al., 2010).

1.6 Research gaps and thesis objectives

Despite significant research on cheetah ecology and conservation, several critical gaps remain. For instance, while tourism is a cornerstone of conservation economies, its specific effects on cheetah hunting behaviour, particularly in high-disturbance areas, are poorly understood. Understanding these effects is vital, as disruptions during hunting can lead to cascading impacts on cheetah fitness, reproduction, and long-term population viability. Similarly, the interplay between environmental variables (such as woody cover, water sources, slope, and elevation) and anthropogenic factors in shaping cheetah movements is of particular importance because these interactions determine access to key resources while avoiding risks. Investigating these gaps is crucial for disentangling the complex drivers of cheetah space use and behaviour, particularly in multi-use landscapes where the balance between human activities and wildlife conservation is increasingly precarious.

This thesis investigates the intricate relationships between human activities and cheetah ecology along the Serengeti borderlands, examining patterns and processes at multiple spatial and behavioural scales. Understanding cheetah ecology requires addressing how large-scale habitat features influence distribution, how movement patterns reflect responses to these features, and how fine-scale behaviours underlie these broader patterns. Specifically, it addresses the following three key research objectives:

i. Large-scale habitat selection: What are the critical habitat features influencing cheetah distribution, and how do anthropogenic and environmental factors affect their space use?

ii. Local-scale habitat selection and movement: How do cheetahs make fine-scale movement decisions, and how are their movement patterns influenced by pastoralism, tourism, and habitat features at localized scales?

iii. Fine-scale behavioural decision making: What are the behavioural mechanisms, including hunting decisions and other activity patterns, that are associated with cheetah responses to human activities at fine spatial scales?

This thesis consists of six chapters. This chapter serves as the general introduction, providing an overview of large carnivore ecology in human-modified landscapes. It explores the interplay between ecological requirements and anthropogenic pressures, highlighting the behavioural and spatial adaptations large carnivores employ to survive in increasingly fragmented habitats. The chapter also explores into the challenges posed by habitat loss, human - wildlife conflict as well as the importance of understanding large carnivore movement ecology, using the cheetah as a study animal.

Chapter 2 explores broad-scale aspects of cheetah space use in relation to the surrounding anthropogenic and environmental conditions. It introduces the key concepts of habitat selection, human-wildlife interactions in cheetahs and the methodologies employed in understanding large carnivore behaviour. The chapter also highlights the broader conservation challenges faced by cheetahs and the significance of studying their spatial ecology in multi-use landscapes.

Chapter 3 delves into understanding the effects of anthropogenic activities on cheetah movement patterns at a local (finer) scale. Using Integrated Step Selection Analysis (iSSA), this chapter investigates how environmental and human-related variables, such as roads, lodges, and bomas, influence cheetah habitat use and movement decisions. The analysis emphasizes the role of these anthropogenic features in shaping cheetah behaviour both at the population and individual level.

In Chapter 4 explores the impacts of tourism on cheetah hunting behaviour. Specifically, this chapter examines how proximity to tourist vehicles affects critical cheetah activities, shedding light on the behavioural mechanisms underlying the patterns of space use and movement observed in Chapters 2 and 3. By combining behavioural data and statistical modelling, I assessed the trade-offs cheetahs face in balancing energy expenditure and disturbance avoidance, providing insights into sustainable tourism practices that can minimize these impacts.

Chapter 5 comprises the general discussion, synthesizing the findings of the data chapters to provide a comprehensive analysis of human impacts on cheetah ecology across multiple spatial and behavioural scales. This chapter explores how fine-scale investigations into cheetah behaviours, such as hunting success and responses to human presence, help explain the broader patterns observed in habitat selection and movement. It also draws comparisons with similar studies on large carnivores, comparing and contrasting their responses to anthropogenic pressures such as pastoralism and tourism. This multi-scale approach not only enhances our understanding of cheetah ecology but also provides understandings into the mechanisms driving their spatial and behavioural strategies.

Finally, Chapter 6 comprises the conclusions and recommendations. The findings from this thesis hold significant implications for both conservation biology and sustainable land-use planning. By elucidating the ways in which anthropogenic activities affect cheetah ecology, this research offers valuable insights for mitigating human-wildlife conflict and promoting coexistence. These recommendations can inform conservation strategies not only for cheetahs but also for other large carnivores facing similar pressures globally.

2 Identifying critical habitat of cheetah space use

Abstract

Cheetahs (*Acinonyx jubatus*) navigate landscapes shaped not only by natural ecological dynamics but also by human influences, selecting habitats that best support their survival amidst varying anthropogenic pressures. As human activities expand in areas adjacent to the core protected areas, understanding how these changes affect cheetah habitat selection is critical, particularly in terms of access to key resources and avoidance of anthropogenic threats. This study explores the habitat selection of cheetahs within the southern borders of Serengeti National Park. Addressing anthropogenic and environmental factors affecting habitat choice, we utilized GPS satellite collar data from ten cheetahs between 2022 and 2024. Our analysis incorporated a range of human-related and environmental covariates, used Generalized Linear Mixed Models (GLMMs) to identify areas selected by cheetahs. Key anthropogenic factors encompassed distances to lodges, roads, and bomas (thorny livestock enclosures used by pastoralist communities) and the environmental variables included woody cover, slope, elevation, relative vegetative greenness, and distance to rivers. The analysis revealed that cheetahs adjusted their movement patterns in response to human activities, avoiding areas near roads and lodges during peak tourist seasons (wet seasons) and steering clear of areas near occupied Maasai bomas during dry seasons. Cheetahs also prefer areas with high tree density, flatter terrains, lower elevations, areas with lower NDVI (less green vegetation), and closer proximity to rivers, particularly in the dry season. These results contribute significantly to the development of cheetah conservation strategies by highlighting the importance of specific landscape features that influence their distributions and may improve our understanding of how cheetahs manage to minimize the impacts of human disturbance across the southern borderlands of the Serengeti ecosystem.

2.1 Introduction

The geographic ranges of large carnivores have undergone severe decline due to combined impacts of habitat loss and degradation, persecution, and overharvesting (Ripple et al., 2014). Because of these anthropogenic activities, large carnivore populations in human landscapes are substantially reduced, particularly outside protected areas (Inskip & Zimmermann, 2009). A combination of their low population densities and wide-ranging behaviour increases their chances of encountering human habitation, and increases levels of conflict (Ripple et al., 2014). However also, in large part, conflicts between humans and carnivores stem from carnivores attacking livestock, which in turn prompts humans to kill them either in retaliation or as a preventive measure (Treves & Karanth, 2003).

In acknowledging severe challenges confronting large carnivores, it is essential to understand the critical role of habitat in their survival. Habitat, including biotic and abiotic components, provide critical resources including food and shelter for an organism's survival and reproductive success (Kearney, 2006). Organisms typically select habitats that enhance their survival and reproductive success, by improving their access to food, mates, and other resources (Klaassen & Broekhuis, 2018). Consequently, animal habitat relationships serve as major drivers in the processes of evolution and speciation (Morris, 2003). However, human activities have significantly modified natural habitats, leading to profound effects on their structure and the availability of resources.

Urbanization, deforestation, and agriculture are among the key human-induced changes that fragment habitats and alter their quality (Mcdonald et al., 2008). These modifications disrupt ecological balances, hinder movement and resource accessibility, and can lead to increased human-wildlife conflict (Carlson et al., 2022). For large carnivores that depend on vast areas for their hunting and reproductive activities, the degradation and fragmentation of habitats are significant barriers to their survival and the effectiveness of conservation efforts (Nisi et al., 2023). Such habitat changes can lead to decreased biodiversity, altered species composition, and diminished populations of key species, underscoring the urgent need for sustainable land-use practices and conservation efforts to mitigate these impacts (Ripple et al., 2014; Treves & Karanth, 2003).

Large carnivores are increasingly adapting their spatial and temporal behaviours to mitigate interactions with humans, often by avoiding anthropogenic features and altering their activity patterns (Abrahms et al., 2016; Suraci et al., 2019). Studies such as Barker et al. (2023) and Carricondo-Sanchez et al. (2020) highlight that while large carnivores prioritize prey acquisition, they simultaneously exhibit strategies to navigate landscapes dominated by human activities, suggesting a complex balancing act between meeting their feeding needs and minimising human encounters. Additionally, the work of Wilmers et al. (2013) illustrates context-dependent behavioural responses in large predators like the puma (*Puma concolor*), indicating that adaptations to human development can vary widely among species and even within populations - suggesting that behavioural plasticity is influenced by local environmental conditions, levels of human disturbance, and individual traits. Frey et al. (2020) investigated the impacts of human landscape disturbance on species activity patterns and temporal niche partitioning and demonstrated that multiple carnivore species became more nocturnal on disturbed landscapes, adding a layer of complexity to our understanding of carnivore adaptations. These findings underscore the intricate ways in which human presence can shape the distribution and behaviour of large carnivores, potentially excluding them from essential resources (Ripple et al., 2014, 2015) and underscoring the sensitivity of many mammalian carnivores to anthropogenic activities (Woodroffe & Ginsberg, 1998).

Sympatric carnivores, for example, use habitat and space differently due to intra-guild competition and interference (May et al., 2008). Oriol-Cotterill et al. (2015) study showed how lions adapt to human-dominated landscapes through spatiotemporal partitioning of their activities. Lions adjusted their movements and behaviour in response to the presence and activities of humans to minimize conflict and the risk of mortality due to human retaliation. They were found to come closer to human settlements (bomas) during times when human activity was lowest, particularly at night when people were asleep. This indicates that lions are able to modify their spatial and temporal patterns of activity to reduce direct contact with humans, thereby mitigating the risk of interactions that can lead to preventative or retaliatory killings by humans. Another study in Anchorage – Alaska, showed that brown bears were primarily nocturnal at sites with higher human usage. The study highlighted the importance of assessing areas separately when developing conflict mitigation interventions and suggested restricting human access or altering recreational activities as potential solutions for reducing human – brown bear encounters (Coltrane & Sinnott, 2015). Another study in Laikipia, Kenya, revealed sub-diurnal variation in the path-selection of lions, indicating that they used space sporadically during the day and significantly at night (Burak et al., 2023).

2.1.1 Cheetah Ecology

Cheetahs occupy relatively large home ranges for their size, often exceeding 800 km^2 in some regions, which is substantially greater than the typical home ranges of species like lions or leopards that are more territorial and often have access to higher prey densities (Van Der Weyde et al., 2017). Most protected areas in Africa are smaller than a cheetah home range, only a handful of protected areas are large enough to support viable cheetah populations (Durant et al., 2017). Cheetah has exceptionally large home range sizes relative to their body size, with reports of ranges exceeding 3,000 km^2 (Marker et al., 2003). The size of cheetah home ranges exhibits substantial variation, predominantly influenced by factors such as prey availability, habitat quality, interspecific competition, and sex (Durant, 2000a). Cheetahs possess exceptional mobility, allowing them to efficiently navigate vast expanses (Broekhuis & Gopalaswamy, 2016). To avoid direct conflicts, cheetahs seek out areas with fewer competing predators; these areas, known as 'competition refuges,' are not fixed in space but change over time as competitors move in search of prey (Durant, 1998). Cheetah mobility is key to avoiding encounters with larger predators, indirectly contributing to their low densities and extensive home ranges (Durant, 2000b). Within the Serengeti ecosystem, cheetahs are found at much lower densities than most other sympatric carnivores, with total abundances constituting only 10% that of lions (*Panthera leo*), 5% that of spotted hyenas (*Crocuta crocuta*), and 25% that of leopards (*Panthera pardus*) (Caro 1994). This tendency to range widely across large areas highlights the importance of mobility in cheetahs' strategy to avoid direct competition with larger, more dominant predators. The low population density of cheetahs necessitates large, multi-use landscapes for their survival (Durant et al., 2017).

Cheetahs are habitat generalists, found in a wide range of habitats and ecoregions, ranging from dry forest and thick scrub through to grassland and hyper arid deserts, such as the Sahara (Durant et al., 2022, 2014, 2017). In the Sahara, where the population density of cheetahs is even lower than in the savannah due to the harsh desert environment, the Saharan cheetah is severely constrained, with population density estimates ranging from 0.21 – 0.55 per 1,000km^2, compared to 10 animals per 1000km^2 in savannah environments (Belbachir et al., 2015). Outside of core protected areas, where most of the wild cheetah population (i.e., 67%) roam, population growth rates are suppressed primarily due to prey and habitat loss and the risk of extinction increases significantly. Nonetheless, the impacts of human-wildlife conflict and loss of prey due to isolated and small population sizes are also contributing factors to the decline in cheetah numbers (Durant et al., 2017). Consequently, cheetahs require the maintenance of large, interconnected habitats in order to coexist with humans. Eventually, the persistence of these free-ranging species depends on their survival across a matrix of protected and unprotected areas.

In the Serengeti, the majority of cheetahs migrate with gazelles as their primary source of food (Durant et al., 2007). Large herds of migratory herbivores, including wildebeest, gazelles, zebras and elands, move across the ecosystem seasonally. In the dry season, Thomson's gazelles migrate from the woodland margins within the Serengeti National Park to the short-grass plains, and in the wet season they regularly move outside of the park (Durant et al., 1988). Since cheetahs follow the migration of the Thomson’s gazelle, they tend to have similar localized seasonal migratory movements. Consequently, most cheetahs leave the core protected area yearly, predominantly to the south and east, exposing them to anthropogenic effects outside the park such as human carnivore conflicts from livestock depredation and habitat fragmentation (Durant et al., 2007).

Borderlands refer to transitional zones between core protected areas and adjacent human-dominated landscapes. These areas are critically important for conservation because they often function as ecological buffers and corridors that facilitate wildlife movement between fragmented habitats (Woodroffe & Ginsberg, 1998; Western et al., 2009). However, they are also sites of intense human activity - such as livestock grazing, road development, tourism, and settlement expansion - which create both opportunities and constraints for wide-ranging species like cheetahs.

In the Serengeti, borderlands are particularly significant due to the high overlap between wildlife movement routes and anthropogenic features. These areas lie outside the strict enforcement and low-impact management regimes found within national park boundaries and thus provide a more variable and human-influenced context to study predator space use. For cheetahs, whose survival depends on vast, connected landscapes and avoidance of dominant competitors, understanding how they navigate these borderlands is key to informing broader conservation strategies.

This study therefore used GPS tracking data from collared cheetahs to assess the influence of anthropogenic and environmental variables on habitat selection in the southeastern borderlands of Serengeti National Park. We tested the hypothesis that cheetah habitat selection is significantly influenced by both human-related and environmental factors. Specifically, we made the following predictions:

- Tourism activities (measured by distance to lodges and roads) will negatively affect cheetah habitat selection, as cheetahs are likely to avoid areas of high human presence and vehicle disturbance.
- Pastoralism activities (measured via distance to bomas) will also be associated with habitat avoidance, especially during the dry season when bomas are actively used and livestock are moved closer to park borders.
- Woody cover is expected to have a positive association with selection, as dense cover provides concealment and refuge from larger predators.
- Proximity to water bodies (rivers) will be positively associated with selection due to prey availability and hydration needs.
- Topographic variation**,** including slope and elevation, may also influence space use, though the expected direction may vary depending on prey distributions and visibility.

By explicitly testing these hypotheses, this chapter aims to uncover the drivers of cheetah habitat preferences in a dynamic, multi-use landscape, with implications for both spatial planning and human-wildlife coexistence.

2.2 Materials and methods

2.2.1 Study area

The primary focus of this research is cheetahs inhabiting the southeastern periphery of the Serengeti Ecosystem (Figure 2.1). Southern Serengeti National Park (SNP), Makao Wildlife Management Area (MWMA), Maswa Game Reserve (MGR), and Ndutu area (a component of Ngorongoro Conservation Area) comprise the principal areas of interest. Serengeti National Park encompasses a vast expanse measuring around 14,750 square kilometres in size. Annual precipitation in SNP increases from 500 to 1100 mm from the southeast to northwest, alongside broad vegetation changes from short grassland to savanna woodland (Holdo et al., 2009a). The park supports a diverse array of fauna, including cheetahs, and is subject to the impacts of numerous human-induced processes, including tourism and human presence for research purposes. Located to the southwest of the study area, the 780 km^2 Makao Wildlife Management Area was established in 2009, comprised of Sapa, Mwangudo, Mbushi, Jinamo, Iramba Ndogo, Makao, and Mwabagimu areas. By linking Maswa Game Reserve, Ngorongoro Conservation Area, and Serengeti National Park, MWMA provides an essential wildlife corridor within the Serengeti ecosystem (Lwankomezi et al., 2023). Due to the reliance of local communities on agriculture and livestock grazing, which can result in habitat degradation and competition for resources, the region is prone to human-wildlife conflict. Maswa Game Reserve, which encompasses an area of 2,200 km^2, functions as a critical buffer zone separating Serengeti National Park from the adjacent regions (Kimaro & Treydte, 2021). The reserve undergoes two periods of heavy precipitation annually: November to December brings brief downpours, and January to May brings prolonged rainfall; the average annual precipitation range is 600 to 1,150 mm (Bartzke et al., 2018). Controlled hunting and grazing are human activities in MGR that have the potential to affect the natural habitat and wildlife populations. Ngorongoro Conservation Area is inhabited by an estimated 100,000 individuals (Yamat, 2018), including both indigenous and non-indigenous NCA inhabitants, and their domesticated livestock such as goats, cattle, and sheep (Lyimo et al., 2020). Pastoralism has been practiced in this region for over two millennia (Homewood & Rodgers, 1991). The NCA was traversed by Maasai people and their livestock around 200 years ago. The Datoga, who were the former pastoralist group found in the NCA, moved out in response to the Maasai, and are now a minority inhabiting the southern corner of the NCA (Linuma et al., 2022). In general, study area is distinguished by its varied habitats and substantial human impacts, which underscore the importance of prudent management in order to reconcile conservation objectives with the needs of local communities.

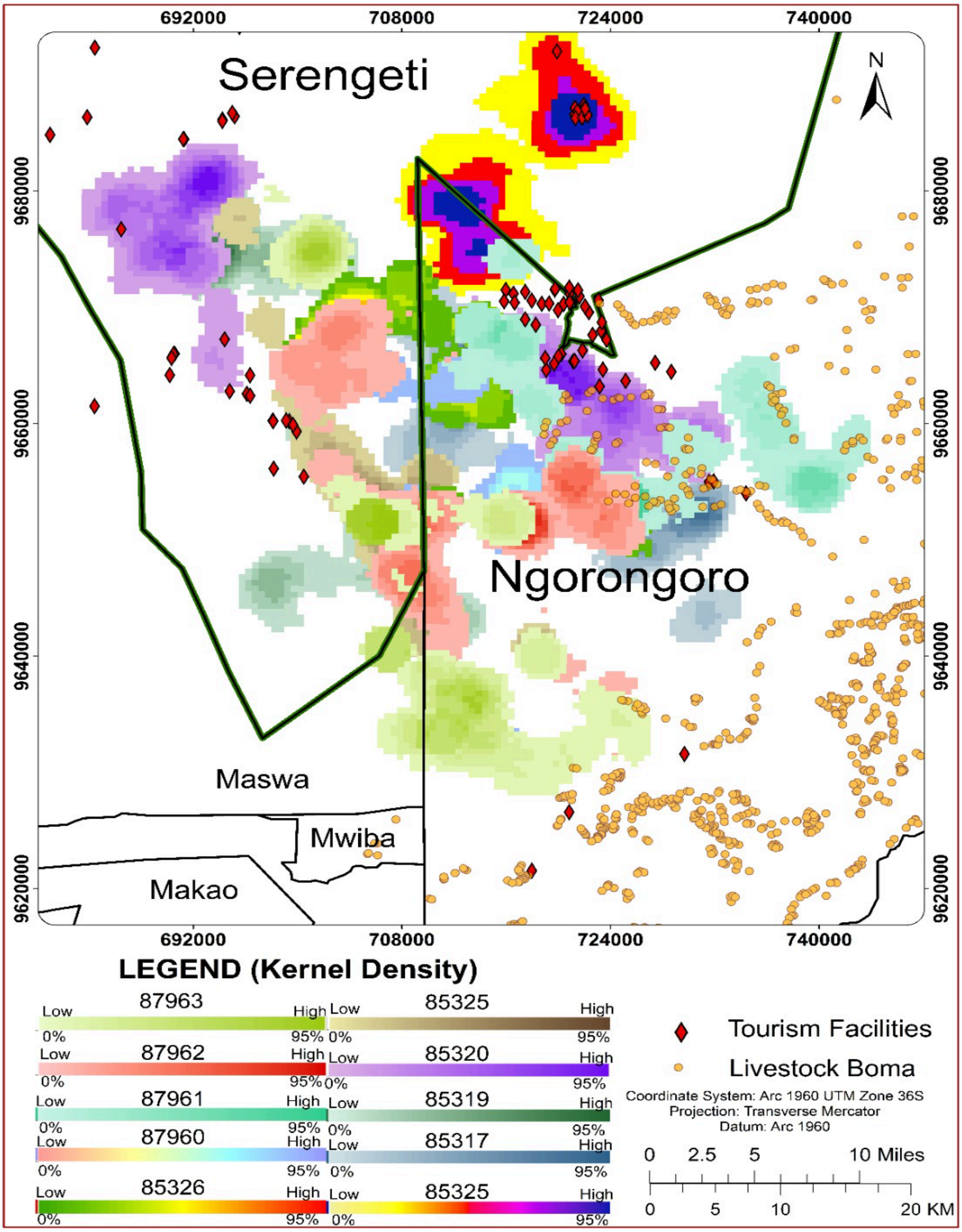


Figure 2.1: Kernel density estimates of GPS locations for ten collared cheetahs within the Serengeti ecosystem, illustrating individual space use patterns. Each colour gradient represents the intensity of location points for a single individual, with warmer colours indicating higher density.

2.2.2 Data collection

2.2.3 Cheetah collaring process

We collected location data from Global Positioning System (GPS) satellite collars deployed on cheetahs across the study area. In April and May 2022, a total of ten cheetahs were fitted with collars (VERTEX Lite -1C IRIDIUM Collar, manufactured by Vectronics), which include an Iridium module, VHF Beacon, Mortality sensor, Temperature sensor and Basic 3-axis Activity sensor. Because cheetahs are largely diurnal, we intensively sampled cheetah locations from 6:00 am to 8:00 pm at two-hour intervals and with an additional location at midnight over one year.
Cheetahs were located through intensive field tracking conducted by the Serengeti Cheetah Project team, using a combination of recent sightings, spoor, and known home ranges from long-term monitoring data. Once located, cheetahs were approached slowly using a 4WD vehicle, a method that exploits the species' general tolerance to vehicles due to long-term habituation in the Serengeti ecosystem. Although such tolerance allows close approaches for research, cheetahs may still be disturbed when multiple vehicles are present. During collaring we minimised disturbance by using only a single approach vehicle prior to darting, with additional research vehicles arriving only once the animal was immobilised. Darting was performed from the vehicle at close range (10-15 m), when the animal was stationary or resting, to ensure safe and accurate administration.

Immobilizations were carried out by veterinarians from the Tanzania Wildlife Research Institute (TAWIRI) and the Ngorongoro Conservation Area Authority using a dart gun and two tranquilizer combinations: Medetomidine 2 mg with Ketamine 100 mg, or Medetomidine 2 mg with Zoletil 50 mg. The reversal (Atipamezole 2.5 mg/Yohimbine 6.25 mg) was administered after approximately one hour, allowing time for the metabolization of the Ketamine or Zoletil. Darts were targeted to large muscle groups (shoulder or rump) for effective uptake. All immobilized individuals recovered fully with no observable adverse effects. Each collared cheetah was tracked and monitored for at least three days afterwards and no effects of the collar were observed (only one individual scratched at the collar occasionally over the first 24-hour period). The configuration of these collars was selected to keep them to 400g or less, which is equivalent to 1.1% of the weight of an average female cheetah (35kg). This ensured that the collars had minimal impact on the animal behaviour

(Laurenson & Caro, 1994). We used location data from the third day after a collar was deployed on a cheetah in order to avoid any anomalous behaviour following recovery from immobilization. The interventions were approved by the ethics committee for animal research at the Zoological Society of London and the research was covered by permits from the Tanzania Wildlife Research Institute.

Figure 2.2: Zara, one of the ten GPS radio collared female cheetahs, photographed immediately after recovering from immobilization.

2.2.4 Habitat selection

Habitat selection was assessed using resource selection functions (RSFs), which are statistical models that estimate the probability of an animal selecting a given habitat type based on its use relative to availability. While similar in concept to species distribution models (SDMs), RSFs are typically applied at finer spatial or behavioural scales and focus on individual or population-level habitat preferences within a defined area of availability. To determine the number of available points required in this analysis, we employed a sensitivity analysis according to (Stabach et al., 2016) and used 20 available points for every observed point. Available points were randomly generated within the 95% home range of the utilized area for each individual collared cheetah using KDE (Kernel Distribution Estimates) in the R programming language. Preference for specific habitat types or selectivity in habitat use was assessed by comparing the habitat conditions at available points to the habitat conditions at locations visited by cheetah.

2.2.5 Covariates

2.2.6 Anthropogenic covariates

In this study, we explored the influence of both tourism and pastoralism activities on cheetah habitat selection. These human activity effects were analysed by examining the impacts of tourism facilities, including lodges and seasonal campsites and the road networks associated with them. We assessed the impact of these features by calculating the distance from both observed and available cheetah GPS locations to the nearest tourist facility and road network. This approach acknowledges the intertwined nature of roads and tourism facilities, as roads facilitate access to these facilities and are also utilized by tourists' vehicles, potentially affecting the behaviour and routines of large carnivores, including cheetahs (Corsi et al., 1999; Kerley et al., 2002). The road networks considered in this study encompass main roads, seasonal roads, and administrative roads, reflecting the various levels of human activity and accessibility within the cheetah's habitat. Pastoralism activities were addressed by the boma (semi-permanent Maasai houses and livestock corral) presence. Boma locations were mapped from Google Earth Pro and then later rasterized with the aim of providing a distance between each boma as a point feature to the nearest cheetah location (Jansson et al., 2024).

