The Impacts of Climate Change and Veterinary Fencing on Savanna Ungulate Populations, Communities, and Behaviors

by

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Graduate Program in Environment
Duke University

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Dissertation submitted in partial fulfillment of the requirements for the degree of
Doctor of Philosophy in the Graduate Program in Environment
in the Graduate School of Duke University
2023

ABSTRACT

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Abstract

As global change pushes ecosystems past climate tipping points, southern African savannas will experience more heat waves and droughts. These ecosystems are home to 90% of the world's large herbivore diversity, millions of livestock, and a rapidly growing human population expected to reach 2 billion by 2040. As a unique vestige of large Pleistocene-era herbivores and a burgeoning powerhouse of global population, it is necessary to understand how African savanna ecological communities will respond to global change. Especially concerning for these communities are more frequent droughts that may dry up key surface water resources; increased heat loads that may overwhelm ungulate thermoregulatory systems; and the expansion of veterinary fencing across the landscape, which currently restricts historic great migrations of millions of ungulates. Large herbivores regulate nutrient cycling and vegetation structure on African savannas in a way that cannot be replaced by smaller herbivores or livestock; therefore, their responses to these threats are of utmost importance to preserving savanna functioning for the future.

This dissertation explores the effects of increasing drought, heat, and veterinary fencing on savanna ungulate communities from the individual to the metapopulation scale. In the Kruger National Park, South Africa, I first address large-scale and long-term questions of drought impacts on rare antelope populations in the context of the full suite of large herbivores in the Kruger Park. I use thirty years of harmonized aerial census data and a Bayesian Generalized Joint Attribute Model to understand how drought,

and its interaction with regional rainfall and surface water supply, drives herbivore community structure and rare antelope survival. In Khaudum National Park, Namibia, I then use a four-year dataset of 33 antelope fitted with GPS collars to answer questions on heat and fencing-induced behavioral changes on two species on opposite sides of a water-dependence spectrum. I investigate how these species differ in their reliance on surface water, cool microclimates, and shifting activity budgets when responding to higher temperatures. I then explore how they differ in their responses to veterinary fencing, and how these responses change seasonally.

As climate change brings more drought and hotter temperatures to southern Africa, the findings of this dissertation indicate that the placement of artificial waterholes on the landscape will be key to rare antelope survival in the Kruger Park; that water dependence is a key factor in antelope responses to heat and fencing; and that the expression of thermoregulatory strategies for two savanna ungulates will intensify under higher temperatures. This dissertation adds these unique findings to the canon of savanna movement and fence ecology literature, and provides multiple points from which future research in this arena can improve on our expectations of savanna ungulate behavioral shifts under climate change.

Dedication

Mom and Dad, you have given me everything. I am so grateful we made it in one piece.

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— Kazuo Ishiguro, *The Remains of the Day*

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Truly, where would I be without those who have made me?

1

Introduction

"There is a crucial need to establish relationships ***between herbivore movements and their changing environments, especially in Africa*** *where most of the world's large herbivore diversity resides. . . . Without [this knowledge], we are likely to see a progressive loss of this legacy, as protected areas lose their effectiveness under shifts in climate, atmospheric carbon dioxide, and human activities plus infrastructure."*

— Owen-Smith et al. 2020

For the ∼2.5 million years since the genus *Homo* evolved in Africa, the fates of savanna biomes, large herbivores, and Earth's climate have been intertwined with human activity. One of the largest consequences of this relationship were the near-synchronous late Pleistocene extinctions (∼50,000–10,000 years before present) of 65% of large mammal genera across the globe (Barnosky et al 2004), driven largely by human hunting and exacerbated in some regions by climatic changes (Faith and Surovell 2009, Koch et al 2006, Sandom et al 2014). Today, the spread of urbanization, agriculture, and organized poaching, as well as the intensifying burden of anthropogenic climate change on the biosphere, threaten many of the planet's remaining large herbivore

species. Despite vulnerability to these threats and African savannas' high biodiversity, large African herbivores are understudied compared to their North American, European, and Asian counterparts. The chapters that follow explore how changing climate, landscapes, and human infrastructure affect the movements and behaviors of large African savanna herbivores.

1.1 African savannas

The history and present of large African mammals, including modern humans (*Homo sapiens sapiens*), are inextricable from the formation of the savanna biome. Savannas are defined by a unique codominance of trees and grasses (<50% tree cover), and form in regions where feedbacks between fire, herbivory, and rainfall prevent tree growth from dominating the herbaceous layer (Scheiter and Higgins 2009, Staver et al. 2011). Savannas are considered *disturbance-driven* ecosystems, where periodic consumption of the vegetative layer, either through burning or herbivory, maintains an otherwise unstable ecosystem state.

The dominance of savannas and grasslands that we see today (over 33% of the Earth's land surface) was made possible in the late Miocene (about 8 Ma) by the almost-synchronous convergent evolution of the C_4 photosynthetic pathway in grasses (Beerling and Osborne 2006, Osborne and Beerling 2006). A major weakness in ancestral C_3 photosynthesis occurs when a key photosynthetic enzyme, RuBisCO, reacts with oxygen instead of carbon dioxide at the leaf's surface. The C_4 pathway physically separates the carbon-gain and sugar-production steps of photosynthesis, moving RuBisCO deep within the leaf where it can be saturated with carbon transported from the leaf's surface in four-C chains (hence, "C_4", Osborne and Beerling 2006). This avoidance of photorespiratory waste provided an energetic advantage for C_4 grasses in the low-CO_2 and high-aridity environments of the late Miocene (Osborne and Beerling 2006).

The spread of C_4 grasses enhanced the fire regime of early savannas, as grasses build up more flammable fuel in the wet season. In addition, full forests can encourage their own microclimate of high rainfall to form; replacing forests with savannas therefore interrupted this high-rainfall feedback and allowed understory grasses to flourish (Beerling and Osborne 2006).

Due to their disturbance-driven structure and highly seasonal climate variation, savannas have a highly irregular distribution of nutrients and other resources. This landscape heterogeneity of African savannas, through an abundance of ecosystem types and interfaces within small areas, promotes the coexistence of a high diversity of flora and fauna (du Toit 2003). Large herbivores are particularly well-supported by landscape heterogeneity, as their size often demands larger ranges that cover a greater diversity of vegetative biomass (Katayama et al. 2014). This effect of heterogeneity crosses many scales. At the feeding patch scale, variation in leaf to stem ratios or plant height can result in spatial separation of herbivores by diet; therefore, vegetatively diverse patches often support more diverse assemblages of ungulates (du Toit 2003). And, at the habitat scale, a mosaic of habitats allows for more opportunities for speciation to occur, as terrestrial mammals are often habitat specific (du Toit 2003, Vrba 1992). These features of the savanna biome have led to its support, in Africa, of 90% of the world's diversity in large herbivores (Owen-Smith et al. 2020).

1.2 Herbivores and their movements

As with the mass mammalian extinctions of the late Pleistocene, large mammals today (n = 74 with mean adult body mass $\geqslant$100kg) are disproportionately threatened: 60% of the world's large herbivores are currently threatened with extinction, compared to 27% of all mammals (IUCN 2023, Ripple et al. 2015). Large mammals are more susceptible to hunting (Venter et al. 2020). Range area generally increases with body size

(Harestad and Bunnel 1979, Reiss 1988, Tucker et al. 2014) and, with human encroachment on wild spaces accelerating each year, the space available to free-ranging mammals shrinks. Finally, large mammals are more likely than small mammals to pose a threat to human lives and livelihoods, with instances of wildlife-human conflict increasing with body size (Mukeka et al. 2019).