2.2.7 Environmental covariates

As previous research demonstrated that cheetahs differentially use habitat (Broekhuis, 2012; Rostro-García et al., 2015), we expected that environmental features such as vegetation cover, normalized difference vegetation index (NDVI), slope, elevation and rivers would affect cheetah space use in our study area. The selection of layers was based on characteristics known to be crucial components of cheetah habitat selection, including vegetation cover and other geographical features (Pettorelli et al., 2009). Woody cover plays a critical role in shaping cheetah habitat selection by influencing concealment, hunting success, and predator avoidance. In this study, woody cover was estimated using tree density data derived from Sentinel-1 C-band radar, which captures seasonal variation in vegetation structure by comparing dry and wet season readings (Thijssen et al., 2025). This approach enhanced our understanding of how vegetation dynamics affect cheetah space use across seasons. We used processed layers from Townshend et al. (2016), where the data have been refined and presented in a ready-to-use format. Although the dataset reflects canopy cover over the past 10 years, it remains a valid and representative indicator of long-term woody vegetation in the Serengeti, where large-scale deforestation is limited. These layers provided a consistent, ready-to-use format that served as a proxy for structural habitat complexity relevant to cheetah movement and selection. Vegetative greenness was anticipated to influence cheetah habitat selection through its effects on prey availability, access to water, hunting cover, thermoregulation, and denning opportunities. To quantify this, we used the Normalized Difference Vegetation Index (NDVI), a widely adopted remote sensing metric derived from red and near-infrared reflectance, which reflects plant biomass and photosynthetic activity (Tucker, 1979). NDVI values were obtained from the Moderate-Resolution Imaging Spectroradiometer (MODIS) aboard NASA’s Terra satellite, at approximately 250 × 250 m spatial resolution and 16-day temporal resolution for the whole study period. To account for short-term fluctuations and departures from typical vegetation patterns, we calculated NDVI anomaly, defined as the Z-score difference between observed NDVI and the long-term monthly mean, normalized by standard deviation. This approach allowed us to identify areas with unusually high or low productivity relative to seasonal expectations, offering insights into temporal variation in habitat quality that may influence cheetah foraging and space-use decisions. Elevation can significantly influence cheetah habitat selection, primarily through its effects on climate, vegetation, and prey availability. Therefore, elevation values were extracted at a resolution of 30 m from NASAs TRM dataset. Finally, we hypothesized that cheetah habitat selection would be influenced by rivers. Even though cheetahs can subsist without water, rivers are important because they affect the distribution of many cheetah prey species, especially during the dry season (Durant, 1998). Thus, at each available and observed cheetah location, we measured distance to the nearest river. These layers were obtained from Serengeti National Park GIS database.

2.2.8 Temporal covariates

Incorporating the variables of seasonality (wet and dry seasons) and time of day (day and night) into our resource selection analysis offers improved understanding of cheetah behaviour and habitat preferences. This approach acknowledges the dynamic nature of the environment and the adaptability of cheetahs to these changes. Seasonality influences the availability of resources, such as water and prey, which in turn affects the spatial behaviour of cheetahs. During the dry season, cheetahs were expected to prefer habitats near water sources, where prey is likely to congregate, while in the wet season, their preferences could shift as water becomes more widespread. Similarly, the inclusion of time of day as a variable intended to recognize the diurnal and nocturnal patterns of both cheetahs and their prey, as well as the impact of human activity, which is higher during daytime. By considering these temporal factors, our analysis provides a more comprehensive picture of how cheetahs interact with their environment in relation to human activities and how they alter their movement and selection strategies in response to varying conditions.

2.2.9 Analysis

All statistical analyses were carried out in R software. Generalized Linear Mixed Models (GLMMs) with a binomial error were fitted to cheetah data and random points, where 1 indicated an observed cheetah GPS location and 0 indicated random points available in a study area. Collar ID was included as a random factor to account for individual differences among cheetahs. Prior to analysis, we scaled all distance explanatory variables to standardise variables to a similar scale, to allow us to assess the relative effect size of each covariate. Collinearity among covariates was assessed using the Variance Inflation Factor (VIF) function from the "*car*" package. Only one variable – ruggedness, had a VIF greater than 5 and was subsequently removed. The remaining variables were retained, as all had acceptable VIF values below the commonly used threshold of 5. The Akaike Information Criterion (AIC) was employed to determine the most parsimonious model with the greatest explanatory power, according to the approach outlined in (Burnham & Anderson, 2004).

2.3 Results

Overall, ~ 24,300 GPS locations were recorded for the ten collared cheetahs over a period of two years, with a minimum number of 1,684 points and a maximum number of 3,788 points, and a mean of 2,025 locations per cheetah over a period of twelve months. There were no mortalities, and all collars remained active for the entire period. The most parsimonious model included environmental variables such as woody cover measured by tree density/woody cover, Digital elevation Model, distance to the nearest river, slope, NDVI (Normalized Difference Vegetation Index), as well as anthropogenic variables such as distances to lodges, roads, and bomas (Table 2.1).

Table 2.1: Comparison of the top 11 candidate GLM models representing cheetah habitat selection in the southern borderlands of the Serengeti, Tanzania. The most complex model was also the best fitting model.

Model structure	AIC	Delta AIC	Model Likelihood	Akaike Weight
Woodycover*season*daynight + Slope + DEM + NDVI + Lodges*season*daynight + Roads*season*daynight + Bomas*season*daynight + Rivers*season*daynight	224649.4	0	1	0.999996
Woodycover * season *daynight + Slope + DEM + NDVI + Lodges* season *daynight + Roads* season *daynight + Bomas* season *daynight + Rivers* season	224674.2	24.85741	4.00E-06	4.00E-06
Woodycover * season *daynight + Slope + DEM + NDVI + Lodges* season *daynight + Roads* season *daynight + Bomas* season + Rivers* season	224717.8	68.43639	1.38E-15	1.38E-15
Woodycover * season *daynight + Slope + DEM + NDVI + Lodges*season*daynight + Roads*season + Bomas*season + Rivers*season	224720.4	71.06961	3.69E-16	3.69E-16
Woodycover *season*daynight + Slope + DEM + NDVI + Lodges*season + Roads*season + Bomas*season + Rivers*season	224751	101.6171	8.59E-23	8.59E-23
Woodycover *season + Slope + DEM + NDVI + Lodges*season + Roads*season + Bomas*season + Rivers*season	224754.4	105.0497	1.54E-23	1.54E-23
Woodycover *season + Slope + DEM + NDVI + Lodges*season + Roads*season + Bomas + Rivers*season	227159.2	2509.858	0	0
Woodycover *season + Slope + DEM + NDVI + Lodges*season + Roads + Bomas + Rivers*season	227255.4	2605.993	0	0
Woodycover *season + Slope + DEM + NDVI + Lodges + Roads + Bomas + Rivers*season	228573.3	3923.929	0	0
Woodycover + Slope + DEM + NDVI + Lodges + Roads + Bomas + Rivers*season	229371.5	4722.131	0	0
Woodycover + Slope + DEM + NDVI + Lodges + Roads + Bomas + Rivers	229957.2	5307.836	0	0

Key: *Woodycover: A measure of tree density, Slope: The slope of the terrain, DEM (Digital Elevation Model): Elevation data, NDVI (Normalized Difference Vegetation Index): A vegetation index, Lodges: Proximity to lodges in the study area, Roads: Distance to roads in the study area, Bomas: Distance to Maasai community thorn bush enclosures,* *Rivers: Distance to the nearest river in the study area, Season: Categorical variable representing wet and dry seasons and Time of the day (daynight): Categorical variable representing day and night.*

In addition to relative model comparisons using AIC, absolute model performance was evaluated. The top-performing model had a marginal R^2 of 0.10 and a conditional R^2 of 0.10, suggesting that the fixed effects accounted for nearly all of the explained variance in cheetah habitat selection. The random effect of individual cheetah ID contributed minimal additional variance, indicating broadly consistent selection patterns across individuals. Specifically, only 0.23% of the variation was attributable to differences between individual cheetahs, as calculated from the difference between conditional and marginal R^2. The model's ability to discriminate between used and available locations, as indicated by the area under the receiver operating characteristic curve (AUC), was 0.659, suggesting modest but meaningful predictive performance.

2.3.1 Effects on cheetah resource selection

2.3.2 Anthropogenic covariates

The data suggested that cheetahs change behaviour in response to specific anthropogenic activities. For instance, during the wet season, with peak tourist activity, cheetahs selected regions that were more distant from the lodges (Figure 2.3a), whereas, in the dry season (with low tourist numbers), there was a slight negative correlation with the distance to lodges, suggesting that cheetahs selected areas closer to lodges. There was a positive relationship between the distance to roads and cheetah locations indicating that cheetahs tended to avoid areas near roads, but this probability peaked at around 2km distance and then dropped off again as distance increased. Nevertheless, there was no significant difference in the selection of areas at a moderate distance from roads based on the time of day. Cheetahs slightly avoided areas close to roads and preferred areas at an intermediate distance and also avoided areas farther away from roads. There was a slight increase in the probability of selection during the dry season compared to the wet season, although the overall probability remained quite low at <8%. (Figure 2.3b). Cheetahs also tended to select areas that were farther away from bomas during the dry season, when bomas are more likely to be occupied by the Maasai (Figure 2.3c). Distances to bomas and lodges showed narrow confidence intervals indicating greater precision in their predictions.

2.3.3 Environmental covariates

The negative effect of woody cover in the dry season suggests that cheetahs preferred locations with relatively low tree density in the dry season and the other way round in the wet season (Figure 2.3d). In the dry season cheetahs showed a preference for the plains and an avoidance of denser vegetation, there was no significant difference in selection during the day and night hours. But in wet season there was a different pattern, cheetahs selected areas with high woody cover, with slightly higher probability of selection at night than during the day. The confidence intervals for woody cover selection in the dry season were narrow, suggesting that predictions had reasonably high precision. Cheetahs also tended to select areas nearer to rivers during both the wet and dry seasons, but with a more marked preference in the dry season than the wet (Figure 2.3e). There was a negative association with slope which suggests that cheetahs prefer flatter terrains than those with steeper slopes (Figure 2.3f). There was a negative correlation with elevation and NDVI, which implies that cheetahs chose lower elevations and less green vegetation (Figure 2.3g and 2.3h respectively).

These results were used to create a habitat suitability map for the study area for both dry and wet seasons (Figure 2.4). The habitat suitability map shows that areas inside the Serengeti national park are more suitable for cheetahs than outside during dry season whereas areas around Ndutu, Maswa GR, Makao WMA and the adjacent areas seems to be more suitable in wet season.

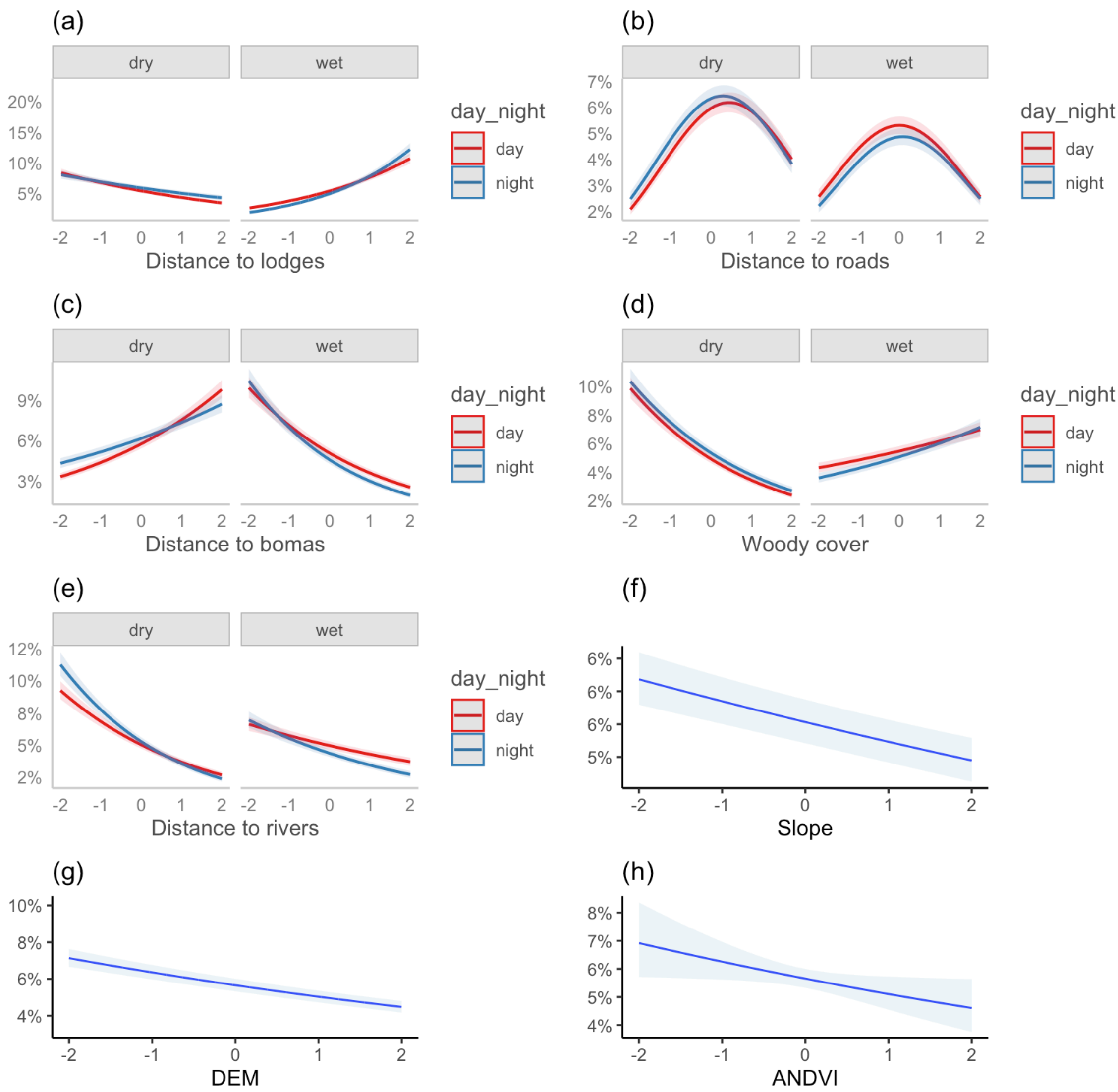


Figure 2.3: The relative probability of selection (Y-axis) by cheetahs in the Serengeti National Park borderlands in relation to (a) Distance to lodges, (b) Distance to roads, (c) Distance to bomas, (d) Woody cover, (e) Distance to rivers, (f) Slope, (g) Digital Elevation Model, (h) Anomaly Normalized Difference Vegetation Index. Note: Predictor variables are in units of standard deviation.

Table 2.2: Coefficient estimates of the selected variables in relation to cheetah habitat selection in Serengeti, Tanzania. This table only includes significant variables, the full table with all covariates is in the appendix, (Appendix A).

Covariates	Estimate	Standard Error	Z value	P value
Intercept	-2.7991	0.0460	-60.8399	<0.001
Woody cover	-0.4859	0.0163	-29.7694	<0.001
Slope	-0.5533	0.0420	-13.1730	<0.001
DEM	-0.1954	0.0099	-19.7574	<0.001
ANDVI	-0.1078	0.0507	-2.1248	0.0336
Distance to lodges	-0.1892	0.0132	-14.3504	<0.001
Distance to roads	0.0535	0.0111	4.8419	<0.001
Distance to bomas	0.3113	0.0134	23.2395	<0.001
Distance to rivers	-0.2883	0.0155	-18.6443	<0.001
Woody cover*Wet	0.7144	0.0177	40.4241	<0.001
Lodges*Wet	0.5036	0.0178	28.3288	<0.001
Roads*Wet	-0.1866	0.0173	-10.7964	<0.001
Bomas*Wet	-0.6334	0.0192	-32.9406	<0.001
Bomas*Night	-0.1060	0.0180	-5.8770	<0.001
Rivers*Wet	0.1780	0.0218	8.1796	<0.001
Rivers*Night	-0.0526	0.0247	-2.1288	0.0333
Bomas*Wet*Night	0.0679	0.0314	2.1639	0.0305

Key: Bomas – Distance to bomas, Lodges – Distance to lodges, Roads – Distance to roads, Rivers – distance to rivers.

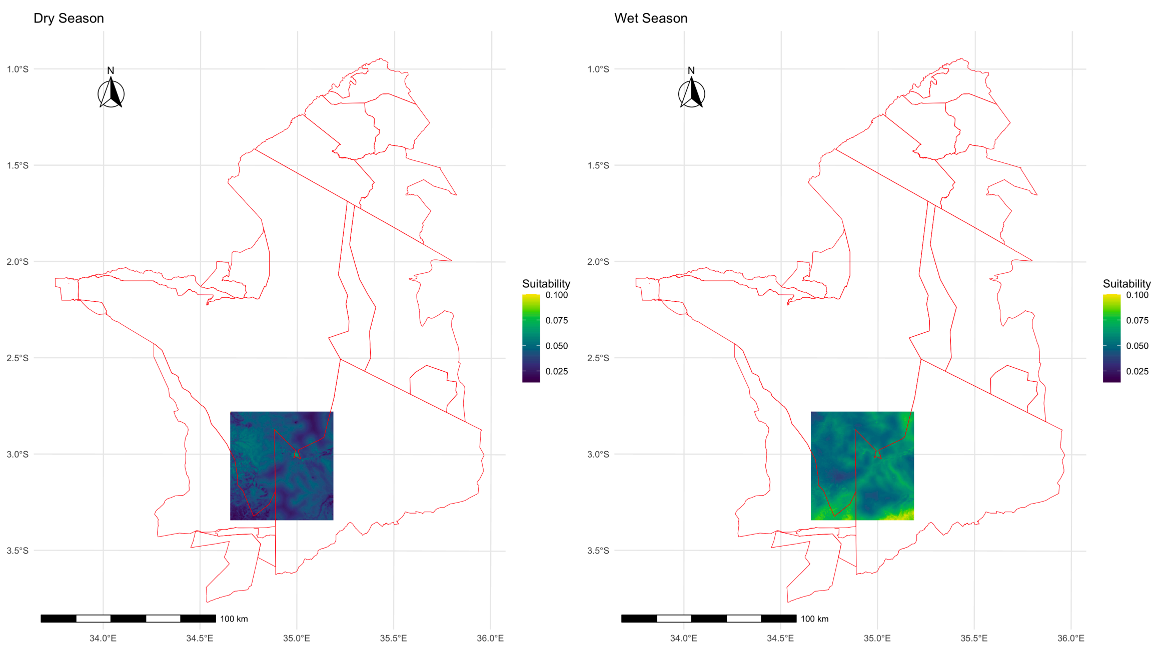


Figure 2.4: Habitat suitability maps for cheetahs in dry and wet seasons along the southern Serengeti ecosystem borderland, based on the following variables: distance to lodges, distance to Maasai bomas, distance to roads, woody cover, slope, distance to rivers, digital elevation model and anomaly normalized difference vegetation index. The map was produced by R software.

2.4 Discussion

Our results provide strong support for our hypothesis that anthropogenic impacts affect the movement patterns of cheetahs across the Serengeti borderlands. We investigated anthropogenic variables such as tourism facilities, roads, and bomas, and found that cheetahs avoided areas with human disturbance, indicating that the presence of humans in these facilities impacts their movements. Notably, cheetahs demonstrated behavioural flexibility in their habitat use, showing avoidance of areas near bomas and lodges during specific seasons. Cheetahs were more likely to avoid bomas during the dry season - when these sites are typically occupied by Maasai pastoralists - and avoided lodges during the wet season, which coincides with peak tourism activity. While I did not directly record boma or lodge occupancy, these seasonal avoidance patterns were captured through interaction terms between anthropogenic variables and season in the RSF models, suggesting that cheetahs adjust their space use in response to temporally varying human activity. Additionally, our research shows that all environmental parameters, including woody cover, NDVI, slope, rivers, and elevation, influenced overall cheetah habitat selection, underscoring that their use of the landscape is not random but influenced by specific anthropogenic and environmental factors. Our research adds to this collection of knowledge by examining specific human activities and environmental drivers that impact the habitat selection of the cheetahs.

2.4.1 Anthropogenic covariates

Anthropogenic factors were the most the influential drivers of cheetah habitat selection. The strong positive association with distance to lodges during the wet season implies that cheetahs tend to avoid areas near the lodges when they are most active. The wet season is the peak tourist season for this part of the Serengeti because the rains provide lush grazing grounds essential for wildebeest calving and nutrition, while also supplying the vital resources needed for their migration (Holdo et al., 2009b; Pennycuick, 1975). Cheetah avoidance of the lodges is therefore most likely due to the disturbances and human activity associated with these tourism facilities. There is a weak relationship in the other direction during the dry season when tourism is low, which suggests a slight preference for areas close to tourist facilities, probably because tourist facilities are sited in areas which hold important dry season resources for cheetah, such as woody cover and water. A study which examined the impact of human infrastructure on male brown bears movement in central Sweden showed that both dispersers and resident bears generally avoided buildings. In addition, dispersers exhibit intensified movement rate in proximity to such structures, suggesting a perception of increased risk (Thorsen et al., 2022). Another similar study in Maasai Mara - Kenya, showed that cheetahs strongly avoided human pressures and show a strong preference to wildlife areas (Klaassen & Broekhuis, 2018).

Cheetahs consistently avoided areas in close proximity to roads (within 2 km) throughout the year, showing a preference for locations situated at farther distances from roads. However, this avoidance was slightly less pronounced during the dry season, which may reflect the reduced intensity of tourism-related disturbance such as vehicle traffic and noise during that time of year. Nevertheless, roads had a much lower explanatory power compared to lodges, with changes in selection probability ranging between 3-7%. Another similar study in Tanzania's Ruaha-Rungwa landscape suggested that variations in lion activity on village land likely reflected avoidance of humans. The lions changed their general activity patterns by limiting road use during times when human presence was more likely (Searle et al., 2021).

In support of our hypothesis, cheetahs tend to avoid areas affected by active pastoralist activities. The bomas, occupied by the Maasai, are densely populated in regions close to essential resources such as water, forage, and plant materials, which are vital for human livelihoods. This indicates a strong correlation between human settlements and the distribution of resources (Luck, 2007). Areas adjacent to the southern borderlands of the Serengeti serve as dry season refuges for pastoralists. Consequently, bomas are largely unoccupied during the wet season, with pastoralists moving in and reoccupying bomas in the dry season. The results showed that cheetahs tended to select areas farther away from bomas during the dry season, when pastoralists were more likely to be present.

Overall, our results indicate that human impacts strongly influence cheetah movement. However, cheetahs adjust their space use in response to human presence and often return to disturbed areas after people have left, demonstrating a capacity to tolerate temporary disturbances. Zanette et al. (2023) demonstrated the anxiety exhibited by wildlife species towards humans, which significantly exceeds their fear of traditional apex predators like lions and placing them in a role of "super predator". This phenomenon emphasizes the profound psychological impact human presence has on wildlife, altering their natural behaviours and habitat preferences. Another study by Suraci et al. (2019) found that lions adjust their movement patterns and activity levels in areas with frequent human activity, further demonstrating the pervasive influence of human presence on wildlife behaviour. These studies collectively illustrate a complex relationship between wildlife behaviour and human influence, where animals not only respond to immediate threats but also adjust their strategies in response to human activities.

2.4.2 Environmental covariates

Different environmental factors including woody cover, slope, elevation, NDVI and proximity to rivers were associated with habitat selection of cheetahs. Our finding of a strong positive association between probability of cheetah presence and woody cover in the wet season supports previous research which has demonstrated that areas with increased tree density or woody cover are likely to be selected by female cheetahs (Bissett & Bernard, 2007; Broomhall et al., 2003; Durant, 2000b) and this is commonly understood as a method for avoiding predators, shade being particularly important during midday, but den sites and scent marking too. Cheetah utilization of enclosed habitats reduce occurrence of kleptoparasitism, by lowering the chances of being detected by lions and other scavengers that are likely to be drawn to cheetah carcasses (Hunter et al., 2007). Cheetahs may have chosen thick cover to maximize their hunting success and minimize chances of losing their kills to other predators. This aligns with the findings of Rostro-García et al. (2015) who observed that cheetahs often selected denser habitats with lower prey densities for their kill sites possibly to avoid detection by dominant competitors, even if it meant hunting in suboptimal areas in terms of prey abundance.

Cheetahs avoided areas with steeper slopes, this is likely because such terrain impedes their hunting activities. This observation aligns with Tagwireyi et al. (2020), who found that cheetahs in Gonarezhou National Park avoided higher slopes, though the effect was weak compared to other drivers of cheetah distribution. Similarly, Klaassen & Broekhuis. (2018) noted that in the Maasai Mara, cheetahs preferred lower slopes, which likely enhanced their hunting abilities.

Our results indicated a weak inverse relationship between elevation and cheetah habitat selection, suggesting that higher elevations are generally avoided by cheetahs. Welch et al. (2015) support this finding, observing cheetahs more frequently at lower elevations, likely due to better prey availability and milder temperatures. Conversely, Tagwireyi et al. (2020) found that cheetahs in Gonarezhou National Park, Zimbabwe, preferred higher elevations for better prey visibility and predator avoidance. However, in the Serengeti, the observed avoidance of high elevations may be explained by the region's topography, where elevated areas are typically steep or rocky hilltops that offer limited visibility, reduced prey availability, or less suitable terrain for cheetahs, which prefer open and gently sloping landscapes.