African large mammals in particular are over-threatened and under-studied. 50% of the largest African mammals (17 of 32 species) have decreasing populations or are extinct in the wild (IUCN 2023, Ripple et al. 2015). Despite these population trends and the high biodiversity of large herbivores in Africa, the amount of research in the region (245 mean articles per species) falls far behind that in North America (1,354), Europe (1,045), and Asia (1,183). Additionally, most African research focuses on only four species: African savanna elephant (*Loxodonta africana*), Cape buffalo (*Syncerus caffer*), white rhinoceros (*Ceratotherium simum*) and black rhinoceros (*Diceros bicornis*); Ripple et al. 2015).

The movement of free-ranging African herbivores across the landscape is critical both to herbivore survival and to the maintenance of savanna functioning. African herbivores are often called *ecosystem engineers*, as their movements significantly shape savanna productivity (Geremia et al. 2019, Holdo et al. 2007), structure (Bakker et al. 2016, Holdo et al. 2009, O'Connor et al. 2020, Staver et al. 2009), and nutrient cycling (McNaughton 1976, Melis et al. 2007, Subalusky et al. 2017). Long-distance migrations allow large herbivores to follow the flush of fresh plant matter that follows the onset of the rainy season (Bischof et al. 2012, Geremia et al. 2019, McNaughton 1976), while local herbivore movements respond to acute climatic conditions such as a higher heat index or local droughts (Boyers et al. 2019).

1.3 Human-caused changes for large herbivores

In the late Pleistocene to early Holocene (~50,000-10,000 years before present), a combination of human over-hunting, climate shifts, and the cascading effects of large herbivore loss brought about the extinction of over 60% of then-extant mammalian species (Barnosky et al. 2004, Koch and Barnosky 2006, Prescott et al. 2012). Megafauna (animals with average adult body mass >1,000kg) were completely extirpated in North America, Australia, and Europe, with only a few species of elephant, rhinoceros, hippopotamus, and giraffe remaining in Africa and southern Asia (Owen-Smith 1987).

Human impacts on herbivores in the Anthropocene adds climate and landscape change to the extractive declines of the Pleistocene. Anthropogenic climate change will cause southern Africa to warm and dry faster than other subtropical biomes (Engelbrecht et al. 2015). Increasing local temperatures will have differential effects on mammalian species depending on their size and thermoregulatory strategy, as larger mammals have more difficulty shedding heat (Bell 1971, Jarman 1974, Owen-Smith 1989).

In addition to climatic changes, human infrastructure dominates the African landscape. As human populations in Africa are expected to reach 2 billion by 2040 (FAO 2023), these features will only increase in density. Veterinary fencing is the largest and fastest-growing linear feature on the Earth's surface (Jakes et al. 2018), and its fragementation of the landscape can have outsized effects on large mammals that need access to large, heterogeneous landscapes. Landscape fragmentation can lower biodiversity (Fahrig 2003) as fragmented landscapes support fewer species (He and Legendre 1996, McIntyre 1995) and increase extinction rates (Wilcox and Murphy 1985). In addition, the physical barriers creating this fragmentation can prevent herbivore seasonal migration into critical habitats (Kauffman et al. 2021).

Finally, the aridization and heating of African savannas will make water access scarcer, yet ever more important, for large African mammals. Ephemeral surface wa-

ter sources in southern Africa may dry more quickly (Bates et al. 2008, Nkemelang et al. 2018), leading to a greater dependence on permanent rivers and human-supplied waterholes. This aggregation around scarce water may increase risks associated with higher herbivore density, such as competition for forage access (Owen-Smith 1998) and increased predation (Cozzi et al. 2012, Fuller 2016).

1.4 Chapters Overview

Chapter 2 combines 30 years of aerial ungulate census data from Kruger NP for the first time, describing long-term population trends in fourteen species. I then use these data along with a Bayesian generalized joint-attribute model (GJAM) to understand how species differed in their responses to drought in the late 1980s and early 1990s, and discuss what this might mean for rare antelope species of special concern today.