In this study, we found a weak negative correlation between the normalized difference vegetation index (NDVI) and cheetah habitat selection, suggesting a slight tendency for cheetahs to use less greener areas, though the effect size was small and should be interpreted with caution. This pattern may reflect broader ecological and behavioural factors. Wildebeests and Thomson's gazelles - the primary prey of cheetahs - follow rainfall patterns in the Serengeti, which in turn attract dominant predators like lions and hyenas to these resource-rich areas (Durant, 2000b; Durant et al., 1988). As a result, cheetahs may avoid such areas to reduce the risk of competition and kleptoparasitism. This interplay between predator-prey dynamics, interspecific competition, and habitat structure underscores the nuanced spatial strategies cheetahs employ in response to environmental pressures.

The significant relationship between proximity to rivers and cheetah presence is due to rivers attracting prey species, which encourages cheetahs to focus their hunting efforts in these areas to maximize their success. This finding has been found previously in the Serengeti ecosystem (Durant 1998) and is supported by Rostro-García et al. (2015) and Valeix et al. (2009). These studies show that cheetahs, despite an elevated risk from lions, utilized areas near water sources because these locations are positively selected by prey. Both dry and wet seasons had similar patterns of effects on cheetah selection, with dry season indicating slightly higher probability of selection. Large carnivores that hunt in arid and semi-arid savannas utilize ambush or chase-and-grab tactics to capture prey (Hopcraft et al., 2005) and therefore, these predators frequently congregate in areas with relatively dense vegetation and water sources. The results of our study provide insight into the complex interplay between cheetahs and their surroundings, mainly emphasizing the influence of anthropogenic factors.

2.5 Conclusion and recommendations

2.5.1 Conclusion

This study has demonstrated the significant impact anthropogenic factors can play on the habitat selection and movement patterns of cheetahs in the Serengeti borderlands. The findings reveal a clear avoidance of areas with high human disturbance; areas with lodges and bomas occupied by Maasai altered cheetah movements significantly. Cheetahs are sensitive to a broad spectrum of human activities, which corroborates findings from similar studies which have shown that human disturbances adversely affect wildlife movements and spatial use (Broekhuis et al., 2019; Klaassen & Broekhuis, 2018). Furthermore, our research confirms the influence of environmental variables such as woody cover, NDVI, slope, rivers, and elevation on cheetah habitat preferences. Cheetahs in the Serengeti landscape demonstrate a preference for habitats that optimize hunting efficiency and reduce predation, which is consistent with prior research (Basille et al., 2013; Bissett & Bernard, 2007; Broomhall et al., 2003; Rostro-García et al., 2015; Welch et al., 2015) and others. The complexity of these interactions highlights the need for conservation strategies that consider both the direct and indirect impacts of human activities on both wildlife and environment. Our study contributes significantly to a growing body of evidence that demonstrates negative relationships between wildlife and human activities and highlights the need for thoughtful and holistic management approaches that can mitigate against these impacts, in order to support the needs of both people and wildlife.

2.5.2 Recommendations

From our findings and based on the considerable value of the Serengeti to the global cheetah population, we recommend:

- The development of a human impact management plan for the region, to provide recommendations to limit additional human activities around tourism facilities and bomas. For example, clustering Maasai bomas and establishing zones around them could be a practical and effective way of preserving critical cheetah habitats and could also help to reduce livestock depredation.

- Careful management of human activities in optimal cheetah habitats to reduce human disturbances. This could, for example, involve managing the number and timing of tourists in the area, as well as regulating the types and intensity of activities allowed in these areas.
- Ensure the connectivity of suitable habitats by creating and maintaining safe wildlife corridors that link fragmented landscapes. This will help cheetahs move freely between different parts of their range and maintain genetic diversity.
- Enforce the existing regulations on wildlife harassment for tourists by including provision of resources and vehicles to rangers and ensuring that penalties are enforced.

In order to implement these steps, it will be crucial for park management to collaborate closely with local communities to develop consensual agreements on the management of the landscape, which should include strategies for boma placement that help to safeguard cheetahs while minimizing risks of livestock depredation. These steps, here and across cheetah distributional range, will be important for maintaining connectivity and coexistence with local communities, whilst ensuring that tourists do not damage the iconic wildlife that they may have travelled miles to see.

3 The impacts of anthropogenic activities on cheetah habitat selection and movement

Abstract

Large carnivores require extensive, interconnected habitats to thrive, but increasing human activities are altering these landscapes, forcing species like cheetahs (*Acinonyx jubatus*) to navigate complex and often fragmented environments. Understanding the shape and strength of these behavioural responses provides insight into the impact of land management on carnivore populations. However, such behavioural information is often lacking for rare or sensitive species, largely due to the logistical challenges of tracking elusive animals and their typically low population densities - challenges that are less pronounced for more common or wide-ranging species. This study investigates the influence of anthropogenic factors, namely pastoralism and tourism infrastructure, as well as environmental and seasonal variables, on fine-scale cheetah habitat selection and movement patterns in the Serengeti ecosystem. Utilizing GPS data from ten collared cheetahs, spanning >24,300 locations recorded across two years, we examined the effects of proximity to bomas, roads, and lodges, alongside environmental covariates such as woody cover, rivers, slope, elevation, and NDVI on habitat selection and movement using Integrated Step Selection Functions (iSSFs) at the individual level. Responses of cheetah to anthropogenic activities varied across individuals. Results reveal significant avoidance of bomas, particularly during the dry season. Responses to lodges varied across individuals and seasons, with cheetahs avoiding areas near lodges during the wet season but occasionally selecting them during the dry season. Proximity to roads showed mixed effects, with some individuals selecting and some individuals avoiding roads, while environmental factors such as woody cover and slope displayed seasonal variation in selection. Proximity to rivers emerged as a consistent driver across individuals and seasons, with cheetahs favouring areas nearer to rivers, presumably because of enhanced resource availability. This study underscores the variable strategies cheetahs employ to mitigate risks and optimize resource use in dynamic shared landscapes. Cheetahs' avoidance of bomas, lodges, and roads at certain times reflects human-induced habitat loss, as these areas become functionally unavailable despite being structurally intact; to ensure the continued viability of the Serengeti cheetah population, there is a need for careful land-use planning that prioritises cheetah habitat.

3.1 Introduction

Large carnivores require extensive habitats spanning a variety of ecosystems to meet their needs for food, shelter, and reproduction. However, habitat loss and fragmentation increasingly bring these predators into contact with human-altered environments, leading to conflicts and potential threats to their survival (Crooks et al., 2011; Ripple et al., 2014). The fragmentation of carnivore populations into isolated groups due to loss of connectivity caused by human activities disrupts their ecological dynamics and heightens their vulnerability to extinction (Carricondo-Sanchez et al., 2020; Linnell et al., 2001). For carnivores, maintaining genetic diversity and reducing the risk of local extinction of populations necessitates the ability to move through fragmented landscapes (Cushman et al., 2018). Yet, these landscapes often comprise areas that are significantly modified by human actions, which while they may provide resources, also impose risks such as persecution, habitat loss, and increased mortality (Woodroffe & Ginsberg, 1998). As the availability of natural prey declines, carnivores may take greater risks that increase their interactions with humans (Schuette et al., 2013). Sustainable management strategies are crucial to mitigate these risks and facilitate the coexistence of wildlife and humans (Pooley et al., 2017).

Human modified landscapes, particularly those on the fringes of protected areas, play important roles in shaping the behaviour and population dynamics of large carnivores. In arid areas, intensive livestock grazing can degrade habitats and elevate resource competition between livestock and wildlife (Reid et al., 2014; Veldhuis et al., 2014), though importantly, this interaction can be neutral or even positive under some conditions (Odadi et al., 2011). Several studies have demonstrated that large carnivores often adjust their spatial and temporal behaviours to navigate human pressures. For instance, Abrahms et al. (2016) and Suraci et al. (2019) highlight that large carnivores shift their movement patterns to avoid high-risk areas or times associated with human presence, suggesting an adaptive strategy to balance resource needs and minimize conflicts. Furthermore, (Frey et al., 2020) revealed that multiple carnivore species, including pumas and wolves, exhibited increased nocturnality in response to human landscape disturbances, indicating a temporal strategy to avoid interactions with people.

Other studies on sympatric large carnivores illustrates how different species use space differently in response to human activities and interspecific competition. For example, Oriol-Cotterill et al. (2015) demonstrated that lions adjust their spatial and temporal activity to avoid human settlements by utilizing these areas at night when human activity is minimal. This spatiotemporal partitioning helps lions to reduce the risk of conflict with humans. Similarly, Coltrane & Sinnott (2015) found that brown bears in Anchorage, Alaska, increased their nocturnal activity in areas with higher human usage, highlighting the behavioural adaptations large carnivores employ to mitigate the risks of human encounters.

Cheetahs (*Acinonyx jubatus*) exhibit notable behavioural plasticity compared to many other large carnivores, allowing them to adjust their space use and activity patterns in response to human disturbance. However, they still face unique challenges due to their low population density, wide-ranging behaviour, and competition with dominant predators (Van Der Weyde et al., 2017). Their strategy of seeking out areas with relatively low densities of prey species is a mechanism to minimize direct competition with other large carnivores (Durant, 1998). Studies by Broekhuis & Gopalaswamy (2016) and Durant (1998) have shown that cheetahs often alter their habitat use to avoid larger predators like lions and hyenas, reflecting their need to find "competition refuges". Moreover, Durant et al. (2017) emphasize that cheetahs require large, interconnected habitats to support their extensive movements, as these landscapes allow them to minimize competition from other predators, find optimal hunting grounds and avoid conflicts. This behavioural flexibility, while beneficial, also brings cheetah into contact with anthropogenic activities and infrastructure, such as human settlements and livestock.

In the Serengeti, cheetahs encounter dynamic challenges posed by human activities. Pastoralism, through livestock grazing, can lead to habitat degradation and reduced availability of prey species due to competition for forage (Msuha et al., 2012; Reid et al., 2014; Veldhuis et al., 2014), though the interaction between wild and domestic ruminant grazers can be neutral or even positive under some conditions (Odadi et al., 2011). The Serengeti's thriving ecotourism industry introduces another potentially intensive form of land-use. While evidence on the direct impacts of high-intensity tourism on cheetahs remains limited, studies suggest that large carnivores, including cheetahs, may alter their behaviour or habitat use in response to human activity (Carter et al., 2012; Oriol-Cotterill et al., 2015). Specific evidence for cheetah avoidance of tourism infrastructure under high human activity is currently lacking. However, given their tendency to avoid areas with high sympatric large carnivore densities and their extensive ranging behaviour, cheetahs are often found outside protected areas. This increases their exposure to anthropogenic pressures, such as habitat fragmentation and human-wildlife conflict (Durant et al., 2017).

Borderland areas, transitional zones between protected regions and human-modified landscapes, provide a unique opportunity to understand how cheetahs respond to such anthropogenic activities. These interface regions are often sparsely monitored by land managers, are expanding in size globally (Sillero-Zubiri et al., 2023), contain essential resources for wildlife and humans, and represent areas where human and wildlife interests overlap most acutely. Understanding how cheetahs adapt their movement patterns in response to pastoralism and tourism in these borderlands is critical for designing effective conservation strategies that ensure long-term viability of cheetah while promoting livelihoods and economic return.

Traditional species occurrence data often fail to capture the underlying movement processes and behavioural decisions animals make in response to their environment. Step selection functions (SSFs), and their extension through integrated SSFs (iSSAs), offer a powerful framework for analysing how animals move through heterogeneous landscapes by comparing used steps with available ones generated from the animal’s movement constraints (Avgar et al., 2016; Signer et al., 2019). This method allows researchers to simultaneously model habitat selection and movement behaviour, offering more nuanced insight than occurrence-based models. By accounting for step length and turn angle distributions, iSSA is particularly well-suited for fine-scale investigations of how animals respond to dynamic features such as human activity or seasonal habitat change. This approach complements the broader-scale resource selection functions (RSFs) employed in Chapter 2 by focusing on local-scale drivers of cheetah behaviour and space use.

This study employs Integrated Step Selection Analysis (iSSA) to assess the effects of human-related activities, particularly pastoralism and tourism, on cheetah movement patterns in the Serengeti. The iSSA approach integrates animal movement data with spatial information on both environmental and anthropogenic factors, providing insights into how cheetahs respond, in terms of habitat selection and movement, to landscape features and human activities (Avgar et al., 2016; Patterson et al., 2008). By using GPS data from collared cheetahs, this research examines how proximity to pastoral settlements and tourism infrastructure influences cheetah movements while also considering key environmental variables such as woody cover, water sources, and topography (Broekhuis & Gopalaswamy, 2016).

Specifically, I predicted that cheetahs would exhibit avoidance behaviour toward areas close to roads, lodges, and bomas, reflected in either shorter step lengths (indicating caution) or increased turning angles (suggesting hesitation or evasion). In contrast, I expected longer steps and more directed movements in areas farther from anthropogenic features, suggesting more relaxed or efficient travel. Regarding environmental covariates, I anticipated preference for moderate woody cover, which offers concealment for hunting but still allows visibility. I also predicted that cheetahs would select areas closer to rivers or water sources during the dry season and that slope and elevation would influence movement patterns by shaping energetically efficient routes. Finally, I expected these patterns to vary by season and time of day, with stronger avoidance responses during daylight hours when human activity is highest.

The goal of this study is to understand how human activities impact cheetah mobility and habitat selection at fine spatial scale and thereby provide guidance for conservation strategies that promote human-wildlife coexistence within the Serengeti. By identifying behavioural responses of cheetahs to human activities, the research aims to inform land-use planning and conservation efforts, ensuring that both community needs and wildlife preservation are balanced (Cushman et al., 2018; Ripple et al., 2015).

3.2 Materials and methods

3.2.1 Study area

This study focuses on cheetah populations in the southeastern periphery of the Serengeti ecosystem, covering Southern Serengeti National Park (SNP), Makao Wildlife Management Area (MWMA), Maswa Game Reserve (MGR), and the Ndutu area within the Ngorongoro Conservation Area. The study area experiences a rainfall gradient, with annual precipitation ranging from approximately 500 mm in the southeast to 1,150 mm in the northwest. Rainfall occurs mainly in two seasons: brief showers between November and December, followed by prolonged rains from January to May. This precipitation gradient fosters a range of habitats, from short grasslands in the southeastern regions to savanna woodlands in the northwest, providing diverse ecosystems that support an array of wildlife, including cheetahs (Bartzke et al., 2018; Holdo et al., 2009a).

Each land management unit has distinct conservation priorities and varying degrees of human activity. Serengeti National Park spans approximately 14,750 square kilometres and remains a core area for wildlife conservation. The Makao Wildlife Management Area, established in 2009 and covering 780 square kilometres, serves as a critical wildlife corridor, linking SNP, MGR, and the Ngorongoro Conservation Area (Lwankomezi et al., 2023). Local reliance on agriculture and livestock grazing in MWMA often leads to habitat degradation and human-wildlife conflicts. Maswa Game Reserve, covering 2,200 square kilometres, acts as a buffer zone, separating SNP from agro-pastoralist areas. Within MGR, controlled hunting and grazing are permitted under regulated conditions (Kimaro & Treydte, 2021). The Ndutu region in the Ngorongoro Conservation Area supports a population of approximately 100,000 people, including both indigenous Maasai pastoralists and non-indigenous residents, who rely on livestock such as cattle, goats, sheep, and, to a lesser extent, camels (Yamat, 2018). This long-standing pastoralist tradition, along with the complex social dynamics introduced by groups such as the Maasai and Datoga, contributes to the area's unique land-use history (Homewood & Rodgers, 1991; Linuma et al., 2022). Pastoralist activities in NCA exhibit strong seasonal patterns, with livestock herds expanding into greener grazing areas during the dry season and retreating closer to settlement centres during the wet season. By contrast, tourism peaks during the annual wildebeest migration, particularly in the wet season, when visitors flock to view high wildlife densities in the Ndutu region.

The southeastern Serengeti ecosystem is characterized by diverse soils, ranging from nutrient-rich volcanic soils in the northwestern areas to more leached and sandy soils in the southeastern grasslands (Reed et al., 2009). This soil variation, combined with the rainfall gradient, plays a key role in shaping the hydrology and vegetation diversity across the landscape. Vegetation varies from short grasses in the nutrient-poor southeastern plains to denser savanna woodlands in the northwest, providing a mosaic of habitats essential for different wildlife (Estes et al., 2012)

The prey base within the Serengeti ecosystem is dynamic, driven by the annual migration of large herbivores such as wildebeest (*Connochaetes taurinus*), zebras (*Equus quagga*), and gazelles (*Eudorcas thomsonii*), which follow seasonal rainfall patterns in search of fresh grazing ground (Fryxell et al., 1988; Sinclair et al., 2000). This seasonal pulse of prey abundance results in high prey density during the wet season when migratory herds concentrate in the southeastern plains, offering ample hunting opportunities for predators like cheetahs. In the dry season, prey density declines as these animals move northwest toward more permanent water sources and pasture (Holdo et al., 2009b). This fluctuation in prey availability is crucial for interpreting seasonal variations in cheetah behaviour, as changes in prey density influence hunting success and movement patterns (Durant, 2000b).

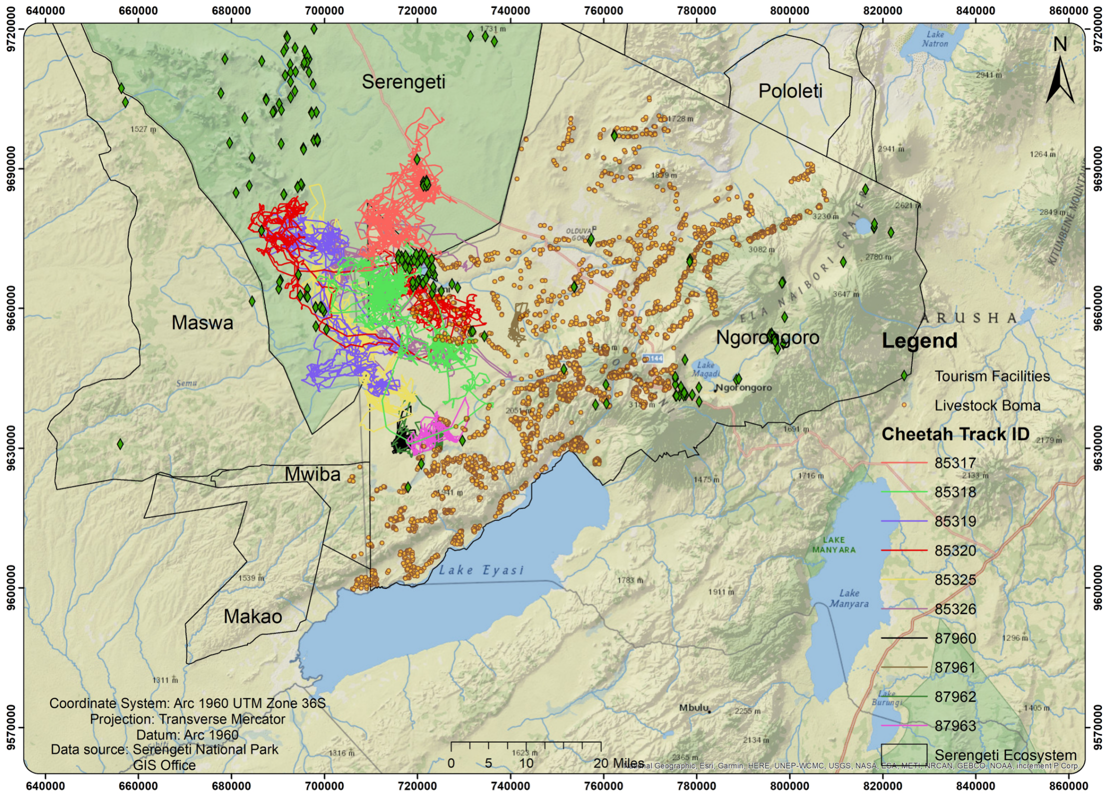


Figure 3.1: Map of the study area showing cheetah telemetry data in relation to anthropogenic and vegetation features. Each individual is represented by its unique track colour.

3.2.2 Data collection

3.2.2.1 Cheetah collaring

We collected locational data by fitting Global Positioning System (GPS) satellite collars to ten adult cheetahs across the study area. The sample included cheetahs from a range of spatial locations to capture variation in habitat use and movement patterns. Given that females have greater demographic importance and range more widely than males (Durant et al., 2007), all ten collared cheetahs were females. The collars used were VERTEX Lite -1C IRIDIUM models, manufactured by VECTRONIC Aerospace GmbH, and were deployed in April and May 2022. The collars were equipped with a basic 3-axis activity sensor, a basic temperature sensor, a mortality sensor, a VHF beacon, and an Iridium communication module. The locations of cheetahs were sampled at two-hour intervals from 6:00 am to 8:00 pm, with an additional location recorded at midnight, over the course of a year, as they are primarily diurnal (Caro, 1994). Veterinarians from the Tanzania Wildlife Research Institute and the NCA employed tranquillizing agents to immobilise cheetahs. The darts administered used a combination of Ketamine (100mg) or

Zoletil (50mg) in combination with Medetomidine (2mg). Atipamezole (2.5mg) or Yohimbine (6.25mg) were administered to reverse the tranquilizers. To guarantee precise shots into the main muscles of the rump or shoulder when the cheetahs were inactive, immobilisations were performed from a close distance of 10-15 metres. All ten cheetahs recovered completely without any indications of discomfort following immobilisation. To guarantee that there were no adverse side effects, each cheetah was monitored and tracked for a minimum of three days following immobilisation. The collars, which weighed 400 grammes (1.1% of the average female cheetah's weight of 35 kg), were selected to minimise any potential impact on the animals' behaviour (Laurenson & Caro, 1994). In order to prevent any behavioural anomalies that may arise during recovery, we ignored the first three days of GPS data. Animal immobilizations were approved by the ethics committee by Zoological Society of London and followed Tanzania Wildlife Research Institute approved guidelines and protocols for animal capture.

Figure 3.2: The Athlete (Collar ID - 85326), one of the ten GPS radio collared female cheetahs, photographed immediately after recovering from immobilization.

3.2.3 Anthropogenic covariates

We evaluated the impact of tourism on the movement patterns of cheetahs. Tourism related infrastructure may influence the behaviour and movement patterns of large carnivores, such as cheetahs (Roe et al., 1997; Van Der Meer et al., 2016). The impacts of tourism facilities (including permanent lodges and special campsites) and the road networks were evaluated by computing the distance between the nearest tourism facility and road to the GPS locations of observed cheetah locations and all locations available to cheetah. This method recognises the interconnectedness of roads and tourism facilities, as roads facilitate access to these facilities and are also used by tourists' vehicles for wildlife viewing opportunities. The road networks that are the subject of this study include administrative roads, game drive roads, and primary roads. Although roads may vary in the degree of human activity, we considered all roads together as game viewing vehicles have access to all roads.

Pastoralist activities were characterised by the presence of “bomas”, a semi-permanent Maasai dwellings and livestock corrals. The central base for livestock herding activities are bomas. Livestock are herded daily away from the bomas to seek water and graze in the nearby vicinity, travelling up to 10 kilometres from the boma, before returning at night (Jansson et al., 2024). We assumed that intensity of pastoralist activities declined with distance from the boma, with the most intense use close to the boma. The locations of bomas were initially mapped using Google Earth Pro and subsequently rasterized to calculate the distance between each cheetah observation to the closest boma as a measure of exposure to pastoralist activities (Jansson et al., 2024).

3.2.4 Environmental covariates

In order to assess the effects of environmental covariates on cheetah movement patterns, our study included landscape features such as woody cover, the normalized difference vegetation index (NDVI), slope, elevation, and rivers. The landscape features were chosen based on the characteristics that are recognised as critical components of cheetah habitat selection, such as woody cover and other geographical features (Minja et al., 2025 *in review*; Pettorelli et al., 2009). The mobility decisions of cheetahs could be influenced by woody cover, which may affect their overall chances of survival. Woody cover plays a critical role in shaping cheetah habitat selection by influencing concealment, hunting success, and predator avoidance. In this study, woody cover was estimated using tree density data derived from Sentinel-1 C-band radar, which captures seasonal variation in vegetation structure by comparing dry and wet season readings (Thijssen et al., 2025). This approach enhanced our understanding of how vegetation dynamics affect cheetah space use across seasons. We used processed layers from Townshend et al. (2016), where the data have been refined and presented in a ready-to-use format. Although the dataset reflects canopy cover over the past 10 years, it remains a valid and representative indicator of long-term woody vegetation in the Serengeti, where large-scale deforestation is limited. These layers provided a consistent, ready-to-use format that served as a proxy for structural habitat complexity relevant to cheetah movement and selection. Vegetative greenness was anticipated to influence cheetah habitat selection through its effects on prey availability, access to water, hunting cover, thermoregulation, and denning opportunities. To quantify this, we used the Normalized Difference Vegetation Index (NDVI), a widely adopted remote sensing metric derived from red and near-infrared reflectance, which reflects plant biomass and photosynthetic activity (Tucker, 1979). NDVI values were obtained from the Moderate-Resolution Imaging Spectroradiometer (MODIS) aboard NASA’s Terra satellite, at approximately 250 × 250 m spatial resolution and 16-day temporal resolution for the whole study period. To account for short-term fluctuations and departures from typical vegetation patterns, we calculated NDVI anomaly, defined as the Z-score difference between observed NDVI and the long-term monthly mean, normalized by standard deviation. This approach allowed us to identify areas with unusually high or low productivity relative to seasonal expectations, offering insights into temporal variation in habitat quality that may influence cheetah foraging and space-use decisions. We hypothesized that cheetah movement patterns might be influenced by elevation, particularly through its effects on climate, vegetation, and prey availability. NASA's Shuttle Radar Topography Mission (STRM) dataset was used to extract elevation values at a resolution of 30m. We also considered the influence of rivers on cheetah movement. Rivers are crucial because they influence the distribution of numerous cheetah prey species, particularly during the dry season, despite the fact that cheetahs can survive without water (Durant, 1998). Therefore, we quantified the distance to the nearest river at each cheetah location and each available location, and we investigated the impact of water availability on the cheetahs' movements. Each of these layers was acquired from the GIS database of the Serengeti National Park (Hopcraft J.G.C, *unpublished*).

3.2.5 Temporal covariates

To better understand the potential influence of seasonal variation on cheetah movement, we incorporated a binary “season” variable in our step selection analysis, distinguishing between wet and dry seasons. This approach allowed us to explicitly test if and how cheetah movements varied with seasonal changes and helped capture the dynamic nature of human activities and environmental conditions across both seasons. By examining the seasonal shifts of cheetah movements in resource availability and human presence, we aimed to provide a more comprehensive picture of how cheetahs interact with their environment. This includes a better understanding of how cheetah adjust their movement strategies in response to seasonal changes, offering deeper insights into their adaptability to varying anthropogenic and environmental pressures.

3.2.6 Statistical Analysis

Key covariates including woody cover, distance to lodges, roads, rivers, slope, NDVI, elevation, and proximity to bomas were extracted from the corresponding raster layers to assess their influence on cheetah movement patterns. GPS data from collared cheetahs were georeferenced and projected into the European Petroleum Survey Group coordinate reference system (EPSG: 21036) to facilitate accurate movement modelling. Location data were cleaned by removing all rows with missing values and duplicate entries, which included identical timestamps and coordinates likely resulting from collar signal errors or repeated data transmissions. Dates were systematically organised aiding in the delineation of seasonal effects on cheetah behaviours within their home ranges.

We employed exponential decay functions to model the decreasing impact of anthropogenic factors on cheetahs with increasing distance (Nielsen et al., 2009). Unlike a negative linear response, which diminishes across distances but remains consistently proportional, the exponential decay function we used is explicitly non-linear, highlighting that the effect of an anthropogenic feature is much more pronounced at close proximity but diminishes rapidly beyond a certain threshold. This behaviour is mathematically described by the equation exp(-dist/decay distance), where "*dist*" represents the distance to the anthropogenic feature, and "decay distance" specifies the rate at which the effect reduces, eventually approaching zero.

We chose a decay threshold of 2 kilometres based on ecological reasoning and evidence from our prior research. In Chapter 2 I showed that disturbances from anthropogenic features, such as roads and human settlements, tend to have the most pronounced effects within a 2-kilometre radius before tapering off (Minja et al., 2025, *in review*). By applying this threshold, we were able to capture the localized impact of anthropogenic factors while ensuring that distant features did not overly influence the results.

To examine cheetah habitat selection at a local (fine) scale, we used integrated step selection functions (iSSFs), comparing anthropogenic and environmental covariates at cheetah locations with those at a random set of available locations along their movement paths (Avgar et al., 2016). The ***amt*** package in R (Signer et al., 2019) was employed to estimate the movement parameters of each cheetah, including its step length and turn angle. All the GPS data were first nested by individual collar ID, allowing for the creation of separate movement tracks for each cheetah. These tracks were resampled at regular intervals (at every 2 hours), generating sequences of steps (i.e. 'bursts') that were then filtered to have minimum of at least 3 steps per burst for robust step selection analysis.

From each used location, we generated 20 random available locations based on the empirical movement characteristics of the animals. Specifically, step lengths were sampled from a gamma distribution, which is appropriate for modelling continuous and positively skewed data, while turning angles were sampled from a von Mises distribution - a circular probability distribution commonly used to represent directional data, such as angles ranging from $-\pi$ to π. These matched sets of one used and twenty available steps formed the basis for constructing the response variable (case_), where used steps were coded as 1 and available steps as 0. These were grouped into strata to allow for a conditional logistic regression design approximated through a Poisson model with a stratum-specific intercept (Fieberg et al., 2021). All covariates were extracted at relevant points (either at the end of each step or at both the start and end) for each individual. Covariate transformations, including a logarithmic transformation of step length and cosine transformation of turn angle, ensured proper scaling. Predictor variables were scaled and centred to facilitate model convergence and interpretation.

Global models were generated for each season, encompassing all predictors. General models included linear terms for anthropogenic features (distance to bomas, lodges, and roads) and environmental features (woody cover, slope, elevation, distance to rivers) measured at the end points of steps, as well as interactions between movement variables (step length, log step length, and cosine of turn angle) and anthropogenic features at the start of steps. To ensure comparability across individuals, the same model structure was applied uniformly to all cheetahs.

On the other hand, the average patterns at the population level were explored, a global integrated step selection model was fit using data pooled from all ten collared cheetahs. This model included the full suite of anthropogenic and environmental covariates, along with interactions with movement parameters. However, most coefficients in this pooled model were statistically non-significant, indicating high individual variation in cheetah responses and a lack of strong generalizable selection trends at the population level (Appendix B). Given this, I focused my analyses on individual-level models to better capture behavioural heterogeneity among cheetahs. This approach allowed me to identify more nuanced and distinct patterns in how different individuals responded to landscape features and human activities.

3.3 Results

A total of ~ 24,300 GPS locations were collected from the ten collared cheetahs over a two-year period. The number of points per cheetah ranged from a minimum of 1,684 to a maximum of 3,788, with an average of 2,025 locations recorded per cheetah over a span of roughly twelve months. There were no cheetah mortalities during the study.

3.3.1 **Response to Anthropogenic Factors**

Cheetahs generally displayed significant avoidance of anthropogenic features, though responses varied by individual and season (Tables 3.1 & 3.2; Figures 3.3 & 3.4). For instance, three individuals (IDs = 85318, 85325 and 87962) significantly avoided areas near bomas during the dry season (β = 0.46 - 95% CI = [0.096, 0.82], β = 1.9 - 95% CI = [0.3, 3.5] and β = 2.8 - 95% CI = [0.25, 5.4] respectively), and 8 out 10 cheetah showed a positive mean coefficient, implying an avoidance of these areas. In the wet season, only one individual (85325) exhibited significant avoidance of bomas (β = 3.2, 95% CI = [0.53, 5.9]), while the overall population-level effect for other cheetahs was marginal selection of areas where unoccupied bomas were. For distance to lodges, there was no significance avoidance or preference in the dry season across individuals, but in the wet season 2 out of 10 individuals (85325 and 87961) demonstrated significant avoidance (β = 0.68, 95% CI = [0.1, 1.3], β = 5.6, 95% CI = [1.7, 9.4] respectively), selecting areas farther from the lodges (Figure 3.3). Conversely, one individual (87960) selected areas near lodges during the dry season (β = -0.56, 95% CI = [-1.11, -0.044]). The step selection functions showed variable relationships with the distance to roads. In the dry season, two out of 10 individuals (85317 and 87962) selected areas near roads in the dry season (β = -0.42, 95% CI = [-0.7, -0.13] and β = -3.9, 95% CI = [-7, -0.89] respectively) whereas two other individuals (85325 and 87961) selected areas that were significantly farther away from the roads (β = 0.3, 95% CI = [0.057, 0.54] and β = 6.4, 95% CI = [0.76, 12] respectively). However, in the wet season, two individuals (85325 and 87960) significantly avoided roads (β = 0.34, 95% CI = [0.078, 0.59] and β = 5, 95% CI = [2.3, 7.7] respectively). In a post-hoc analysis, I found no consistent spatial pattern in the way individual cheetahs responded to anthropogenic effects. This suggests that cheetah responses may be context-dependent, potentially shaped by local conditions such as prey availability, the presence of dominant competitors, or individual experience. Territory-level factors or fine-scale variation in human activity may also influence behavioural responses in ways not captured by broader landscape metrics. Responses varied across individuals, with some showing positive, negative, or neutral associations with anthropogenic features, but no overarching trend emerged. However, the small sample size (n = 10 individuals) may have limited the ability to detect statistically significant or consistent effects.

3.3.2 Movement vs Anthropogenic interactions

Interactions between movement metrics (step length and turn angle) and continuous distance-to anthropogenic variables revealed nuanced differences in cheetah movement strategies. These responses varied significantly among individuals and seasons, reflecting how cheetahs navigated gradients of human-modified landscapes (Tables 3.1 & 3.2).

3.3.2.1 Step Length

Significant interactions between step length (*sl_*) and distance-to bomas were observed for several individuals. In the dry season, individual 85318 showed increased step lengths as distance from bomas increased (β=0.00035,95% CI= [0.0002,0.0005]) indicating avoidance behaviour, where the cheetah moved more rapidly and covered greater distances away from bomas. Similarly, individuals 85319 and 85320 exhibited shorter step lengths closer to bomas (β=-0.00096, 95% CI=[-0.002,-0.00021]) and (β=−0.00014,95% CI=[−0.0003,−7.3e−06]) respectively, reflecting localized activity such as increased caution or vigilance near bomas. Together, these patterns suggest that cheetahs tend to move cautiously near bomas but increase their speed and range as they distance themselves from these anthropogenic structures.

In the wet season, interactions between step length and distance to lodges were observed, highlighting individual variation in cheetah responses. For instance, individual 85317 exhibited longer step lengths farther away from lodges (β = 0.00016, 95% CI = [2.3e-06, 0.00031]), indicating avoidance behaviour. In contrast, individual 85319 displayed shorter step lengths closer to lodges (β = -0.00016, 95% CI = [-0.0003, -3.5e-07]), suggesting localized activity or cautious movement near the lodges. In the dry season, only individual 85320 strongly avoided lodges, as indicated by longer step lengths with increasing distance (β = 0.00021, 95% CI = [3.6e-05, 0.00038]). Other collared cheetahs selected areas near the lodges during the dry season, with shorter step lengths, although these effects were only marginally significant

In the dry season, individual 87961 exhibited longer steps (β = 0.0047, 95% CI: [0.0001, 0.009]) as the distance to roads increased, indicating that this individual moved in longer strides farther away from roads. Nonetheless, in the wet season, individual 85326 displayed a decrease in step length as the distance to roads increased (β = -0.002, 95% CI: [-0.001, -2.2e-05]), suggesting shorter steps or localized movement pattern farther from roads. In contrast, individual 87960 showed an increase in step length with increasing distance from roads (β = 0.0042, 95% CI: [0.001, 0.0073]), indicating a preference for more extensive movement farther from roads in the wet season.

3.3.2.2 Turn Angle

Turn angle (*cos_ta_)* interactions with distance-to anthropogenic features also varied by individual and season. For instance, in the dry season, 85325 (-0.77, 95% CI=[-1.3, -0.21]) indicated that as the distance to bomas increases, this cheetah tends to make sharper turns. On the other hand, individual 85326 and 87961 exhibited less pronounced turns as the distance from the bomas increased (β=0.13, 95% CI=[0.0062, 0.26]) and more persistent in direction (β=1.8, 95% CI=[0.056,3.5]) away from the bomas respectively.

In the dry season, individuals 85326 and 87961 exhibited persistence in directional movement as the distance from roads increased, with β values of 0.12 (95% CI= [0.021, 0.22]) and 3.7 (95% CI= [0.051, 7.4]), respectively. Conversely, cheetah 85318 showed more tortuous movement as the distance from roads increased (β = -0.1, 95% CI= [-0.18, -0.025]). In the wet season, individuals 85325, 87963, and 87960 demonstrated consistent responses by moving more directly as the distance from roads increased, with β values of 0.15 (95% CI= [0.028, 0.26]), 0.89 (95% CI= [0.26, 1.5]), and 6 (95% CI= [3.3, 8.6]), respectively.

For lodges, in the dry season, individuals 85325 and 87961 displayed more tortuous movement as the distance to lodges increased, with β values of -0.11 (95% CI: [-0.2, -0.021]) and -3.8 (95% CI: [-7.3, -0.36]), respectively. However, in the wet season, individual 85317 (β = 0.21, 95% CI: [0.091, 0.33]) demonstrated more persistent directional movement as the distance from lodges increased. In contrast, individual 87960 (β = -21, 95% CI: [-32, -9.4]) exhibited highly tortuous movement as the distance from lodges increased.

3.3.3 **Response to Environmental Factors**

The step selection function revealed a significant negative association with woody cover during the dry season for some individuals, such as 85318, 85320, and 85325, with β values of -0.22 (95% CI: [-0.34, -0.089]), -0.37 (95% CI: [-0.56, -0.19]), and -0.46 (95% CI: [-0.63, -0.3]), respectively, suggesting a selection for areas with less woody vegetation (Figure 3.4). However, in the wet season, the overall woody cover influence was weaker and hence insignificant, except for 85317 and 85326 who selected denser areas compared with the other eight cheetahs (β = 0.25, 95% CI = [0.095, 0.41] and β = 0.2, 95% CI = [0.06, 0.33] respectively). The step selection function indicated that elevation had an overall weaker effect on cheetahs during the dry season. However, in the wet season, individual step selection functions for cheetahs 85325, 87962, and 87960 showed a preference for higher elevations, with β values of 0.59 (95% CI: [0.24, 0.94]), 0.47 (95% CI: [0.043, 0.89]), and 1.2 (95% CI: [0.39, 2]), respectively.

Overall, cheetahs selected areas close to rivers in both seasons, although the relationship was weak. However, individual step selection functions for cheetahs 85319, 85325 (both seasons), and 87961 showed a positive association with proximity to rivers, with β values of -0.4 (95% CI: [-0.64, -0.16]), -0.24 (95% CI: [-0.42, -0.057]), -0.18 (95% CI: [-0.36, -0.0048]), and -0.43 (95% CI: [-0.66, -0.2]), respectively. Cheetahs generally avoided steeper slopes across the study area. Even though the slopes effect was weaker to more than a half of the studied cheetahs, there were a couple of individuals that showed significant effects. For instance, 85325 and 87962 avoided steep slopes in the dry season (β = -0.28, 95% CI = [-0.46, -0.1] and β = -1.4, 95% CI = [-2.3, -0.46] respectively). NDVI also influenced cheetah step selection, even though its significance at the population level was marginal, more than half of the cheetahs avoided greener areas in both seasons (Figure 3.4). Individual cheetahs such as 85325 selected greener areas with higher NDVI during the dry season (β = 0.5, 95% CI = [0.21, 0.78]) and avoided such areas in wet season (β = -0.62, 95% CI = [-0.91, -0.34]) shows a fine scale behaviour of reacting differently to the same environmental variable compared to 87960 who significantly avoided greener areas in both seasons.

Table 3.1: Dry season coefficient estimates (with 95% CI in parentheses) from integrated step selection functions fit to data from GPS collars of 10 individual cheetah (IDs along top row) in the Serengeti Ecosystem (2022-2024). Significant coefficients in bold. Anthropogenic and environmental variables were scaled and centred prior to analysis, so effect sizes are comparable.

					DRY SEASON					
Variables	85317	85318	85319	85320	85325	85326	87963	87962	87961	87960
Bomas_end	0.68 (-0.055,1.4)	**0.46 (0.096,0.82)**	0.69 (-1.6,3)	0.41 (-0.19,1)	**1.9 (0.3,3.5)**	0.19 (-0.39,0.77)	-0.81 (-1.6,0.037)	**2.8 (0.25,5.4)**	**-1.7 (-3, -0.31)**	0.88 (-1.7, 3.5)
Lodges_end	-0.17 (-0.49,0.16)	0.031 (-0.33,0.39)	0.23 (-0.4,0.86)	0.052 (-0.23,0.34)	-0.016 (-0.28,0.25)	-0.14 (-0.67,0.39)	0.25 (-1.2,1.7)	-2.4 (-6.9,2)	-2.6 (-8.6,3.4)	-3.8 (-8.5, 0.87)
Roads_end	**-0.42 (-0.7, -0.13)**	-0.14 (-0.38,0.098)	0.15 (-0.11,0.41)	0.069 (-0.2,0.33)	**0.3 (0.057, 0.54)**	0.13 (-0.097, 0.36)	-0.14 (-1.6,1.3)	**-3.9 (-7, -0.89)**	**6.4 (0.76,12)**	1.6 (-0.38, 3.6)
Woodycover	-0.01 (-0.21,0.18)	**-0.22 (-0.34, -0.089)**	-0.17 (-0.47,0.13)	**-0.37 (-0.56, -0.19)**	**-0.46 (-0.63, -0.3)**	0.3 (-0.093, 0.69)	-0.16 (-0.68,0.36)	-2.1 (-4.3,0.16)	-0.29 (-0.73,0.16)	-0.98 (-3, 0.99)
Rivers	-0.054 (-0.2,0.093)	-0.15 (-0.37,0.076)	**-0.4 (-0.64, -0.16)**	-0.077 (-0.28,0.12)	**-0.24 (-0.42, -0.057)**	-0.17 (-0.38, 0.045)	0.34 (-0.41,1.1)	-1.6 (-4.5,1.3)	-0.16 (-0.52,0.21)	0.29 (-0.56, 1.1)
Slope	0.03 (-0.16,0.22)	-0.022 (-0.18,0.14)	0.0063 (-0.19,0.21)	0.067 (-0.093,0.23)	**-0.28 (-0.46, -0.1)**	0.14 (-0.031, 0.31)	-0.19 (-0.64,0.27)	**-1.4 (-2.3, -0.46)**	0.037 (-0.42,0.49)	0.44 (-0.091, 0.98)
Ndvi	-0.062 (-0.17,0.049)	0.033 (-0.14,0.21)	-0.18 (-0.57,0.21)	-0.18 (-0.47,0.11)	**0.5 (0.21, 0.78)**	**-0.38 (-0.6, -0.16)**	-0.055 (-0.42,0.31)	0.98 (-0.027,2)	0.11 (-0.92,1.1)	**-0.9 (-1.6, -0.19)**
DEM	-0.065 (-0.4,0.27)	-0.52 (-1,0.0075)	-0.36 (-0.95,0.24)	-0.084 (-0.54,0.37)	-0.22 (-0.61,0.17)	-0.53 (-1.1, 0.02)	-0.27 (-0.92,0.37)	**3 (1.3,4.7)**	-0.18 (-1.1,0.72)	0.92 (-0.33, 2.2)
sl_	**-0.00013 (-0.00026, -1e-05)**	0.00015 (-1.9e-06,0.00031)	0.00025 (-3e-04,8e-04)	6e-05 (-1e-04,0.00022)	6.8e-05 (-0.00018,0.00031)	**-0.00049 (-0.00071, -0.00026)**	-0.00027 (-0.0014,0.0009)	-0.0014 (-0.016,0.013)	-0.00036 (-0.008,0.007)	-0.00072 (-0.0038, 0.0024)
log_sl_	0.014 (-0.015,0.042)	0.033 (-0.0067,0.073)	-0.019 (-0.16,0.12)	-0.024 (-0.059,0.01)	0.09 (-0.011,0.19)	0.05 (-0.0031,0.1)	0.25 (-0.076,0.57)	-5.9 (-28,16)	1.6 (-1.5, 4.7)	-0.0018 (-0.74, 0.73)
cos_ta_	-0.056 (-0.15,0.036)	0.087 (-0.037,0.21)	0.12 (-0.28,0.51)	0.049 (-0.062,0.16)	**0.38 (0.075,0.69)**	-0.062 (-0.2,0.079)	**1.1 (0.064,2.1)**	6.3 (-6.8,19)	2.2 (-2.9,7.3)	-0.14 (-2.1, 1.8)
sl_:Bomas_start	-5.9e-05 (-0.00037,0.00025)	**0.00035 (0.0002, 0.0005)**	**-0.00096 (-0.002, -0.00021)**	**-0.00014 (-0.0003, -7.3e-06)**	-2e-04 (-0.00065,0.00025)	6.8e-05 (-0.00015,0.00028)	0.00013 (-0.00036,0.0006)	0.0022 (-0.0066,0.011)	0.0016 (-0.0007, 0.004)	2.2e-05 (-0.004, 0.004)
log_sl_:Bomas_start	0.011 (-0.058,0.081)	0.012 (-0.015,0.039)	0.026 (-0.16,0.22)	**0.026 (0.0018, 0.05)**	-0.12 (-0.31, 0.058)	**0.05 (0.012,0.087)**	**0.14 (0.00017,0.28)**	-7.7 (-21,5.7)	0.63 (-0.46, 1.7)	-0.23 (-1.2, 0.7)
cos_ta_:Bomas_start	0.2 (-0.03,0.44)	0.055 (-0.032,0.14)	-0.26 (-0.81,0.3)	-0.027 (-0.11,0.055)	**-0.77 (-1.3, -0.21)**	**0.13 (0.0062,0.26)**	0.41 (-0.034,0.86)	2.4 (-5.1,9.8)	**1.8 (0.056, 3.5)**	-0.28 (-2.8, 2.2)
sl_:Lodges_start	4.2e-05 (-0.00014, 0.0002)	-5.8e-05 (-2e-04, 8.7e-05)	0.00025 (-1.3e-05,0.00052)	**0.00021 (3.6e-05, 0.00038)**	-7.7e-05 (-0.00018, 2.2e-05)	3e-04 (-3.7e-05,0.00063)	-0.00043 (-0.0018,9e-04)	0.022 (-0.00064,0.044)	-0.0016 (-0.006, 0.003)	-0.00027 (-0.0078, 0.0072)
log_sl_:Lodges_start	-0.0067 (-0.044, 0.03)	8.3e-05 (-0.031,0.031)	-0.048 (-0.098,0.0028)	-0.012 (-0.043, 0.019)	-0.0081 (-0.037, 0.02)	-0.078 (-0.16,0.0053)	-0.078 (-0.28,0.12)	-24 (-61,12)	-0.062 (-0.87, 0.75)	0.074 (-1.5, 1.6)
cos_ta_:Lodges_start	0.052 (-0.067, 0.17)	0.041 (-0.055,0.14)	0.018 (-0.11,0.14)	0.086 (-0.0061, 0.18)	**-0.11 (-0.2, -0.021)**	-0.095 (-0.32,0.13)	0.55 (-0.3,1.4)	2.6 (-12,17)	**-3.8 (-7.3, -0.36)**	0.46 (-3.9, 4.8)
sl_:Roads_start	1.8e-05 (-0.00017,0.00021)	-7.7e-05 (-2e-04,5e-05)	-6.9e-05 (-0.00024,1e-04)	8.9e-05 (-9.6e-05, 0.00027)	8.8e-06 (-9.2e-05, 0.00011)	-6.4e-06 (-0.00016,0.00014)	0.00073 (-5e-04,0.0019)	-0.0027 (-0.0091,0.0038)	**0.0047 (0.0001,0.009)**	0.0014 (-0.0008,0.0036)
log_sl_:Roads_start	0.0081 (-0.032,0.048)	-0.0016 (-0.027,0.023)	0.027 (-0.0078,0.061)	0.011 (-0.024, 0.046)	-0.017 (-0.047, 0.014)	**0.04 (0.0053,0.075)**	0.11 (-0.081,0.3)	9.2 (-0.63,19)	0.23 (-0.74,1.2)	-0.028 (-0.35, 0.3)
cos_ta_:Roads_start	-0.078 (-0.21,0.053)	**-0.1 (-0.18, -0.025)**	0.077 (-0.018,0.17)	0.048 (-0.056, 0.15)	0.075 (-0.018, 0.17)	**0.12 (0.021,0.22)**	-0.11 (-0.88,0.66)	0.43 (-4.4,5.3)	**3.7 (0.051,7.4)**	-0.19 (-1.3, 0.89)

Table 3.2: Wet season coefficient estimates (with 95% CI in parentheses) from integrated step selection functions fit to data from GPS collars of 10 individual cheetah (IDs along top row) in the Serengeti Ecosystem (2022-2024). Significant coefficients in bold. Anthropogenic and environmental variables were scaled and centred prior to analysis, so effect sizes are comparable.