Chapters 3 and 4 use GPS collar data from two antelope species in Khaudum NP, roan (*Hippotragus equinus*) and gemsbok (*Oryx gazella*), to investigate how climate change and human infrastructure intersect with antelope thermoregulatory strategies to alter movement behaviors. **Chapter 3** investigates changes in the intensity of thermoregulatory strategy in roan and gesmbok, modeling the strength of roan dependence on surface water and gemsbok dependence on shifting activity budgets under low and high ambient temperatures. **Chapter 4** investigates how seasonal movement strategies affect roan and gemsbok interactions with veterinary fencing at the eastern boundary of Khaudum NP.

1.5 Study regions: Kruger NP, South Africa and Khaudum NP, Namibia

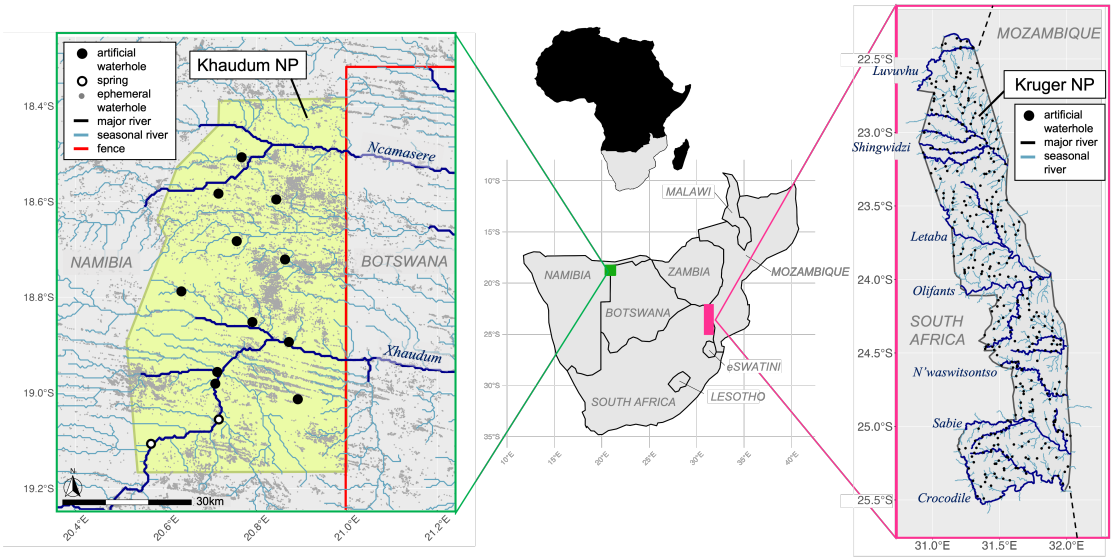
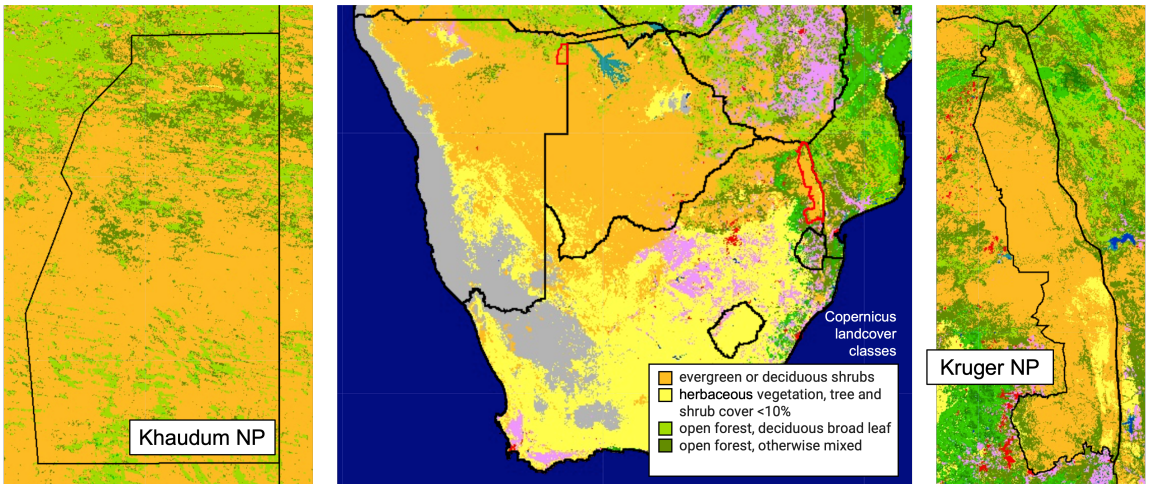