	WET SEASON									
Variables	85317	85318	85319	85320	85325	85326	87963	87962	87961	87960
Bomas_end	0.97 (-0.15,2.1)	0.13 (-0.54, 0.81)	-0.53 (-3.1, 2.1)	-0.18 (-0.6, 0.25)	**3.2 (0.53, 5.9)**	0.3 (-0.11,0.7)	-0.29 (-1.1, 0.48)	**-0.99 (-1.7, -0.24)**	-1.1 (-2.4, 0.13)	4 (-0.55, 8.5)
Lodges_end	-0.32 (-0.65,0.011)	0.69 (-0.35, 1.7)	**-0.56 (-1.1, -0.044)**	0.084 (-0.23, 0.4)	**0.68 (0.1, 1.3)**	0.25 (-0.14,0.65)	-0.47 (-1.5, 0.59)	1.7 (-0.003, 3.5)	**5.6 (1.7, 9.4)**	-5.6 (-13, 1.8)
Roads_end	-0.15 (-0.5,0.2)	0.09 (-0.3, 0.48)	-0.061 (-0.35, 0.23)	0.1 (-0.22, 0.43)	**0.34 (0.078, 0.59)**	-0.0031 (-0.26,0.25)	-0.18 (-1.2, 0.86)	0.14 (-0.81, 1.1)	-1.1 (-3.3, 1.1)	**5 (2.3, 7.7)**
Woodycover	**0.25 (0.095,0.41)**	-0.23 (-0.57,0.11)	-0.1 (-0.24, 0.03)	0.0092 (-0.18, 0.19)	-0.0054 (-0.13, 0.12)	**0.2 (0.06, 0.33)**	0.096 (-0.24, 0.43)	0.36 (-0.41, 1.1)	-0.046 (-0.55, 0.45)	-1.3 (-2.7, 0.16)
Rivers	-0.09 (-0.24,0.055)	-0.087 (-0.35,0.18)	-0.2 (-0.41, 0.018)	0.062 (-0.1, 0.22)	**-0.18 (-0.36, -0.0048)**	-0.036 (-0.2,0.13)	0.16 (-0.38, 0.7)	0.083 (-0.4, 0.57)	**-0.43 (-0.66, -0.2)**	0.043 (-0.46, 0.54)
Slope	-0.081 (-0.28,0.12)	**0.41 (0.14, 0.69)**	0.057 (-0.13, 0.24)	-0.14 (-0.47,0.19)	-0.08 (-0.26, 0.096)	-0.021 (-0.14,0.098)	-0.2 (-0.51, 0.11)	**-0.35 (-0.6, -0.095)**	**-0.65 (-1.2, -0.088)**	**0.45 (0.11, 0.78)**
Ndvi	-0.089 (-0.25,0.077)	0.31 (-0.0052, 0.63)	-0.033 (-0.34, 0.27)	-0.12 (-0.45, 0.21)	**-0.62 (-0.91, -0.34)**	**0.19 (0.013, 0.37)**	**-0.31 (-0.56, -0.054)**	-0.013 (-0.28, 0.25)	-0.034 (-1, 0.96)	**-1 (-1.7, -0.37)**
DEM	-0.16 (-0.51,0.19)	-0.015 (-0.8, 0.78)	0.097 (-0.58, 0.78)	0.58 (-0.25, 1.4)	**0.59 (0.24, 0.94)**	0.16 (-0.26,0.58)	0.28 (-0.18, 0.73)	**0.47 (0.043, 0.89)**	-0.19 (-1.1, 0.72)	**1.2 (0.39, 2)**
Sl_	2.8e-06 (-0.0003,0.00027)	-0.00013 (-0.00035, 9.7e-05)	0.0012 (5e-04, 0.0018)	0.00025 (-9.3e-05, 0.00059)	0.00015 (-0.00072, 0.001)	**0.0002 (6.5e-05, 3e-04)**	-0.0005 (-0.001, 0.0006)	-0.0003 (-9e-04, 0.0002)	-0.003 (-0.006, -0.0003)	-0.00052 (-0.0018, 0.001)
log_sl_	**0.12 (0.014, 0.23)**	-0.0045 (-0.052, 0.043)	0.27 (-0.0073, 0.55)	0.019 (-0.075, 0.11)	0.25 (-0.05, 0.55)	**0.068 (0.019, 0.12)**	-0.064 (-0.27, 0.14)	0.1 (-0.026, 0.23)	**2.9 (1.1, 4.7)**	-0.071 (-0.55, 0.4)
cos_ta_	0.16 (-0.12, 0.44)	-0.097 (-0.25, 0.053)	0.019 (-0.61, 0.65)	0.038 (-0.22, 0.29)	-0.99 (-2, 0.00067)	**0.25 (0.12, 0.38)**	-0.33 (-0.95, 0.29)	**0.53 (0.082, 0.97)**	-0.23 (-2.6, 2.1)	0.88 (-0.47, 2.2)
sl_:Bomas_start	0.00015 (-2e-04, 5e-04)	-0.00018 (-0.00041, 5.2e-05)	-0.0013 (-0.0021, -5e-04)	0.00012 (-8e-05, 0.00032)	3.4e-05 (-0.00096, 0.001)	**0.00016 (8.7e-06, 0.00032)**	0.0002 (-0.0003, 0.001)	-0.00015 (-0.00055, 0.00024)	-0.00093 (-0.0034, 0.0015)	0.0053 (-0.0025, 0.013)
log_sl_:Bomas_start	-0.13 (-0.26, 0.0052)	0.0088 (-0.03, 0.054)	-0.25 (-0.56, 0.061)	-0.0062 (-0.055, 0.043)	-0.27 (-0.6, 0.052)	**0.074 (0.024, 0.12)**	-0.0055 (-0.13, 0.12)	0.045 (-0.049, 0.14)	1.1 (-0.011, 2.2)	**-4 (-7.6, -0.51)**
cos_ta_:Bomas_start	0.11 (-0.24, 0.47)	-0.0052 (-0.16, 0.15)	0.066 (-0.64, 0.77)	0.015 (-0.13, 0.16)	**1.2 (0.15, 2.3)**	**0.19 (0.033, 0.34)**	0.24 (-0.13, 0.6)	**0.47 (0.14, 0.8)**	-0.9 (-3.1, 1.3)	**10 (3.4, 18)**
sl_:Lodges_start	**0.00016 (2.3e-06, 0.00031)**	-0.00017 (-0.00053, 0.00019)	**-0.00016 (-0.0003, -3.5e-07)**	-6.4e-06 (-0.0002, 0.0002)	-2.8e-05 (-0.00018, 0.00013)	-0.00013 (-0.00034, 7.4e-05)	-0.0005 (-0.002, 0.001)	0.00041 (-6e-04, 0.0014)	0.0068 (-0.00032, 0.014)	-0.01 (-0.022, 0.0022)
log_sl_:Lodges_start	0.0064 (-0.028, 0.041)	0.0094 (-0.073, 0.092)	0.019 (-0.031, 0.068)	-0.019 (-0.057, 0.019)	-0.064 (-0.13, 0.0037)	-0.039 (-0.11, 0.033)	-0.045 (-0.25, 0.16)	-0.046 (-0.29, 0.19)	1.5 (-0.41, 3.5)	4.4 (-0.49, 9.2)
cos_ta_:Lodges_start	**0.21 (0.091, 0.33)**	0.035 (-0.23, 0.3)	0.072 (-0.056, 0.2)	-0.064 (-0.17, 0.047)	-0.091 (-0.3, 0.12)	0.015 (-0.21, 0.24)	-0.64 (-1.3, 0.05)	0.33 (-0.45, 1.1)	4.9 (-0.93, 11)	**-21 (-32, -9.4)**
sl_:Roads_start	-1.4e-05 (-0.00018, 0.00015)	-2.4e-05 (-0.00021, 0.00016)	-6.3e-06 (-0.00015, 0.00014)	0.00014 (-0.00018, 0.00045)	-1.2e-05 (-0.00011, 8.6e-05)	**-0.002 (-0.001, -2.2e-05)**	0.002 (-0.0005, 0.002)	0.00023 (-0.00024, 7e-04)	-0.00094 (-0.0058, 0.004)	**0.0042 (0.001, 0.0073)**
log_sl_:Roads_start	0.0063 (-0.038, 0.05)	0.032 (-0.00024, 0.064)	-0.002 (-0.047, 0.043)	0.039 (-0.032, 0.11)	-0.014 (-0.048, 0.021)	**0.075 (0.029, 0.12)**	0.12 (-0.078, 0.31)	0.051 (-0.037, 0.14)	-1.2 (-2.7, 0.3)	-0.48 (-1.4, 0.4)
cos_ta_:Roads_start	-0.1 (-0.25, 0.047)	0.02 (-0.084, 0.13)	0.0061 (-0.11, 0.12)	-0.015 (-0.22, 0.19)	**0.15 (0.028, 0.26)**	0.016 (-0.12, 0.16)	**0.89 (0.26, 1.5)**	0.0015 (-0.34, 0.34)	-2.9 (-6.8, 0.93)	**6 (3.3, 8.6)**

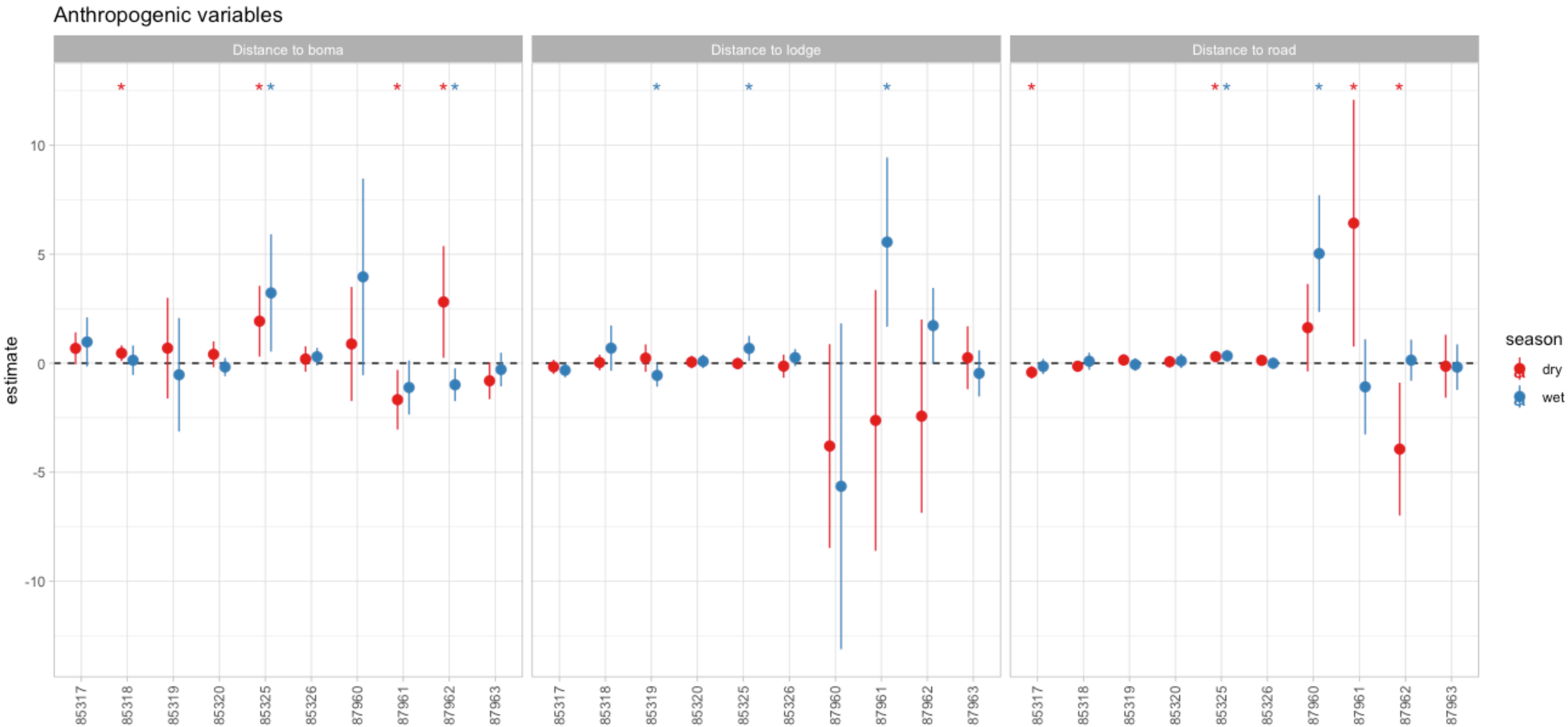


Figure 3.3: The estimated coefficients (with 95% CI) for the effects of anthropogenic variables on cheetah step selection in dry and wet seasons. Stars indicate significance at the p < 0.05 level, Red dots correspond to the dry season, Blue dots correspond to the wet season.

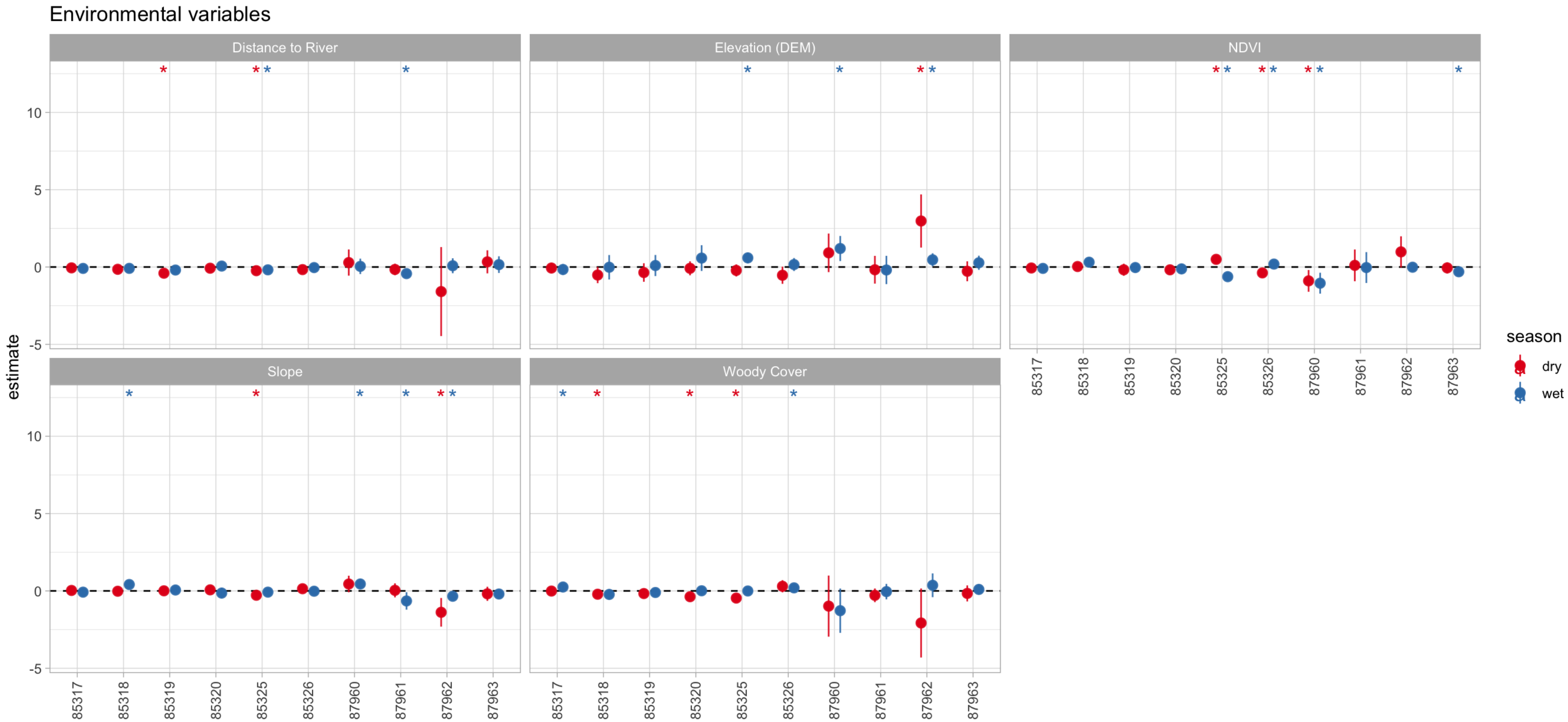


Figure 3.4: The estimated coefficients (with 95% CI) for the effects of environmental variables on cheetah step selection in dry and wet seasons. Stars indicate significance at the p < 0.05 level, Red dots correspond to the dry season, Blue dots correspond to the wet season.

3.4 Discussion

The movement patterns of large carnivores are shaped by a complex interplay of human activities and environmental features (Abrahms et al., 2016; Oriol-Cotterill et al., 2015). For cheetahs, whose survival depends on their ability to navigate vast landscapes while avoiding conflict with humans and other sympatric predators, understanding the impact of anthropogenic and environmental factors on movement is critical. This study investigated cheetah movement patterns in relation to human infrastructure (bomas, lodges and roads) and landscape features (slope, NDVI, woody cover, rivers and elevation), using integrated step selection functions to demonstrate how cheetahs respond to both human presence and environmental variability. The most important finding from this chapter is that cheetahs, on average, tended to avoid areas near bomas at the local scale of movement decisions, while their responses to other anthropogenic features such as lodges and roads were more variable across individuals. While Chapter 2 identified general habitat preferences using broader-scale resource selection models, this chapter builds on those findings by revealing how cheetahs respond to specific features in real time, as they move through the landscape. This finer-scale approach captures immediate decision-making and behavioural flexibility, offering a more detailed understanding of how human activities influence movement patterns on the ground.

3.4.1 Anthropogenic covariates

Cheetahs exhibited strong but variable avoidance of bomas, particularly during the dry season. This population-level pattern, evidenced by positive responses to distance to bomas, may reflect increased direct harassment by herders and herder dogs, disturbances due to noise and smell of livestock herding activities, and indirect displacement of prey and water caused by herding activities. This result aligns with studies on other carnivores, such as lions and African wild dogs, which similarly show animals avoiding settlements to minimize conflict and retaliatory killings (Abrahms et al., 2016; Oriol-Cotterill et al., 2015). Notably, this avoidance was more pronounced in the dry season, likely due to increased Maasai incursions into the core protected areas during this season (Minja et al., 2025, *in review*). Not all individuals showed negative effects of bomas, and this variable response may imply that there are some benefits of being close to bomas, such as being a source of prey and of providing a human shield for large conflict with lions and hyenas.

Intriguingly, it may also indicate that there may be personality differences between different individuals, with some individuals being bolder than others (Greenberg & Holekamp, 2017; Harris & Knowlton, 2001; Heffernan et al., 2007). Nonetheless, our overall findings underscore the need for conservation strategies that mitigate human-wildlife conflict in areas of overlap between pastoralist activities and cheetah habitat.

Response to lodges was more nuanced, with cheetahs showing seasonal variability and, in some cases, a neutral effect. During the dry season, individuals like 87960 selected areas near lodges, possibly due to reduced human disturbances during the low tourism season (Figure 3.3). In contrast, during the wet season, which coincides with peak tourism, several individuals, including 85325 and 87961, avoided lodges. These tourism facilities are located in resource-rich areas, such as rivers and lakes, which are attractive to wildlife, including cheetah prey. As a result, any avoidance of these areas indicates a stronger impact of human activities than might initially be assumed. Increased tourism activity during this period, such as vehicle traffic, dust, noise from lodges, and prey disturbances, likely disrupts cheetah space use. This simultaneous attraction to and avoidance of high-quality habitats reflects a duality often observed in other species, where wildlife are drawn to resource-rich areas but adjust their behaviour or distribution in response to human activity levels. For example, brown bears exhibit increased avoidance of human infrastructure during periods of heightened human activity (Thorsen et al., 2022). Similarly, mountain ungulates in the Alps shift their habitat use in response to ski resorts and other recreational infrastructure, highlighting how cumulative human activities impact wildlife distribution (Naylor et al., 2009). These findings emphasize the importance of managing tourism activities (including facilities) to minimize disturbances during sensitive periods such as peak tourism season, particularly in areas of high cheetah density.

Roads elicited mixed responses from cheetahs, highlighting the role of individual behaviour and ecological context. Some individuals, such as 87962 and 85317, selected areas near roads, while others, including 85320 and 85325, actively avoided them (Figure 3.3). The former individuals were denning at the time, consistent with findings by Durant (1998), who demonstrated that cheetahs often accept suboptimal habitats when lactating, as their restricted mobility requires them to return to the den site daily. Nonetheless, this variability is also consistent with findings in African wild dogs, which use low-traffic roads for efficient travel but avoid high-traffic roads due to disturbance and increased mortality risks (Abrahms et al., 2016). Similarly, lions in the Ruaha-Rungwa landscape adapted their road use to avoid human activity during periods of high traffic, highlighting the context-dependent nature of road impacts (Searle et al., 2021). Studies on brown bears in North America and Europe have also documented variable responses, with some individuals using roads as travel corridors while others avoid them, influenced by factors such as traffic volume, road type, and proximity to human settlements (Northrup et al., 2012; Thorsen et al., 2022).

3.4.2 Environmental covariates

During the dry season, cheetahs in this study largely avoided areas with dense woody cover, a pattern that contrasts with findings by Durant (1998), who observed cheetahs using woody habitats more frequently in the dry season as prey species retreated into these areas following the departure of the wildebeest migration. This discrepancy may suggest that other factors, such as human activity, could influence cheetah habitat use in this region. Open plains, while offering better hunting visibility, may also expose cheetahs to increased tourist pressure, potentially altering their behaviour. Cheetahs use trees along the woodland edge for resting during the day to avoid heat and reduce exposure to predators (Bissett & Bernard, 2007), however, they predominantly move to open areas for other activities, such as hunting. This shift toward open habitats exerted by 85318, 85320 and 85325 may be due to enhanced visibility for prey detection and facilitate high-speed pursuits, a strategy also observed in cheetahs in South Africa and Botswana, where preferences for open grasslands were linked to optimized hunting opportunities (Mills et al., 2004; Wilson et al., 2013).

Conversely, in the wet season, cheetahs tended to select areas with more woody cover. This behaviour was particularly evident in individuals 85326 and 85317 and supports findings suggesting that dense vegetation provides essential resources, including shade, reduced predator encounters, and opportunities for scent-marking (Bissett & Bernard, 2007; Broomhall et al., 2003). Furthermore, enclosed habitats may lower the risk of kleptoparasitism by reducing visibility to scavengers such as lions and hyenas (Hayward & Kerley, 2005; Hunter et al., 2007). These seasonal variations in habitat selection highlight the ecological flexibility of cheetahs in adapting to dynamic landscapes, likely influenced by the dual pressures of resource acquisition and risk avoidance, with tourism activities potentially playing a significant role.

Slope significantly influenced cheetah movement, with negative coefficients reflecting their avoidance of steep terrains. Steep slopes impose greater energetic costs during movement and restrict cheetahs' ability to maintain the high speeds required during hunting (Klaassen & Broekhuis, 2018). This was evident in individuals like 85325, 87961, and 87962, who showed pronounced avoidance of steeper slopes across different seasons (Figure 3.4). Tagwireyi et al. (2020) similarly observed subtle avoidance of steep slopes by cheetahs in Gonarezhou National Park but noted that other factors, such as prey availability, played a more prominent role in shaping their spatial distribution. Supporting this, Moqanaki & Cushman (2017) found that Asiatic cheetahs in Iran preferred moderately rugged terrain, such as hilly areas and eroded foothills, while avoiding both flat and very steep landscapes. These findings emphasize that topographical complexity can provide optimal conditions for cheetah movement and hunting efficiency by reducing energetic costs and enhancing connectivity within landscapes.

Seasonal preferences for elevation further illustrate the ecological flexibility of cheetahs. In the wet season, cheetahs largely selected higher elevations compared to the dry season (Figure 3.4). Elevated terrains also provide strategic advantages in detecting prey and avoiding encounters with dominant predators. Similar preferences for elevated habitats have been observed in cheetahs in Gonarezhou National Park, Zimbabwe, and other predators that benefit from vantage points in complex landscapes (Tagwireyi et al., 2020). The preference for lowlands during the dry season aligns with observations by Welch et al. (2015), who found cheetahs more commonly occupying lower elevations, likely due to improved prey availability and more favourable temperatures. Similarly, Durant (1998) reported that cheetahs concentrated around river valleys during the dry season, where prey gathered near remaining water sources and grazing resources.

NDVI, an indicator of vegetation greenness, exhibited varying effects on cheetah step selection. Negative coefficients in individuals such as 87960, 87963, 85326, and 85325 indicated avoidance of areas with higher vegetation greenness (Figure 3.4). This behaviour may stem from the presence of dense prey populations in such areas, which, while providing abundant hunting opportunities, also attract larger predators like lions and hyenas (Durant, 2000b; Durant et al., 1988) The increased competition and predation risks in these predator-dense regions likely drive cheetahs to select habitats with lower prey densities, balancing hunting opportunities with minimizing chances of losing their kills.

Proximity to rivers had mixed effects across individuals, with some showing significant selection for areas closer to rivers in both dry and wet seasons, while others displayed no notable response. This variability could reflect a correlation with elevation, as cheetahs may prefer lowland areas in river valleys for hunting but avoid areas immediately near water where lions and other predators may concentrate (Figure 3.4). This variability suggests that the relationship between cheetah movement and distance to rivers may be influenced by individual-specific factors or local ecological conditions. In some cases, selection for areas near rivers could be linked to prey availability, as these areas are resource rich. However, avoidance behaviour in others might reflect the risks posed by higher densities of dominant predators, such as lions and hyenas, which also congregate near rivers (Durant et al., 1988; Hayward & Kerley, 2005). This complex dynamic underscores the trade-offs cheetahs face between resource acquisition and predator avoidance.

3.5 Conclusion

3.5.1 Individual Variability in Responses to Anthropogenic Factors

The observed variability in individual responses to anthropogenic factors in our study highlights the complexity of cheetah behaviour and the challenges in predicting population-level impacts. While some individuals showed strong avoidance or behavioural shifts in the presence of humans or human-related activities, others appeared to tolerate human impacts. This variability could stem from differences in past experiences, heritable characteristics or social contexts, none of which were directly measurable in our study.

It is plausible that some cheetahs exhibiting strong responses had previous negative encounters with humans or vehicles, such as harassment or disturbances, which may have heightened their sensitivity to these stimuli. Conversely, individuals showing no discernible responses might have habituated to human presence, never experienced such adverse interactions, or possess different underlying personalities. While a majority of individuals showed limited responses, even a small subset of the population demonstrating strong behavioural shifts could have significant implications. For a rare and sensitive species like the cheetah, population-level consequences might arise if such behaviours lead to reduced fitness, altered habitat use, or diminished hunting success.

Finally, it is important to acknowledge caveats in interpreting these results. The study's temporal and spatial scope may not fully capture the nuances of individual behavioural adaptation over time. Additionally, our inability to account for individual histories limits our understanding of the root causes of observed individual behaviour variability. Future studies combining the long-term monitoring information from studies such as the Serengeti Cheetah Project with genetic analyses could shed light on these dynamics.

3.5.2 Conservation Implications and Strategies

The observed patterns emphasize the flexible strategies cheetahs employ to navigate landscapes shaped by human activities and environmental variability. Avoidance of bomas, dense woody cover, and steep slopes highlights the critical role of open, low-disturbance habitats in maintaining cheetah populations. Similarly, the variable effects of lodges and roads suggest that human infrastructure should be carefully managed to minimize its impact on cheetah movement. Seasonal dynamics in responses to rivers and elevation further underscore the need for spatially and temporally informed conservation strategies. For example, during the dry season, cheetahs may rely on areas that retain water and attract prey. Conservation actions could include ensuring the protection of critical water sources, such as marshy areas and lakes in Ndutu, and reducing human disturbances, such as livestock grazing in these areas during dry months. Similarly, in the wet season, cheetahs may move to higher elevations to avoid disturbances from tour cars, high densities of wildebeest, and other migrating wildlife across the Ndutu plains. Additionally, they may be displaced from open areas due to their high visibility, which increases the likelihood of harassment. Identifying and safeguarding these seasonally preferred habitats, as well as mitigating potential conflicts with human activities like grazing or settlement expansion in higher-elevation zones, is vital.

Managing human-carnivore conflict through community engagement and improved livestock practices could also significantly reduce disturbances in key cheetah habitats. Measures such as predator-proof enclosures (e.g., chain-link fences with mesh roofing to prevent predator access), proper night-time kraaling of livestock, and deploying guard animals like trained dogs can help deter predators and reduce livestock loss. Supporting community-led grazing management plans, such as designated grazing zones and rotational grazing systems, can help balance the needs of livestock herding with wildlife conservation. During severe dry seasons, bottlenecks often arise, and land managers could collaborate with communities to establish set-aside grazing areas that provide a vital resource during drought years.

Preserving open landscapes and maintaining connectivity between habitats are essential for supporting cheetah movement, hunting, and overall survival. To address the issue of Maasai incursions into protected areas, collaborative efforts involving park authorities and local communities are essential. Establishing buffer zones around protected areas, where controlled grazing is permitted, could reduce pressures on core cheetah habitats. Additionally, regulated tourism infrastructure and road development is necessary to prevent further habitat fragmentation caused by increased human activity.

Given the variability in cheetah personality and individual responses to environmental features, conservation strategies should adopt species-specific and context-sensitive approaches. These measures could include limiting road expansion and regulating traffic in core cheetah habitats. Collaborative efforts between conservationists, local authorities, Maasai communities, and the tourism sector are essential to achieve a sustainable balance between development, tourism activities, pastoralism, and the conservation of cheetahs and other sympatric carnivores.

3.5.3 Future Work

Future research should explore how diel activity patterns influence cheetah responses to human infrastructure and environmental features. Incorporating accelerometer data, prey dynamics and other predator densities and movement would provide deeper insights into the drivers of cheetah habitat selection. Long-term studies monitoring changes in habitat use in response to expand infrastructure and climate variability are also essential for predicting and mitigating future challenges to cheetah conservation and for understanding how past experiences of cheetah shape their future responses.

Figure 3.5: A cheetah relocating her cubs from an unoccupied Maasai boma in Ndutu after being harassed by tour cars.

4 Tourism activity effects on cheetah hunting success

Abstract

Tourism activities, while supporting conservation through funding and awareness, may often disrupt wildlife behaviour. This study investigates the impact of tourist vehicle presence on cheetah (*Acinonyx jubatus*) hunting success in the southeastern Serengeti ecosystem. Over 110 hours of observations, including 6,600 sample points, revealed that cheetah hunting behaviour is significantly influenced by tourism-related disturbances. Generalized Linear Mixed Models (GLMMs) demonstrated a strong negative relationship between vehicle presence and hunting probability, with hunting likelihood dropping from 20% in the absence of vehicles to nearly 0% when vehicles were present. Additionally, engine noise was a critical predictor, with hunting probability declining sharply as the number of running engines increased. Behavioural shifts were also evident, with cheetahs displaying passive behaviours, such as lying down or sitting up, in response to vehicles. These disturbances mimic predation risk, causing cheetahs to conserve energy and abandon hunting efforts, similar to avoidance behaviours exhibited around dominant predators. The demographic consequences of these disturbances, including reduced hunting success and potential impacts on cub recruitment, underline the long-term risks to cheetah population viability. This study underscores the urgent need for integrated conservation strategies. Recommended measures include limiting the number of vehicles near hunting cheetahs, reducing engine noise by mandating engine shutdowns during stops, enforcing minimum distance regulations, and establishing robust reporting systems for wildlife harassment.

4.1 Introduction

Anthropogenic activities exert profound impacts on large carnivores by influencing their behaviour, distribution, and survival (Graham et al., 2005). The expansion of tourism, urban development, and agriculture has resulted in habitat fragmentation and increased human-wildlife interactions. Such disturbances can lead to habitat avoidance, changes in daily activity patterns, and increased stress levels for large carnivores like lions, leopards, spotted hyenas and cheetahs (Ripple et al., 2014). Tourism, particularly in protected areas, has a unique dual role: it supports conservation efforts through funding and education (Buckley, 2011), but at the same time it can disrupt natural behaviours of animals around humans by reducing their fearfulness and antipredator responses towards humans (Geffroy et al., 2015).

There is growing evidence of the diverse ways in which tourism impacts large carnivores and other wildlife. For instance, tourist activities can disrupt natural behaviours, leading to changes in stress levels and body condition. Brown bears, for example, have been observed to alter their foraging behaviour and reduce food intake when exposed to tourism activities (Rode et al., 2006). Similarly, dolphins are known to decrease their resting time and stay active longer in the presence of tourist boats, which can disrupt their natural activity patterns (Constantine et al., 2004). In African ecosystems, lions have been reported to show increased stress indicators, such as higher breathing rates and disturbance behaviours, when tourists are present, suggesting that even habituated animals are affected by close human observation (Hayward & Hayward, 2009). The examples above demonstrate that tourism affects both predators and their prey, often in interconnected ways. For instance, snowmobile tourism has been shown to elevate stress levels in wolves, a top predator, and elk, their prey, underscoring the ripple effects of human activities on entire ecosystems (Creel et al., 2002).

Large carnivores, despite being key attractions for tourism and generating significant revenue that supports conservation efforts (Di Minin et al., 2013; Goodwin & Leader-Williams, 2000), also play a vital ecological role in structuring ecosystems. Through their influence on prey behaviour and distribution, often referred to as the "landscape of fear", they can shape habitat use, prevent overgrazing, and support plant diversity, which in turn benefits a wide array of other species. For example, in North American forests, wolves influence deer movement and foraging patterns, contributing to the maintenance of forest structure and biodiversity (Ripple et al., 2014). In African savannas, lions' predation on large herbivores like wildebeest and zebra affects their distribution and grazing patterns, which shapes vegetation cover and influences the habitat availability for other species (Estes et al., 2011). Apex predators contribute to maintaining ecological balance, but their interactions within ecosystems are influenced by a range of natural and anthropogenic factors (Everatt et al., 2015; Ripple et al., 2014). These predators can exert significant pressure on subordinate carnivores by competing for prey and through behaviours such as kleptoparasitism (Hunter et al., 2007). These multiple and diverse natural interspecies interactions can be significantly altered by human presence, which may particularly affect shy or easily displaced species like cheetahs. Cheetahs, for instance, occur at lower densities due to their need to range widely to avoid dominant predators like lions and hyenas, making them particularly vulnerable to human impacts (Durant, 2000b). Their sensitivity to threats, which is crucial for avoiding confrontations with dominant predators, may also heighten their perception of humans as a threat, leading to avoidance behaviours and altered habitat use. This heightened sensitivity, combined with their low population densities, increases their susceptibility to human disturbances such as tourism, habitat fragmentation, and human-wildlife conflict. As a result, these factors can significantly influence their movement, hunting success, and ultimately their survival, posing unique challenges for their conservation.

Cheetahs are highly specialised hunters, equipped with adaptations for speed and stealth (Laurenson & Caro, 1994; Wilson et al., 2018). Their hunting success relies heavily on their ability to approach prey within a close range before initiating a high-speed chase (Hilborn et al., 2012). Despite their adaptations, cheetahs are vulnerable to losing their kills to other predators (Laurenson & Caro, 1994). Studies show that cheetahs frequently abandon hunts or vacate kill sites early when dominant carnivores are present, as competition from the other sympatric predators compels them to prioritise survival over feeding (Hunter et al., 2007). Predator avoidance behaviour is thus a critical component of cheetah ecology, influencing both their hunting success and spatial distribution within the ecosystem. Durant (2000b) demonstrated that cheetahs actively avoid areas where they can detect the presence of lions or hyenas through sight and/or sound. This predator-sensitive foraging behaviour was demonstrated through audio playback experiments in which cheetahs exhibited clear avoidance in response to lion and hyena sounds (Durant, 2000b). Human activities add another layer of complexity to cheetah behaviour (Durant et al., 2017).

Human disturbances pose significant challenges to cheetahs due to their diurnal activity patterns, which set them apart from most other large carnivores that are primarily nocturnal or crepuscular. Their need to closely stalk prey before initiating a chase (Laurenson & Caro, 1994) makes them particularly vulnerable to disruptions caused by tourist activities. Unlike other large carnivores that might become habituated to human presence, cheetahs exhibit heightened sensitivity and avoidance behaviours in response to such disturbances. Even cheetahs that appear calm and habituated to tourists can alter their behaviour due to the disruptions caused by tourist vehicles. For instance, tourists might alter cheetah behaviour such as hunting time or prey handling times and this could have demographic consequences on recruitment or cub survival (Broekhuis, 2018). Another study by Rönn (2002) analysed the influence of tourist vehicles on cheetah behaviour, specifically examining how the number of vehicles and their proximity affected the animals. The findings indicated that behaviours such as movement and resting were significantly impacted by tourist presence. Cheetahs tended to move less when vehicles were nearby. Additionally, when vehicles approached within 30 meters, cheetahs would stop moving and lie down more frequently, suggesting increased stress levels. When vehicles got as close as 5 m or less the situation became too stressful and cheetahs started to move again, trying to get away from that stressful situation (Rönn, 2002). While there is growing evidence that tourism can influence large carnivore behaviour - such as changes in movement, vigilance, or denning patterns - the specific effects of tourism on cheetah hunting behaviour in the wild remain poorly understood. In particular, it is unclear how factors like vehicle presence, engine noise, or tourist proximity influence hunting initiation, success, or abandonment in real time.

By conducting hour-long follows of cheetahs during their peak activity periods in the morning, this study aimed to build on existing research by examining the effects of varying levels of human disturbances on cheetah hunting processes in the southeastern boundaries of Serengeti National Park. Specifically, we examined the hypothesis that cheetahs would minimise their hunting activities when tour cars are around and be more active in the absence of the cars. This study also aimed to assess whether there were thresholds of tour car presence that significantly suppress cheetah hunting decisions and other behavioural activities, with the goal of developing recommendations to the impact of tourism activities on wildlife.

4.2 Materials and methods

4.2.1 Study area

This study focused on how tourism activities influence cheetah hunting success in the southeastern periphery of the Serengeti ecosystem, encompassing Southern Serengeti National Park (SNP), Makao Wildlife Management Area (MWMA), Maswa Game Reserve (MGR), and the Ndutu area within the Ngorongoro Conservation Area (NCA) (Figure 1). The study area spans a gradient of habitats, from short grasslands to savanna woodlands, shaped by annual precipitation patterns ranging from 600 to 1,150 mm (Bartzke et al., 2018; Holdo et al., 2009a). The MWMA, established in 2009, serves as a critical wildlife corridor linking MGR, NCA, and SNP. Its landscape is influenced by agriculture and livestock grazing, activities that can impact wildlife movement and behaviour (Lwankomezi et al., 2023). Similarly, Maswa Game Reserve, a 2,200 square kilometres area bordering SNP, functions as a buffer zone, with controlled human activities such as regulated hunting and grazing permitted.

The Ndutu region, within the NCA, forms an integral part of this study area and represents a unique interface between wildlife and human activity. The NCA supports an estimated population of 100,000 people, including both indigenous Maasai and Datoga communities as well as non-indigenous residents. These communities engage in livestock keeping, with animals such as camels, cattle, goats, and sheep commonly seen across the landscape (Yamat, 2018). The NCA is also a hub for tourism activities, with tour vehicles being particularly abundant during the wet season. These vehicles, along with human activities like grazing and small-scale agriculture, introduce anthropogenic pressures that may shape cheetah hunting behaviour and foraging success.

Management practices across the study area vary: SNP enforces strict wildlife conservation policies with minimal human interference, while the MWMA and MGR permit controlled activities like grazing and trophy hunting, and the NCA supports coexistence of wildlife and humans through regulated use of natural resources. This complex mosaic of habitats, management practices, and human influences provides a useful opportunity for exploring the impacts of tourism activities on cheetah behaviour.

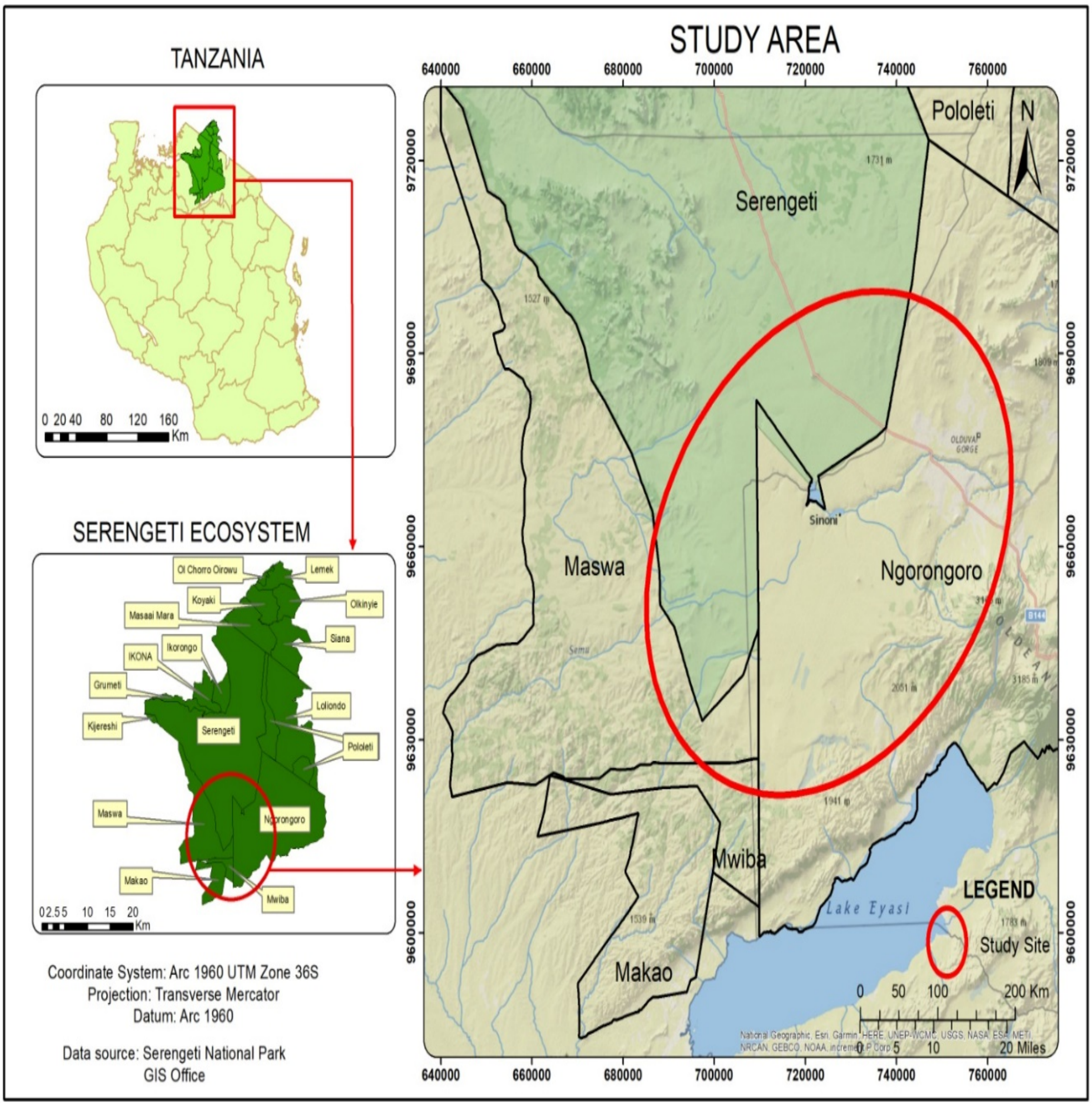


Figure 4.1: Map of the study area within the Serengeti ecosystem where all observational data was collected.

4.2.2 Data collection

4.2.2.1 Cheetah collaring

A total of ten cheetahs were fitted with VERTEX Lite - 1C IRIDIUM collars from Vectronics and were followed on the ground between the period of January 2023 and June 2024. The collars featured a 3-axis activity sensor, a temperature sensor, a mortality sensor, a VHF beacon, and an Iridium module. Among these ten collared cheetahs, we managed to locate and follow on the ground nine individuals to collect observational behaviour data; one cheetah lived in inaccessible areas away from tourism activity. To collar the cheetahs, veterinarians from the Tanzania Wildlife Research Institute and the NCA used tranquilizer darts, administering a combination of Ketamine (100mg) and Medetomidine (2mg), or Medetomidine (2mg) and Zoletil (50mg). Immobilizations were performed from a close distance of 10-15 meters, aiming for the main muscles of the rump or shoulder while cheetahs were inactive. The effects of the drugs were counteracted using Atipamezole (2.5mg) or Yohimbine (6.25mg) after an hour of anaesthesia, ensuring complete recovery without signs of discomfort. The darting procedures were approved by the ethics committee for animal research at the Zoological Society of London, ZSL and the Tanzania Wildlife Research Institute, TAWIRI. Each cheetah was monitored for at least three days post-collaring to ensure that there were no adverse side effects. Each collar weighed 400 grams, equivalent to 1.1% of the average female cheetah's body weight were selected to minimise any potential impact on the animals' behaviour (Laurenson & Caro, 1994).

Figure 4.2: Indi with her three sub adult cubs, one of the ten GPS radio collared female cheetahs, photographed eating a young wildebeest after a successful hunt.

4.2.3 Tourism covariates and behavioural observations

In this study, we examined the impact of tourism on cheetah hunting behaviour. We used each cheetah's 6:00 am GPS location as a reference point to locate individuals in the field. Once located, we employed instantaneous sampling techniques to record behavioural and tourism-related observations at one-minute intervals over two-hour sessions (Bateson, 2017). These observations included the number of tourist vehicles within proximity, their distance from the cheetah, the presence of people standing on vehicle roofs, and any loud human noises.

To assess the effects of tourism on hunting, we carefully documented each hunting attempt, recording its outcome (successful or unsuccessful), duration, GPS location, and distance covered. None of the cheetahs were on kills when first located. Hunting behaviour was defined as a sequence of activities that included stalking (slow, low movement toward prey), chasing (rapid pursuit of prey), and eating (consumption of prey post-capture). These behavioural categories were defined according to established ethological principles, ensuring consistency with prior studies on large carnivore hunting behaviour (Caro, 1994). To minimise observer effects on cheetah behaviour, all data were collected from stationary vehicles positioned at a non-intrusive distance using binoculars. This approach ensured that the presence of the researcher did not confound the assessment of how tourism affected natural hunting behaviour.

4.2.4 Analysis

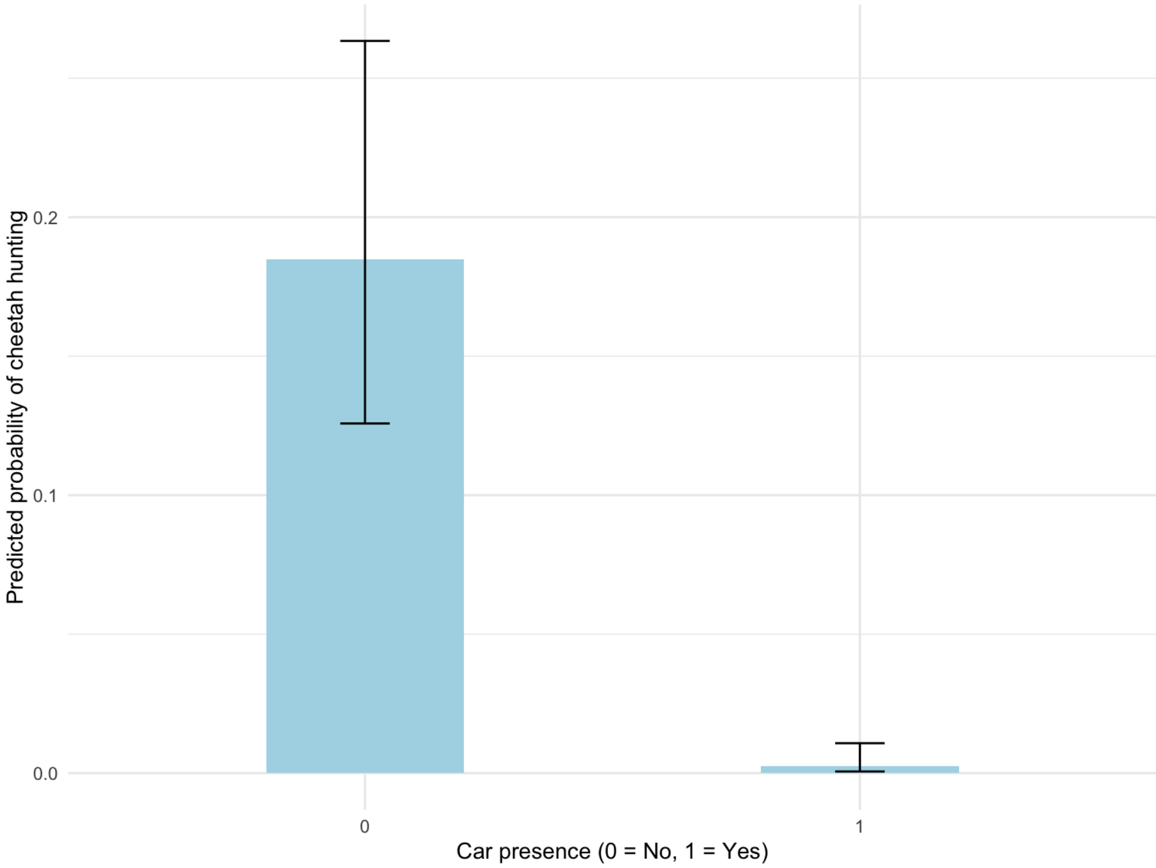
Our analysis focused on cheetah hunting behaviour in relation to tour car presence. Collar ID and cheetah activity were treated as factors and cheetah activities were recoded into 4 descriptive categories: lying down, walking, sitting up, and eating (as a result of a successful hunting). To explore factors influencing cheetah behaviour, we summarised the data by creating a subset of data which contained the events of car presence/absence and observation of a cheetah with a kill or without a kill. All statistical analyses were performed using R software (version 4.4.1). All variables were standardised, and collinearity was assessed using a correlation matrix. Car presence was highly correlated with car distance, and engine running was highly correlated with engine start. To avoid multicollinearity, car distance and engine start were excluded from the models. To assess how cheetah hunting behaviour was influenced by vehicle-related disturbance, we fitted a binomial Generalised Linear Mixed Model (GLMM) using the *glmer()* function. Hunting (Yes/No) was used as the response variable, with car presence, engine running, and people on the roofs included as fixed effects. Cheetah ID was added as a random effect to account for individual variation. In a separate analysis, a multinomial logistic regression was used to model the effect of car presence on broader cheetah activity categories, including lying head up, sitting up, walking, running, and eating. This analysis aimed to evaluate shifts in activity patterns in relation to the presence or absence of cars, offering a more detailed understanding of cheetah behavioural responses to human disturbance.

4.3 Results

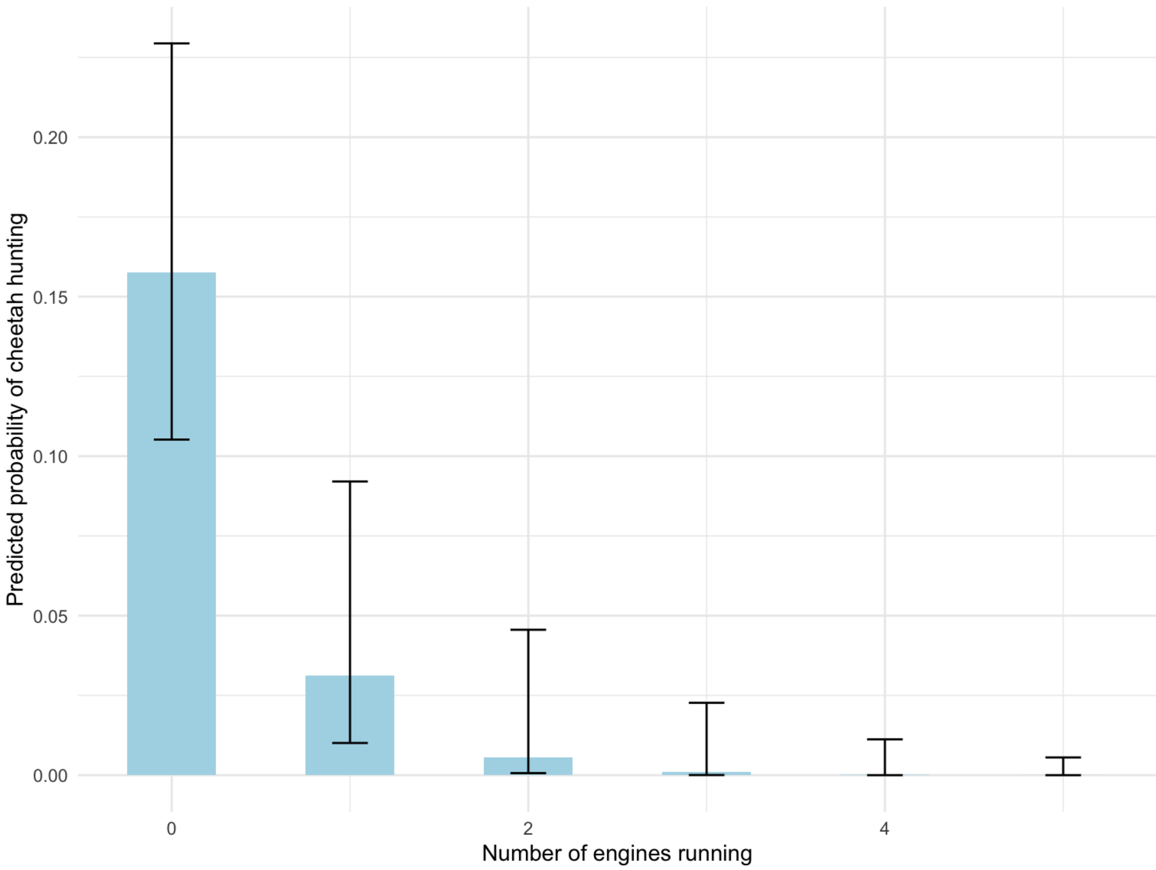
4.3.1 The influence of Tourism on Cheetah Feeding Behaviour

A total of 110 hours of cheetah observations were recorded, with 97.52 hours (88.7%) spent in the absence of tourists and 12.48 hours (11.3%) in their presence. This yielded 6,600 sample points, with 5,851 points (88.7%) recorded in the absence of tourists and 749 points (11.3%) in their presence. The GLMM analysis revealed a significant negative relationship between the presence of tourist vehicles and the probability of cheetahs engaging in hunting ($\beta = -5.22$, $p < 0.001$; Table 1). The predicted probability of a cheetah hunting was approximately 20% in the absence of vehicles, but this dropped to nearly 0% when tourist vehicles were present (Figure 4.3.a). Similarly, the number of engines running was found to be a significant predictor of cheetah hunting behaviour ($\beta = -1.77$, $p < 0.001$; Table 2). When no engines were running, the predicted hunting probability remained around 20%, but as the number of engines increased, hunting probability dropped sharply, reaching nearly 0% with five or more engines running (Figure 4.3.b). In the presence of vehicles, cheetahs were more likely to exhibit passive behaviours, such as lying down or sitting up, rather than engaging in active behaviours like hunting (Figure 4.3.c). Model comparisons indicated that excluding the variable "people on the roof" resulted in a better model fit, as evidenced by a lower AIC value compared to the full model. To visualise the distribution of observation effort and vehicle presence across time, a stacked bar chart was plotted to show total observation hours per month, divided into sessions with and without tourist vehicles present (Figure 4.3.d).