FIGURE 1.1**:** Map of study areas and surface water sources in the context of Southern Africa. Khaudum National Park (left) covers about 385,000ha of semi-arid savanna habitat in northeastern Namibia. Kruger National Park (right) covers almost 2 million ha of semi-arid savanna habitat in northeastern South Africa. Although about five degrees of latitude separate these two national parks, they both have similar climates (about 500mm of rainfall, hot wet season, cool dry season) and vegetation cover (mostly shrubby savanna with more sandy, dystrophic soils in the north and more eutrophic soils in the south.



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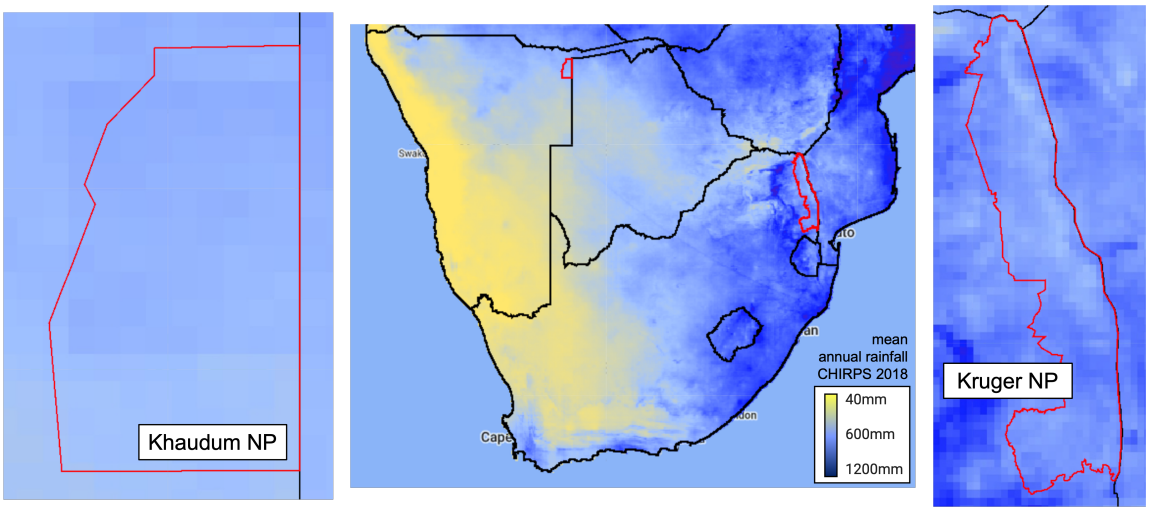

FIGURE 1.3**:** Map of study areas and surface water sources in the context of Southern Africa. Khaudum National Park (left) covers about 385,000ha of semi-arid savanna habitat in northeastern Namibia. Kruger National Park (right) covers almost 2 million ha of semi-arid savanna habitat in northeastern South Africa. Although about five degrees of latitude separate these two national parks, they both have similar climates (about 500mm of rainfall, hot wet season, cool dry season) and vegetation cover (mostly shrubby savanna with more sandy, dystrophic soils in the north and more eutrophic soils in the south.

2

Rare antelope as two groups rely on waterholes during drought on a southern African savanna

Margaret E. Swift, Steven I. Higgins, Gareth P. Hempson, Sandra MacFadyen, Sam Ferreira, Izak P.J. Smit, James S. Clark

2.1 Introduction

As climate change pushes ecosystems past climate tipping points (Armstrong McKay et al. 2022), large herbivores are experiencing an anthropogenic threat not seen since the late Pleistocene extinctions. Southern African savanna ungulates will be at particular risk, as the region is expected to undergo warming and drying at faster rates than other subtropical regions (Engelbrecht et al. 2015). Few studies offer the long-term perspective needed to understand the impacts of changing water and food availability on species that vary widely in diet breadth, size, life span, survival, and reproductive rates. On the one hand, intensifying drought could shift large herbivore communities toward

increasing dominance of browsers that exploit water-rich woody plants as grazers suffer from drying, seasonally available grasses (Abraham et al. 2019, Kihwele et al. 2020, Staver et al. 2021). At the same time, drought and fire can decrease savanna woodiness, especially in small trees, making browse less accessible (Higgins et al. 2007). Furthermore, species dependent on surface water sources, which are likely to dry due to aridization (Chamaillé-Jammes et al. 2007), are especially vulnerable. The role of food and water depends not only on diet but also species' life history differences: Large size, long life, and long gestation and juvenile phases could buffer the effects of episodic recruitment failure during drought in the form of resistant adult survival. These same traits that could lend resistance could also slow recovery: large size and long life often come with slow population growth needed to rebound from population declines. Finally, small populations with positive density-dependent growth rates (the "Allee effect") may decline under large variations in food and water availability (Roques et al 2008, Owen-Smith and Ogutu 2012). In this study we synthesize multi decade census records from one of southern Africa's largest wildlife refuges to quantify drought impacts on the full megaherbivore community. A joint analysis of drought decline and recovery shows community transformation shaped by diet and water availability and flexibility, as mediated by life histories that range from the impala to the savanna elephant.

The long-term herbivore monitoring project in the Kruger National Park, South Africa, provides an opportunity to understand large herbivore community responses to climate variation. The Kruger Park's savanna herbivore populations have been surveyed annually (although with changing methods and scope) over 40 years of extreme dry and wet periods. In particular, the late 1980s saw the North Atlantic Oscillation (NAO) and El Niño-Southern Oscillation (ENSO) bring a decade of drier-than-average conditions to the Kruger Park (Ogutu and Owen-Smith 2003), followed by one of the wettest rainy seasons on record, between 1999 and 2000 (more than 400mm of rainfall above aver-

age). This decade of low rainfall has been cited as a major cause of population declines in tsessebe (*Damaliscus lunatus*; Dunham et al. 2004), greater kudu (*Tragelaphus strepsiceros*; Owen-Smith 1990), sable antelope (*Hippotragus niger*; Owen-Smith et al. 2012), and roan antelope (*Hippotragus equinus*; Harrington and Conover 2006), among others (Ogutu and Owen-Smith 2003).

While population declines were seen across taxa, the high rainfall of the late 1990s, and especially the year 2000, led to the recovery of many herbivore populations, with three notable exceptions. Sable, roan, and tsessebe had been three of the rarest ungulate species in the Kruger Park before the 1980s, but the droughts of 1982 and 1993 reduced their populations dramatically, with roan numbers in particular falling to 10% of their pre-drought levels by 1996 (Harrington et al. 1999, Wilson and Hirst 1977). The fate of these rare antelope, and the impact of their loss on park biodiversity, has long been a concern for park management (Grant et al. 2002). Yet, a study of climate responses of rare antelope (compared to the whole ungulate community) using the entirety of the Kruger Park's long-term census data has until now been unapproachable due to incongruities in data collection methods. The population declines of tsessebe, sable, and roan antelope are well-documented, but the causes and correlates of the declines, and the extent to which these populations have and will continue to recover, remain uncertain. Here, we outline the impacts of climate and management on herbivore populations, discuss the herbivore census data, and offer a three-decade analysis of ungulate, and especially rare antelope, responses to climate variation.