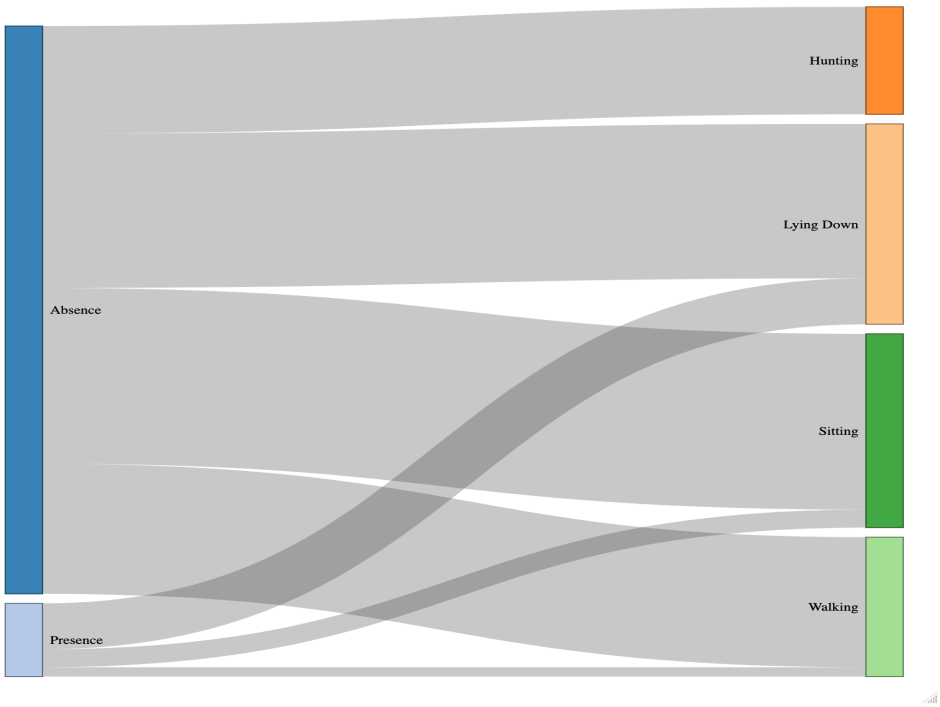
(a)


Predicted probability of cheetah hunting
0.2
0.1
0.0
0
1
Car presence (0 = No, 1 = Yes)

(b)


Predicted probability of cheetah hunting
0.20
0.15
0.10
0.05
0.00
0
2
4
Number of engines running

(c)



(d)

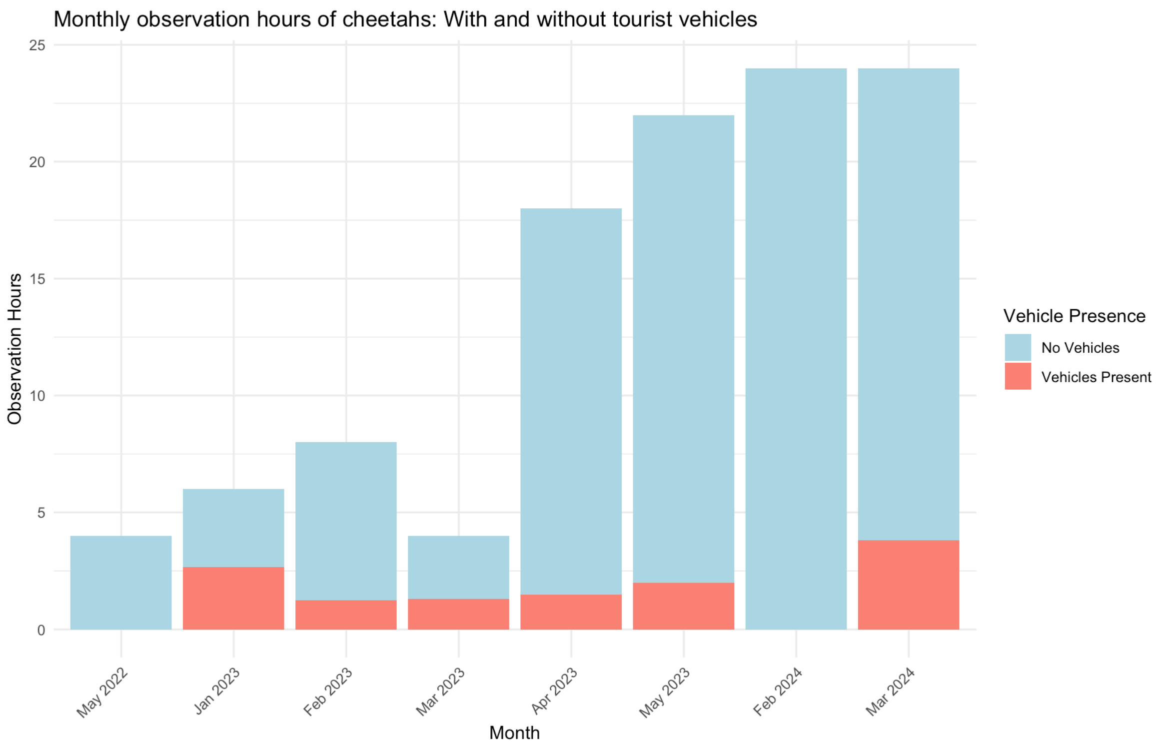


Figure 4.3: (a) Predicted probability of cheetah hunting in relation to tourist vehicle presence, (b) Predicted probability of cheetah hunting in relation to the number of engines running, (c) Sankey diagram illustrating the effect of tour car presence/absence (left) on cheetah behaviour shifts (right), (d) Stacked bar chart showing monthly observation hours of cheetahs divided by presence and absence of tourist vehicles.

Table 4.1: Coefficient estimates of the car presence in relation to cheetah behaviour Serengeti, Tanzania.

Covariates	Estimate	Standard error	Z value	P value
Intercept	-1.472	0.235	-6.273	<0.001
Car presence	-5.224	0.972	-5.374	<0.001

Table 4.2: Coefficient estimates of the engine running in relation to cheetah behaviour Serengeti, Tanzania.

Covariates	Estimate	Standard error	Z value	P value
Intercept	-1.666	0.239	-6.971	<0.001
Engines running	-1.772	0.538	-3.295	<0.001

4.4 Discussion

This study provide compelling evidence that tourism activities negatively impact cheetah behaviour, particularly their hunting activities. When tourist vehicles were present, cheetahs significantly reduced their hunting efforts, often stopping altogether, and became less active overall. Additionally, engine noise exacerbated these effects; the more engines were running, the less likely cheetahs were to engage in hunting activities. These disturbances may trigger avoidance behaviours similar to those employed by cheetahs to evade dominant predators like lions and hyenas. The noise and movement of tourist vehicles could be perceived as a threat, mimicking the presence of other sympatric predators and prompting cheetahs to modify their behaviour accordingly (Durant, 2000a).

Frid & Dill (2002) explored how human-caused disturbances act as a form of predation risk, with wildlife often responding to human activities in a way that mirrors their responses to natural predators. The study introduced the “risk-disturbance” hypothesis, suggesting that wildlife perceives non-lethal disturbances, such as noise, vehicles, or human presence, as potential threats, prompting avoidance behaviours like fleeing, vigilance, and changes in habitat selection. These responses can have direct fitness costs, such as reduced feeding time or increased energy expenditure. In the context of this study, the presence of humans, particularly tourists around cheetahs can be seen as analogous to predation risk. Cheetahs may engage in risk-avoidance behaviours, such as reducing their hunting activity, in response to perceived threats from human disturbances. However, rather than fleeing, they often conserve energy and rest, waiting for vehicles to leave before resuming their activities.

Nonetheless, the findings of this study demonstrate that cheetah behaviour is significantly influenced by the presence of tourist vehicles, leading to reduced hunting activities. This aligns with patterns observed in other species. For instance, Hebblewhite et al. (2005) found that in Banff National Park, high levels of human activity led to the partial exclusion of wolves, altering the behaviour of prey species like elk. This example highlights how intense human presence can cause top predators to abandon certain areas, similar to how cheetahs may alter their movements to avoid tourist hotspots (Minja et al., 2025. *in review*). Likewise, Nevin & Gilbert (2005) observed that brown bears in ecotourism areas changed their foraging and resting behaviours to minimise human contact, a pattern that resonates with our findings. Geffroy et al. (2015) demonstrated that large mammals may even modify their activity patterns, becoming more nocturnal to avoid human disturbances. Ciuti et al. (2012) also showed that human disturbances can have more significant effects on animal behaviour than natural predators, underscoring that tourist presence can disrupt cheetahs' ability to hunt effectively and suggesting a substantial negative impact on their foraging efficiency.

The effects of human presence on wildlife behaviour are not always uniformly negative. Shannon et al. (2014) found that ungulates in Grand Teton National Park used areas with higher human activity as refuges from predators, illustrating the 'predator shelter hypothesis. Similarly, there have been anecdotal reports of cheetahs using tour vehicles as cover to approach prey, suggesting that, in certain situations, human presence could have a positive impact on hunting success. Nevertheless, even if this occurs, our findings show that the overall impact of human disturbances is substantially negative, with significant reductions in cheetah foraging rates when tourist vehicles are present.

Moreover, the demographic consequences of reduced foraging opportunities due to non-lethal disturbances are profound, extending beyond immediate dietary impacts to affect long-term population dynamics. The study by Broekhuis (2018) indicates that high tourist activity in cheetah habitats correlates with significantly reduced cub recruitment. This reduction is particularly evident in areas with heavy tourism, where disturbances from vehicles not only decrease hunting success but also impact cub survival rates. Lactating females with cubs in the den face high energetic costs, which drives them to increase their hunting success and focus on larger prey (Laurenson 1995), however, if they were unable to meet these energetic demands because they were unable to find sufficient prey, then mothers were forced to abandon cubs (Laurenson 1994). This indicates how a reduction in hunting success due to tourism, can directly lead to a reduction in cub recruitment and hence have impacts on population dynamics and, hence, overall population viability. Such an understanding of how these anthropogenic activities affect cheetah behaviour and their ecological roles, particularly across the borderlands of the Serengeti, is crucial for developing effective conservation and wildlife management strategies. Our study thus highlights the urgent need for integrated conservation strategies that include managing tourist numbers and enforcing strict wildlife viewing protocols. By understanding and mitigating the impact of human activity on cheetah reproduction and survival, conservation efforts can be more effectively targeted to support both the immediate and future viability of cheetah populations in protected areas.

4.5 Conclusion

The findings of this study underscore the need for careful management of wildlife tourism in protected areas. Cheetahs' reduced hunting activity in the presence of tourist vehicles may be driven by several factors. Like other predators such as hyenas or lions, cheetahs might avoid hunting if they anticipate losing their kill immediately afterwards, making the effort to capture the prey seem futile. Additionally, the presence of vehicles can disrupt hunting activities particularly stalking and the chasing process, cheetahs may remain lying down to avoid harassment or detection, especially if they feel exposed. Furthermore, the noise and movement from vehicles could increase prey vigilance, making it harder for cheetahs to approach and initiate a hunt. Each of these factors exerts different impacts: for instance, the inability to stalk prey due to vehicle disturbance may deter hunting even when prey are nearby, while disruption during movement may discourage cheetahs from actively searching when prey are sparse.

On the basis of our findings, we recommend the following measures to mitigate the negative impacts of tourism on cheetah hunting behaviour:

- Restrict the number of vehicles allowed near cheetahs during hunting activities to minimize disturbance and maintain a more natural hunting environment.

- Reduce engine running by requiring vehicles to turn off engines when stationary near cheetahs, thereby lowering noise levels.
- Limit vehicle movement in areas where cheetahs are actively hunting to prevent disruptions during stalking or chasing phases.
- Enforce minimum distance regulations between vehicles and cheetahs to reduce the perceived threat and allow cheetahs to behave naturally.
- Establish robust communication channels, such as park management social media accounts, ranger posts, or direct phone lines, to report wildlife harassment and ensure better enforcement of regulations.

Implementing these measures is crucial for preserving the ecological balance of predator-prey dynamics in the Serengeti and ensuring the survival of vulnerable species such as cheetahs. By regulating tourism activities in this way, protected areas can continue to support both conservation and tourism objectives in a sustainable manner.

5 General discussion

Cheetahs are iconic symbols of the savanna wilderness, renowned for their speed and elegance. However, their populations have declined significantly across their historical range in recent decades, with an estimated range contraction of over 90% and fewer than 7,000 individuals remaining globally (Durant et al., 2017). While other large carnivores in the region, such as lions and hyenas, have also faced population pressures, cheetahs are particularly vulnerable due to their low population densities, large home range requirements, and sensitivity to both habitat fragmentation and competition from cooccurring predators. Human activities are frequently implicated in cheetah population decline, yet the specific mechanisms through which humans disrupt cheetah behaviour remain poorly understood and difficult to quantify. The rarity and behavioural sensitivity of cheetahs particularly their tendency to avoid areas with high human activity or dominant competitors make field research particularly challenging, further complicating efforts to address these issues.

The overarching aim of this thesis is to improve our understanding of the relationship between cheetah movement ecology and anthropogenic activities and environmental features in a multi-use landscape. By combining habitat selection, movement, and behavioural analyses across different scales, this study provides critical insights into the mechanisms driving cheetah space use, movement patterns, and hunting behaviour. The study of habitat selection offers a broader-scale perspective on how cheetahs interact with their environment while responding to human-induced changes, shedding light on their spatial distribution and resource preferences. Movement patterns and step selection, analysed at a more local scale, reveal how cheetahs navigate their environment in response to human presence and the resources available at specific locations and times, bridging the gap between habitat selection and fine-scale movement decisions. At a finer scale, the analysis of hunting behaviour provides insights into the decisions and strategies cheetahs employ, offering a deeper understanding of the mechanisms underlying the patterns observed at larger scales. Thus, the finer-scale behaviours provide explanatory power for the broader-scale patterns, allowing us to link individual actions to broad scale distribution patterns and identify key drivers of cheetah space use and their movements across a human-dominated landscape. In this section, the findings are synthesized to understand emergent patterns across spatial scales, elucidate the broader ecological and demographic implications, and place the results in a wider context of large carnivore conservation.

RQ 1: How do anthropogenic and environmental factors influence cheetah space use at landscape scales?

The findings reveal a nuanced, and seasonal, interplay between anthropogenic activities and environmental factors in how they shape cheetah space use across the landscape. Cheetahs exhibited avoidance of anthropogenic features such as bomas, roads, and lodges, but the strength and direction of effect depended strongly on season. The avoidance was more pronounced at the time of year when human activities near these features was greatest, i.e. during the wet season for lodges and dry season for bomas. Interestingly, during these respective periods, cheetahs avoided lodges and bomas with equivalent strength (i.e. effect sizes were nearly identical). These effects suggest that cheetahs perceive anthropogenic features as riskier during periods of heightened human presence, which can influence their spatial distribution on a seasonal basis, and which constitute a form of habitat loss for cheetah. The combined loss of areas near lodges during the wet season, and near bomas during the dry season, imply a year-round loss of habitat due to humans, albeit in different locations. Additional environmental features such as woody cover, slope, elevation and proximity to rivers emerged as key drivers of cheetah habitat selection too. Woody cover provides concealment for stalking prey, our results indicate that they used woody cover disproportionately more during the wet season. This pattern may suggest that, beyond hunting concealment, cheetahs utilize woody cover as a strategy to minimize human disturbance, such as avoiding detection by tourists. Cheetahs exhibited a preference for areas closer to rivers, with this tendency being stronger during the dry season compared to the wet season. Additionally, cheetahs showed a clear avoidance of steeper slopes, favouring flatter terrains instead. This negative association with slope suggests that flat areas may provide better conditions for prey availability, cheetah movement or successful hunting, compared to steeper, more challenging landscapes. Our habitat selection analysis led to a prediction of habitat suitability across the range of cheetah in both wet and dry seasons. Suitability is generally assumed to relate directly and positively to a population's demography (Matthiopoulos et al., 2015) and can inform decision-making about the most and least impactful places to allow future anthropogenic activities, such as new roads, tourist infrastructure and bomas.

RQ 2: What are the impacts of anthropogenic activities on cheetah local scale habitat selection and movement patterns?

At a more local scale, movement patterns using step selection analysis provide insights into how cheetahs navigate their surroundings in response to human presence and the resources available at specific locations and times, linking broader habitat selection to detailed movement decisions. I found that overall, cheetahs exhibited avoidance of bomas, particularly during the dry season when bomas were more likely to be occupied. Short steps near bomas and longer steps away from bomas indicated that cheetahs were taking precautions when they moved near active bomas, and step lengths became unconstrained when cheetah were far from bomas. Thus, during the dry season, either the costs of being near bomas appear to increase for cheetah or the resource benefits decrease. This may reflect an avoidance of disturbance due to people at or near bomas, but could also reflect other effects, which could also be correlated with disturbance, such as limited access of prey and limited water resources. Similarly, seasonal responses to lodges revealed that cheetahs selected areas near the lodges in the dry season, likely due to reduced human activity, but avoided them in the wet season when tourism activities peak, likely due to increased vehicle traffic and noises. One of the oldest lodges in the area (Ndutu Lodge), for example, has between 10 and 20 tourists per day in the dry season (low season), but increases up to 80 in the wet season, an increase by as much as 700% *(source: Ndutu Lodge Manager).* Responses to roads varied with some cheetahs selecting areas near roads in the dry season when traffic is low, while others avoided them year-round due to disturbances or perceived risks. Finally, most cheetahs avoided livestock bomas, with the exception of one individual which consistently stayed near bomas in both seasons. The reasons for this exception are unclear but one hypothesis might be to avoid larger predators via a 'predator shield' (Prugh et al., 2023) and illustrate the importance of individual differences in response to anthropogenic effects. Overall, however, findings from this chapter and the previous one suggest that pastoralism and tourism influence cheetahs' local-scale movement decision-making. Cheetahs respond to human presence and tour vehicles in similar ways to their responses to dominant predators such as lions and hyenas.

RQ 3: What are the effects of tourism on cheetah hunting probability?

At an even more detailed scale, there was a significant influence of tourism activities on cheetah behaviours, particularly their hunting patterns. The presence of tourist vehicles near cheetahs often caused cheetahs to reduce or stop hunting altogether, accompanied by an overall decrease in activity levels. Engine noise intensified these disruptions, suggesting that such disturbances may be perceived at best as a nuisance and worse as a threat, similar to the presence of co-occurring dominant predators. Rather than fleeing, cheetahs often responded by conserving energy and waiting for the disturbance to leave before resuming hunting activity. Human disturbance, such as vehicle noise and tourism activities can hinder cheetah hunting efficiency through multiple mechanisms, including distracting the cheetah, disturbing prey and increasing prey vigilance and hence their detection of cheetah. Such impacts on hunting will affect foraging efficiency and hence body condition and individual fitness, with knock on impacts on cheetah survival, reproduction and population dynamics. Hence, these disruptions extend beyond immediate behavioural changes, underscoring the long-term consequences for cheetah populations and the importance of mitigating tourism impacts on critical activities essential to their survival.

5.1 From behaviour to broader ecological contexts

The findings from the behavioural analysis (Chapter 4) provides a critical lens through which the patterns observed at local (Chapter 3) and large scales (Chapter 2) can be understood. By investigating cheetah behaviour at the finer scale, the insights into how tourism activities influence cheetah behaviours reveal the mechanisms supporting the broader patterns of movements and space use observed across the landscape. This multi-scale approach enhances our understanding of the significant relationship between anthropogenic pressures and environmental factors shaping cheetah ecology.

The disturbances from tourism activities led to reduced hunting efforts or complete cessation of hunting activities, with cheetahs often adopting energy-conserving strategies until the disturbance dwindled. Lactating female cheetahs, in particular, have high metabolic needs, and operate on the edge of starvation, so these disruptions may have severe consequences (Laurenson, 1995), potentially reducing survival of nursing cubs due to insufficient energy acquisition. Similarly, these finer-scale responses can explain the avoidance behaviours observed at the local scale, where cheetahs were shown to avoid lodges and high-use areas during the wet season, a period coinciding with peak tourism activities. The avoidance of these areas is likely a behavioural adaptation to mitigate the negative impacts of frequent disturbances that directly affect their daily activities including hunting. Tourist vehicles, and hence disturbance, will be strongest nearer to lodges. However, importantly, the avoidance of lodges at local scales may involve additional mechanisms other than simply interfering with hunting behaviour. Thus, the overall impact of tourists may be stronger than what is suggested by simply extrapolating fine-scale effects of vehicles.

This connection between behaviours and local-scale movement patterns extends to the observed variability in cheetah responses to roads. The behavioural findings suggest that some cheetahs may perceive roads as low-risk areas during the dry season when traffic is minimal. However, during periods of high tourism activities, tour vehicles use roads to move around in search of wildlife; thus, a cheetah near a road is more likely to be spotted and then, once spotted, may be subject to observation and harassment throughout the day. This pattern is particularly strong if the cheetah has cubs or is next to a kill (*Pers. obs*). These seasonal responses to roads emphasize the individual-level variation in risk perception and the trade-offs cheetahs face between avoiding human disturbances and accessing critical resources, such as prey, while avoiding co-occurring predators.

At the large scale, the findings of seasonal variation in space use with increased avoidance of tourist infrastructures during the wet season can be directly linked to the behavioural disruptions observed at the fine scale. The heightened presence of humans and vehicles during the wet season amplifies the risks associated with these features, reinforcing cheetah avoidance. Conversely, the selection of areas close to lodges during the dry season, observed in the large-scale analysis, reflect lower disturbance and greater preference for these areas during this period. This preference may reflect the fact that the lodges themselves were built in areas with high suitability for cheetah and, possibly, their prey. This seasonal shift emphasises the dynamic interaction between human activity patterns and cheetah space use, manifested by fine-scale behavioural adjustments.

Environmental drivers, such as proximity to rivers, woody cover, slope, elevation (DEM), and NDVI, further contextualize these patterns. At the behavioural scale, cheetahs overall selected areas close to rivers in both seasons. The reliance on rivers aligns with the large-scale observation of increased selection for areas near rivers, particularly during the dry season. Similarly, the avoidance of steep slopes observed at the large scale reflects the fine-scale need for flat terrains to optimize movement and hunting efficiency, as steep slopes may hinder successful predation attempts. Woody cover was shown to provide critical concealment for cheetahs when stalking prey or avoiding detection by competitors, aligning with behavioural strategies to balance predation risk and hunting success. This study found that cheetahs selected woody cover more frequently during the wet season, contrasting with Durant's (1998) findings that cheetahs more strongly preferred woody habitats in the dry season due to prey retreating into woodlands. This raises the possibility that the discrepancy between these findings may be attributed to human-related factors, such as increased visibility on open plains during high tourist pressure, prompting cheetahs to retreat into woodlands. If changes in habitat preferences by cheetah, a top predator, in response to tourism pressure are confirmed by further study, this raises the possibility of cascading ecological impacts.

A negative correlation was found between the normalized difference vegetation index (NDVI) and cheetah habitat selection, indicating that cheetahs avoid green areas. At a fine scale, step selection analysis provided further insights into this pattern, showing that cheetahs actively avoided green areas during their movement decisions. This behaviour may be influenced by several ecological and behavioural factors. Wildebeest and Thomson’s gazelles, which are the main prey of cheetahs, follow the rains in the Serengeti, and both lions and hyenas are attracted to these migratory herds. Cheetahs, however, avoid with high prey densities, which are usually also areas of high productivity, to minimize competition and predation risks (Durant, 1998). Additionally, elevation (DEM) was observed to influence habitat selection, with cheetahs favouring areas of lower elevation that may facilitate ease of movement and reduce energetic costs associated with traversing rugged terrain.

Finally, the behaviours observed at the fine scale provide the foundation for understanding cheetah responses at broader spatial scales. Tourism disturbances directly influence cheetah behaviours, shaping movement patterns and habitat selection at the local and landscape levels. Seasonal dynamics and individual variation further add complexity, highlighting that not all individuals respond in similar ways to navigating anthropogenic pressures. Whether individual variability is driven by past experiences or physiological differences in perception of risk is unknown but would be an intriguing area of future exploration in cheetah and other species that live near and within human dominated landscapes. This multi-scale approach underscores the importance of mitigating human disturbances, particularly during peak tourism seasons, to support cheetah conservation efforts and ensure the persistence of this iconic species in the Serengeti ecosystem.