2.1.1 Climate and management drivers of herbivore population dynamics

Climate drives herbivore population trends primarily through its impacts on the vegetative layer (Seydack et al. 2012). In the short term, increasing temperatures can cause surges in plant growth, therefore supporting higher densities of herbivores. However, this initial growth can lead to nitrogen dilution and reduced carbon storage due to N

limitation, culminating in overall poorer quality forage for inflated herbivore populations (Seydack et al. 2012). Conversely, a combination of higher temperatures and CO2 levels may increase net carbon gain and encourage grass storage of biomass in the roots, leaving fewer nutrients in aboveground forage (Scheiter and Higgins 2009). In addition to these nutrient concerns, the quick and extensive desiccation of grasses during drought (Staver et al. 2019) may also limit large water-dependent grazers such as wildebeest, zebra, and buffalo. These large grazers are predicted to be replaced by smaller species that are less dependent on surface water (Veldhuis et al. 2019) and more able to switch their diets to more water-rich forbs (Abraham et al. 2019). Extended droughts may also cause grazers to decouple from the grazing lawns that they maintain in favor of tussock grass communities (Donaldson et al. 2020). Finally, intense droughts will impede plant hydraulics and photosynthesis (Anderegg et al. 2015, McDowell 2008), reduce surface water availability (Chamaillé-Jammes et al. 2007), and alter fire frequency by alternately lowering fuel loads or increasing the probability of catching fire (Pausas and Fernández-Muñoz 2012, Wilcox et al. 2020). These differential effects on grazers may also be enhanced by the longer growing periods, higher fecundity, and domination of woody plants that is predicted for savannas under future climate scenarios (Buitenwerf et al. 2012, Scheiter and Higgins 2009).

Climate change also influences herbivores directly through high temperatures and subsequent increases in water needs. Higher thermoregulatory costs for large-bodied megaherbivores (Owen-Smith 1989) may cause community composition to shift towards smaller-bodied, generalist mixed feeders (species that can switch from grazing to browsing; Abraham et al. 2019, Staver et al. 2021). In addition, herbivores must make a trade-off between thermoregulation and safety from predation (Ogutu et al. 2014, Veldhuis et al. 2019). Many herbivores rely on drinking surface water daily to supplement water lost through sweating and panting, and rising temperatures can lead to higher herbivore concentrations—and therefore, higher predator concentrations—about the

sparse surface water resources on the landscape (See Chapter 3 for a more thorough review and investigation of the thermoregulation-hydration-safety balance). This water may also become sparser under future drying, leading to the concentration of more individuals around fewer resources (Redfern et al. 2003). Herbivores may also respond to these widespread changes by favoring landscapes with more available food (Riginos 2015) or shade (Veldhuis et al. 2019) over those with better predator visibility, again increasing the risk from predators.

Concurrent with these drought-induced declines, Kruger scientists also became concerned about previous park managers' proliferation of artificial waterholes across the landscape. In the 1960s, artificial waterholes were drilled across the Kruger Park in an attempt to open the dry landscape to species that depend on daily drinking and mitigate drought-induced mortalities caused by migration interruption by park fencing. These waterholes brought these more common species such as zebra (*Equus quagga*) into the northern rangelands previously far from water sources, which had been primarily used by rare antelope species as a refuge from predation and competition (Chirima et al. 2013, Harrington et al. 1999). Because of this increased risk for rare antelope of competition and predation, more than half of the waterholes were closed in the late 1990s (Grant and van der Walt 2000, Pienaar et al. 1997, Smit 2011). Despite these closures and despite the vegetative layer recovered after rain in the early 2000s, populations of these three species remained at low densities throughout the park (Grant et al. 2002), prompting suspicions of positive density dependence (an "Allee effect") inhibiting population recovery (Owen-Smith et al. 2012). These declines and the following lack of recovery may have continuing climatic contributions, however, which can be addressed through an analysis of population trends and community sensitivities over the long term.