5.2 Contextualizing findings in the wider literature

The findings of this study align with, and contribute to, the broader understanding of how anthropogenic activities and environmental features influence large carnivore ecology. Reduced food intake by cheetahs, as demonstrated by disruptions caused by tourist activities, will not only impact where cheetahs choose to move but will likely have demographic consequences through cub recruitment. This aligns with Laurenson's (1995) work, which shows that cheetah mothers abandon cubs if they must travel too far to find food. Broekhuis (2018) further emphasizes these dynamics by demonstrating that high tourist densities negatively affect cheetah cub recruitment, with mothers raising significantly fewer cubs to independence in areas with elevated tourist activity. This link between the time spent foraging by mothers and the survival of their young at a nest or den is seen in other species that must navigate human-dominated landscapes (Doherty & Driscoll, 2018). Human access to protected areas has been shown to negatively impact cub survival in large carnivores, such as tigers *(Panthera tigris)* in Russia, where increased human activity was associated with lower survival rates of tiger cubs (Kerley et al., 2002). Similarly, harvesting has been shown to decrease recruitment in wolves *(Canis lupus)* in Alaska, the number of pups per pack declined after the initiation of harvesting (Ausband et al., 2015). Conversely, wolves preferred denning sites located farther away from villages, forest edges, and high-traffic roads (Theuerkauf et al., 2003).

While this study did not directly measure cheetah responses to Maasai activities, there was spatial avoidance, and hence it is likely that the behavioural responses observed in the presence of tourists are likely to lead to analogous responses to bomas. For instance, increased human activity near bomas may indirectly reduce food intake due to reduced hunting and intensify cheetahs' energetic challenges, mirroring the pressures created by tourism (Lewis et al., 2021). A study by Murphy et al. (2021) demonstrated that anthropogenic disturbances influenced spatiotemporal co-occurrence across multiple scales, leading to increased overlap among species such as black bears *(Ursus americanus)*, coyotes *(Canis latrans)*, bobcats *(Lynx rufus)*, and white-tailed deer *(Odocoileus virginianus)*, while simultaneously reducing available niche space for wildlife in Pennsylvania forests. Leopards (Panthera pardus) in central Kenya provide an example of the disruption of predator-prey interactions by strongly avoiding areas with high human activity during the day while showing variable selection for these areas at night (Van Cleave et al., 2018). Additionally, in India tiger reserves, tourism pressure causes significant stress in tigers *(Panthera tigris),* leading to behavioural and physiological responses that may impact their overall well-being and reproductive success (Tyagi et al., 2019). These examples demonstrate that there may be additional effects of human disturbance through modification of prey and competitor behaviour and distribution that were not measured by this study and deserve further investigation.

Illegal poaching and snaring, along with other human activities, can also significantly disrupt predator-prey relationships by sharply decreasing prey populations. For instance, in the Greater Kafue Ecosystem (GKE), once a key habitat for wild dogs, intense poaching has lowered herbivore densities far below expected levels, leading to a severe decline in wild dogs' primary prey (Schuette et al., 2018; Vinks et al., 2020). This prey depletion has also resulted in lower lion and hyena densities and a convergence in prey composition across the predator guild (Creel et al., 2018), illustrating the far-reaching consequences of human-induced disturbances on ecosystem processes. Disruptions such as these, if substantially intensified, could lead to other ecological impacts, further limiting access of predators to critical resources. This broader complexity of cheetahs and other large carnivores to human presence, could lead to cascading effects on population dynamics and ecology, and reinforces the need for management strategies that account for both direct and indirect impacts of human activity (Estes et al., 2011; Ripple et al., 2014).

The role of environmental features such as rivers and woody cover as key drivers of habitat selection also resonates with findings from other studies. Rivers, which provide critical resources such as water and prey, are frequently selected by large carnivores during dry seasons (De Boer et al., 2010). Similarly, in our study, cheetahs demonstrated selection for areas near rivers especially during the dry season. Woody cover, which cheetahs use for concealment, complements findings from other carnivore studies which also rely on suitable vegetation for stalking prey (Gorini et al., 2012). For example, Hopcraft et al. (2005) showed that lions, in the Serengeti, preferred hunting in areas with good cover rather than high prey density. Many solitary felids that use a stalk-and-ambush hunting strategy depend heavily on dense cover to effectively approach their prey (Balme et al., 2007; Beier et al., 1995; Schmidt et al., 2023).

Overall, the findings of this study contribute to the growing body of literature (Barker et al., 2023; Gorman et al., 2024; Mills et al., 2023; Tucker et al., 2023; Whittington et al., 2022) on predator responses to anthropogenic and environmental pressures, emphasizing the importance of multi-scale analyses to uncover the link between fine-scale mechanistic understanding and large-scale drivers of spatial distribution. Comparisons with other large predators illustrate both shared and unique responses, reflecting the diverse ecological adaptations within the carnivore guild. Future research should continue to explore these dynamics, particularly in the context of increasing human-wildlife interactions in rapidly changing landscapes.

5.3 The significance of limited data in cheetah conservation

A notable limitation of this study is the relatively small sample size of collared cheetahs observed over time. This constraint is not uncommon in field-based ecological studies involving rare and elusive species such as cheetahs, whose naturally low densities, large home ranges, and cryptic behaviours make them difficult to locate and monitor (Durant et al., 2004; Broekhuis et al., 2017). In this study, data were obtained from a limited number of individuals due to logistical constraints, collaring challenges, and the inherently low population density of cheetahs in the Serengeti ecosystem. Consequently, the statistical power to detect certain effects, particularly at finer scales or in relation to less frequent behaviours (such as hunting), may be limited.

However, small sample sizes do not render findings irrelevant. In fact, studies of rare species often require adapted thresholds for inference due to the difficulty of obtaining large datasets (Johnson, 2002; Hebblewhite & Haydon, 2010). In such cases, ecologically meaningful patterns, even if marginally significant or observed in a subset of individuals, can still inform management decisions and conservation interventions. For instance, the finding that some cheetahs ceased hunting in the presence of tourist vehicles - despite the small sample carries important implications for how tourism is managed near cheetahs. Similarly, the consistent avoidance of lodges and bomas in seasonally relevant periods, even if based on fewer observations, highlights a clear behavioural response that may contribute to habitat loss and stress at the population level.

Given the precarious status of cheetah populations globally - with fewer than 7,000 individuals remaining in the wild (Durant et al., 2017) even small-scale disturbances can have outsized demographic consequences. Field-based behavioural ecology studies often demonstrate that marginal findings, especially when they align with ecological reasoning or previous research, may serve as early warning signs of broader-scale processes (Lindenmayer & Likens, 2010). This study's findings, although derived from a limited number of animals, highlight real and repeatable patterns of anthropogenic disturbance, warranting conservation concern. Indeed, conservation science must often act under conditions of uncertainty, where precautionary action is preferable to inaction, particularly when the stakes involve threatened species with limited buffering capacity against human pressures.

The interpretation of these findings therefore benefits from a precautionary approach, where even subtle behavioural disruptions - such as increased resting time or reduced hunting probability in response to human presence - are viewed as cumulative risks to fitness and survival. Moreover, individual-level variation in response to human disturbance, as documented in this study, suggests that some cheetahs may be more vulnerable than others. This reinforces the need for adaptive, individual-aware management strategies, even if population-wide patterns cannot yet be fully generalized.

In conclusion, while the limited sample size imposes constraints on generalisability, it does not diminish the ecological or conservation relevance of the findings. On the contrary, in the context of a rare and sensitive species like the cheetah, small sample sizes may be the norm and finding - however modest - can still provide critical insights that guide urgent conservation action.

5.4 The role of prey and competitors: A missing piece

Another important limitation of this study is the absence of direct data on some of the major ecological factors known to influence cheetah movement and behaviour - specifically, prey distribution and the presence of dominant competitors such as lions and spotted hyenas. These species exert strong top-down pressures on cheetahs through kleptoparasitism, predation on cubs, and interference competition, all of which can shape space use, movement, and hunting behaviour (Durant, 1998; Broekhuis et al., 2013). Similarly, prey availability is a key determinant of carnivore habitat selection and foraging decisions. Although environmental proxies such as NDVI and proximity to rivers were included to partially capture patterns in primary productivity and prey accessibility, these are indirect and do not account for spatial or temporal dynamics in actual prey abundance and movements. The lack of these data constrains inference by making it difficult to disentangle the relative influence of anthropogenic factors versus natural ecological drivers. For example, avoidance of certain areas may be influenced both by human presence and by high densities of competitors. Moreover, prey depletion or aggregation may modify the perceived costs and benefits of habitat use near anthropogenic features. Future research that integrates spatial data on prey densities and competitor activity - e.g., through camera traps, prey transects, or GPS collaring of other carnivores - would help refine these analyses and provide a more complete picture of cheetah ecology in multi-use landscapes (Vanak et al., 2013; Schuette et al., 2013). Nonetheless, even in the absence of these ecological layers, the patterns observed here still offer valuable insights into anthropogenic impacts, which may compound or interact with natural pressures to shape cheetah space use and behaviour.

5.5 Comparison of landscape and local-scale selection analyses

The resource selection analysis in Chapter 2 and the step selection analysis in Chapter 3 offer complementary insights into cheetah habitat preferences, yet they differ in resolution, focus, and implications. At the landscape scale, cheetahs showed broad patterns of selection for areas with low human disturbance, such as regions farther from bomas and roads, and with higher environmental suitability (e.g., moderate woody cover and proximity to water sources). These patterns reveal general habitat preferences and are useful for identifying priority conservation zones and corridors.

In contrast, the local-scale step selection analysis captured finer behavioural responses to immediate surroundings and movement decisions. While there was general consistency with the landscape-scale findings - such as avoidance of human infrastructure - step selection models also highlighted behavioural plasticity. For example, some cheetahs exhibited tolerance to proximity to roads or lodges during certain times of day or in specific contexts, likely reflecting short-term trade-offs between risk and access to prey. Moreover, interactions between movement parameters (e.g., step lengths, turn angles) and anthropogenic features suggested changes in movement efficiency or vigilance when navigating human-modified areas, nuances not detectable in the broader-scale models.

These differences underscore the value of integrating multiple spatial scales when informing conservation. Landscape-scale data are useful for protected areas design and land-use planning, while step-level models provide critical insights into how animals actually behave within those spaces. Importantly, GPS collar data are essential for both levels of analysis, offering spatial and temporal resolution that cannot be achieved through camera traps or indirect signs alone. While some general patterns of habitat use could be inferred without collars, fine-scale behavioural responses to anthropogenic pressures - and their conservation implications - would likely remain undetected.

5.6 Future work

Building on this study to further advance our understanding of cheetah behaviour in relation to human activities and their environment, I propose the following future research directions:

5.6.1 Expand GPS collar data collection

More collars deployed for more years will improve population-level understanding. This would also give insight into long-term responses of individuals, including the effect of past experiences on behaviours to help elucidate why individuals varied in their response. The landscape is changing quickly and there is a need for long-term monitoring of movements

5.6.2 Utilize accelerometer data

Further research should incorporate triaxial accelerometer data into movement and behavioural studies to investigate fine-scale activities of cheetahs. These devices record high-frequency measurements of body acceleration along three axes (X, Y, and Z), enabling the detection of subtle behavioural states such as resting, walking, stalking, and high-speed chases. When combined with GPS data, accelerometers can help identify when specific behaviours occur, assess energy expenditure associated with different activities, and reveal how cheetahs allocate their time and effort across the landscape. This approach holds great potential for uncovering how anthropogenic disturbances - such as tourism pressure or proximity to settlements - alter behaviour, activity budgets, and hunting efficiency. For instance, accelerometry could help distinguish whether cheetahs are merely present in a habitat or actively engaging in key behaviours like hunting or resting, providing deeper ecological insight beyond location data alone.

5.6.3 Assess Maasai impacts

The research above indicates that bomas have a similar magnitude of impact on cheetah behaviour and movements as tourism. However, fine-scale mechanisms of disruption were only studied in context of tourism; I would therefore like to replicate the study of cheetah hunting behaviour in relation to pastoralist activities to explore the specific mechanisms by which bomas in the high-use periods alter cheetah activity patterns. Ultimately, I would want to translate these behavioural and activity changes into an understanding of demographic impacts, with the long-term goal of informing the limits to sustainable coexistence.

5.6.4 Examine the role of cover

In the Serengeti, the availability and quality of vegetation cover are influenced by various factors, including climate variability, grazing by livestock, and anthropogenic activities such as tourism and agriculture. Additionally, the spread of invasive plant species like *Gutenbergia cordifolia* and *Solanum incanum* is altering vegetation structure and composition. While this dense cover may provide concealment for cheetahs, it could also lead to prey avoidance due to reduced visibility of approaching predators. To study the effects of such vegetation change, it is essential to assess the spatial and temporal distribution of vegetation cover in relation to cheetah habitat use and human activities. Advanced remote sensing technologies, such as LiDAR, could provide high-resolution data on vegetation structure and canopy height, enabling researchers to quantify changes in vegetation height and cover over time and across different landscapes. Combining LiDAR data, prey distribution, field observations and cheetah GPS movement data would allow for a more detailed understanding of how vegetation cover influences cheetah behaviour and habitat selection.

5.6.5 Evaluate cheetah habitat shifts and ecological cascades

Future research should explore how cheetah habitat shifts during the high tourist season (wet season) might influence broader ecological dynamics, particularly potential trophic cascades resulting from altered habitat use and predator-prey interactions. For example, a significant shift toward woodland areas due to tourism pressure could reshape prey distributions, competition dynamics, and vegetation structures, warranting further investigation.

5.7 Conservation implications

5.7.1 Cheetah vulnerability to human disturbance

I found a strong signal of human disturbance on cheetah at different scales of analysis, demonstrating that cheetahs avoid areas with human disturbances such as active Maasai bomas, lodges in the high tourism season and, to a lesser extent, high traffic roads. At the large scale, these effects constitute habitat loss for cheetah, and these losses occur year-round, due to tourism and pastoralism occurring at peak intensities in different seasons. These areas lead to a reduction in use and a decrease in hunting opportunities. Together, the research indicates that human activities, even those intended to support conservation (e.g., tourism), if not well managed, can disrupt natural cheetah behaviours such as space use, movements and hunting decisions. There is a need for improved planning around human infrastructure and management of interactions between tourism vehicles and cheetah in order to mitigate these human impacts on cheetah behaviour and ecology.

5.7.2 The role of behavioural flexibility

While cheetahs exhibit a degree of behavioural flexibility that allows them to navigate human-modified landscapes, this adaptability has clear limits - particularly in areas with intense or sustained human activity, such as densely populated settlements near protected area boundaries. This behavioural sensitivity to frequent disturbance can constrain their access to otherwise suitable habitats and increase their vulnerability in fragmented landscapes. Their avoidance of certain anthropogenic features likely reflects an adaptive survival strategy. However, when avoidance leads to reduced access to high-quality habitats - such as areas with abundant prey or water - it may also indicate a sensitivity to habitat degradation, as these areas become functionally unavailable despite being structurally intact. This has implications for their long-term resilience in increasingly human-dominated landscapes.

5.7.3 Habitat heterogeneity as a conservation priority

Cheetahs depend on diverse and heterogenous habitat features, which reflects their need to find sufficient prey while avoiding other predators. Thus, conserving heterogeneous landscapes is critical. Degradation or loss of key habitat types such as wooded patches, water sources and high-quality grasslands attractive to herbivore prey, could disproportionately affect cheetah populations and limit their ability to adapt to changing conditions. Grasslands in parts of the study area used by livestock show increasing presence of invasive plants (*Pers. obs*), such as *Gutenbergia cordifolia* and *Solanum incanum*, suggesting the area may be overgrazed. From a cheetah’s perspective, these invasive species can reduce visibility and alter prey availability by displacing preferred forage species for herbivores, potentially lowering prey densities and making hunting more difficult in heavily degraded habitats.

5.7.4 Spatial and temporal avoidance pattern

This study's findings suggest that cheetah responses to human activities vary spatially (e.g., avoidance of roads, lodges, and bomas), seasonally (wet vs. dry) and, to a smaller extent, diurnally (daytime vs. nighttime). This highlights the importance of considering spatial, seasonal and temporal dynamics when designing conservation strategies for cheetah and other sympatric large carnivore.

5.7.5 Ecosystem-wide conservation needs

This study highlights that cheetah conservation cannot occur in isolation. Cheetahs are just one of many sensitive species in the Serengeti Ecosystem, alongside others such as black rhinos, lions, caracals, and ground pangolins, all of which are vulnerable to similar threats. Protecting cheetahs, therefore, requires addressing broader ecosystem processes and implementing conservation measures that benefit the entire community of species sharing this landscape. This includes mitigating human-wildlife conflicts, ensuring connectivity across the wider Serengeti landscape, and carefully planning human infrastructure to prevent further encroachment on critical wildlife habitats. Such holistic conservation strategies are essential to support not only cheetahs but also the broader biodiversity of the Serengeti.

6 Conclusion

This thesis underlines the complex interplay between cheetahs and their environment within a human-modified landscape in the Serengeti ecosystem, Tanzania. Despite unavoidable limitations such as a small number of collared animals, the findings offer valuable, and consistent, insights into cheetah ecology and the broader implications of human activities on large carnivores. The research highlights the importance of prioritizing sustainable tourism, sustainable pastoral activities along borderlands, and community engagement to foster coexistence between humans and cheetahs. Cheetah survival is likely to be intricately linked to their ability to adapt to human-induced pressures, which pose both immediate and long-term challenges. Observed patterns of avoidance of sites associated with human activities, such as active Maasai bomas, roads with high tour car traffic, tourist lodges, and areas with dense tour car activity and engine noises, highlight the significant impact of human presence on cheetah behaviour. These findings emphasize the critical need to minimize human disturbances, particularly in vital habitats.

While cheetahs demonstrate remarkable behavioural flexibility, their reliance on specific habitat features makes them vulnerable to habitat loss and fragmentation. This emphasises the necessity of maintaining habitat heterogeneity across large landscapes to support diverse prey populations and provide cheetahs with opportunities to evade both natural predators and human impacts.

Ultimately, this research highlights that the coexistence of cheetahs and humans depends on a balanced approach that integrates ecological requirements with sustainable land-use practices. By addressing both anthropogenic pressures and environmental needs, it is possible to create landscapes that promote the resilience and long-term survival of cheetahs and other large carnivores in the Serengeti ecosystem.

6.1 Recommendations

Based on the findings of this research, the following recommendations are proposed to enhance cheetah conservation and foster coexistence between humans and wildlife in the Serengeti borderlands:

6.1.1 Human Activity Management:

- Regulate human activities across the zones of coexistence.
- Develop, through consultation with key stakeholders, management and conservation zoning systems that cluster Maasai bomas and tourism facilities to allow cheetahs to move and hunt freely in areas in between developed areas.
- Control the spatial expansion of camps and restrict building of new permanent tourist facilities to areas of high suitability for cheetah.
- Develop and distribute interpretation materials to raise awareness of the impacts of tourism on cheetah, and to provide guidelines on cheetah-friendly observation practices for tourists and guides.
- Strictly ban shouting, radios and running engines in the vicinity of cheetah to minimize noise pollution and reduce disturbance of cheetahs, particularly for mothers with cubs or showing signs of lactation. Ensure these bans are enforced by ranger patrols to ensure cheetah friendly observation practices in highly visited areas.

6.1.2 Community Engagement:

- Develop educational programs to raise awareness about cheetah conservation and the socio-ecological benefits of coexisting with wildlife. The Serengeti Cheetah Project and park management can collaborate to identify effective methods for sharing and transferring knowledge and information related to cheetah conservation.

6.1.3 Policy and Regulation Enforcement:

- Strengthen enforcement of existing wildlife harassment laws, including clear penalties for violations by tourists or local stakeholders.
- Allocate adequate training workshops to park rangers and conservation officers to monitor and manage human activities effectively.

By implementing these recommendations, park management can mitigate the negative impacts of human activities, enhance the ecological integrity of the Serengeti ecosystem, and secure the long-term survival of cheetahs and other wildlife species. This approach will also support the Serengeti's dual role as a world-renowned biodiversity hotspot and a vital resource for local communities and economies.

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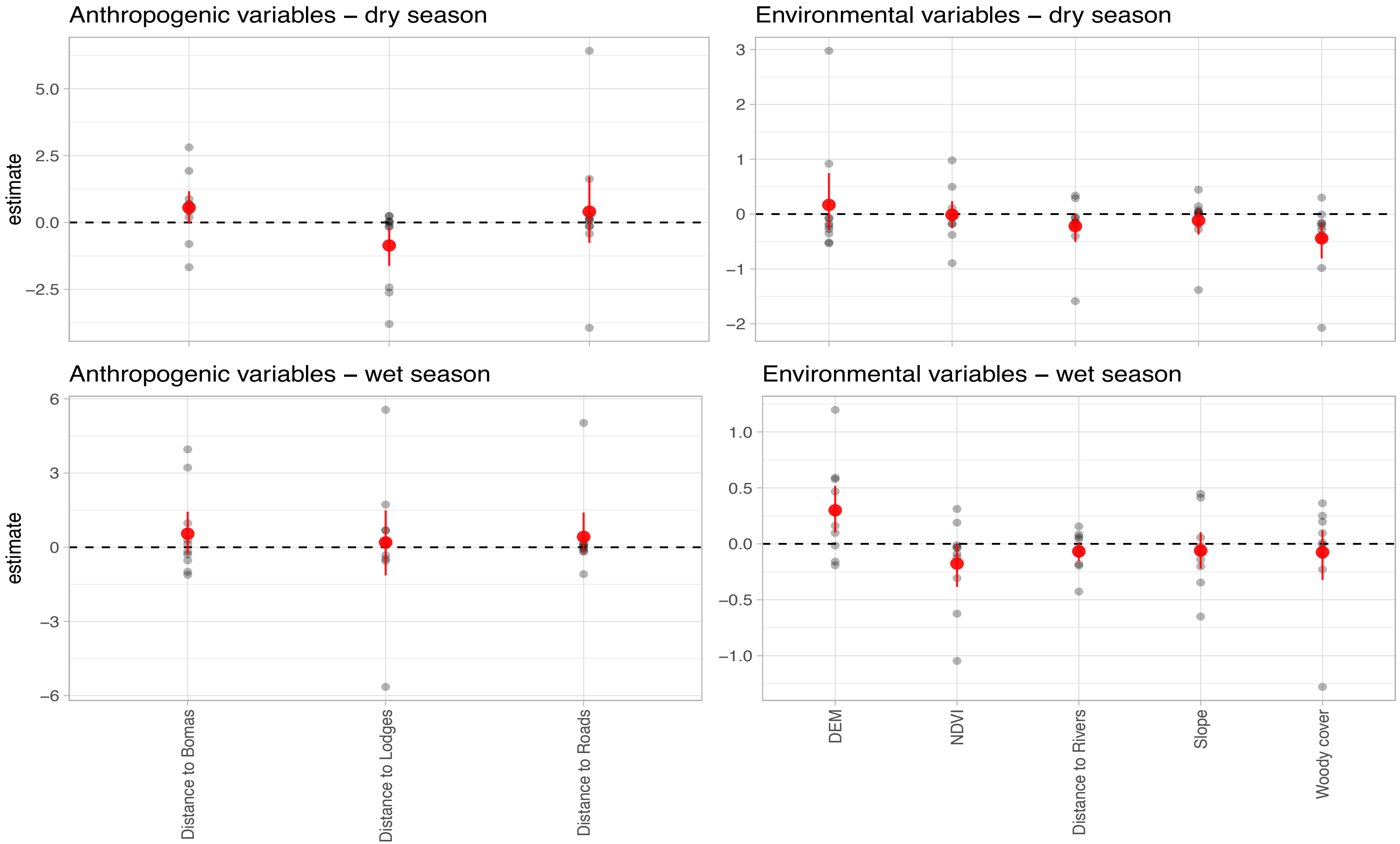
Appendix

Appendix A: The complete output table of coefficient estimates for selected variables related to cheetah habitat selection in Serengeti, Tanzania.

Covariates	Estimate	Standard Error	Z value	P value
Intercept	-2.7991	0.0460	-60.8399	<0.001
Woody cover	-0.4859	0.0163	-29.7694	<0.001
Slope	-0.5533	0.0420	-13.1730	<0.001
DEM	-0.1954	0.0099	-19.7574	<0.001
ANDVI	-0.3622	0.0446	-8.1129	<0.001
Distance to lodges	-0.1892	0.0132	-14.3504	<0.001
Distance to roads	0.0535	0.0111	4.8419	<0.001
Distance to bomas	0.3113	0.0134	23.2395	<0.001
Distance to rivers	-0.2883	0.0155	-18.6443	<0.001
Woody cover*Wet	0.7144	0.0177	40.4241	<0.001
Lodges*Wet	0.5036	0.0178	28.3288	<0.001
Roads*Wet	-0.1866	0.0173	-10.7964	<0.001
Bomas*Wet	-0.6334	0.0192	-32.9406	<0.001
Bomas*Night	-0.1060	0.0180	-5.8770	<0.001
Rivers*Wet	0.1780	0.0218	8.1796	<0.001
Rivers*Night	-0.0526	0.0247	-2.1288	0.0333
Bomas*Wet*Night	0.0679	0.0314	2.1639	0.0305
Woody cover*Night	0.0176	0.0231	0.7618	0.4461
Lodges*Night	0.0658	0.0229	2.8752	0.0040
Roads*Night	-0.0569	0.0023	-2.4936	0.0126
Woody cover*Wet*Night	0.0362	0.0303	1.1970	0.2313
Lodges*Wet*Night	0.0519	0.0305	1.6988	0.0893
Roads*Wet*Night	0.0881	0.0334	2.6355	0.0084
Rivers*Wet*Night	-0.0086	0.0324	-0.2664	0.7899
Wet	0.1422	0.0220	6.4575	<0.001
Night	0.0399	0.0186	2.1461	0.0319
Wet*Night	-0.1382	0.0286	-4.8332	1.3431



Appendix B: Estimated coefficients (±95% CI) from the global integrated step selection model for all cheetahs, showing the effects of anthropogenic and environmental variables during the dry and wet seasons.