2.1.2 Census data and modeling for large mammalian herbivores in the Kruger Park

Long-term ecological monitoring of these complex systems is necessary to address the interacting effects of climate change, vegetative responses to climate variation, and management decisions on ungulate communities. For four decades, scientists in the Kruger National Park have continuously censused its herbivore populations across two million hectares of habitat. Data extend from 1977 to 2017 across three major multi-year aerial surveys, each with different collection methods, time periods, focal species, and stated goals: The Total Count census (TCC, 1977-1997), Distance Sampling census (DST, 1998-2017), and the Megaherbivore and Rare Game census (MRG, 1985-2017) (see Table 1 for a list of ungulates censused). Despite the effort and expense of collecting these data, the differences in methodology make species abundances difficult to compare across data sources; many research projects therefore rely on subsets of the data that used one methodology (Chirima et al. 2012, Ogutu and Owen-Smith 2005, Seydack et al. 2012, Smit et al. 2007). But, to understand climate trends in southern African savanna herbivore communities, researchers need access to the full breadth of Kruger censuses. A data harmonization solution, accompanied by a cross-method climate response analysis, will be an invaluable addition to our scientific understanding of savanna ecosystems under climate change.

A Generalized Joint Attribute Model (GJAM, Clark et al. 2017) is one such Bayesian approach that jointly models species responses to environmental covariates and explicitly includes survey effort in its framework. GJAM provides individual species' responses (here, population trends), sensitivity of species' responses to these covariates, and correlations between species responses at the data scale. The flexibility of inputs and variety of community-level outputs provided by GJAM can help answer key questions about the Kruger ungulate community's response to climate change, and especially that of declining rare antelope species.

2.1.3 Goals of this study

Much is already known about the well-studied herbivore populations of the Kruger National Park; however, the limitations of herbivore census data have left a knowledge gap for long-term herbivore community responses to slow climate change. Research on individual rare antelope species has revealed a reliance on rainfall-induced food availability for tsessebe (Dunham et al. 2004), negative effects from waterhole-induced competition from zebra for sable and roan (Chirima et al. 2013, Grant et al. 2002, Harrington et al. 1999), and a possible Allee effect on sable populations (Owen-Smith et al. 2012). Previous ungulate community studies have uncovered quasi-periodic population oscillations tied to rainfall (Ogutu and Owen-Smith 2005), greater impacts of artificial waterholes on grazer populations (Smit et al. 2007), and high association in large grazer populations with rainfall-determined food quantity (Seydack et al. 2012). And, in recent years, grazers have concentrated less about rivers and more on basaltic substrate (Chirima et al. 2012). Finally, some studies have suggested that small-bodied mixed feeders and browsers may replace large-bodied grazers as the climate favors more droughts and bush encroachment (Abraham et al. 2019, Staver et al. 2021, Veldhuis et al. 2019).

Still, there remains a gap in understanding the slow responses to climate change from the Kruger Park's decades-long dataset. In this paper, we continue the work of these predictive studies on drought effects (Abraham et al. 2019, Staver et al. 2021, Veldhuis et al. 2019), expanding on their diet- and size-level analyses to include life history rates, and pose the following hypotheses:

1. Dietary flexibility to replace dry grasses with more water-rich woody plants is predicted to help buffer browsers and mixed feeders from drought effects. Therefore, we expect grass-dependent (obligate and variable grazers) and water-dependent species will decline more in the drought period than species that do not depend on grass or surface water.

2. Slow life histories may buffer sensitive juvenile stages with long life of insensitive adult stages. Therefore, we expect that large species with slow life histories (elephant, rhinoceros, buffalo) will recover from drought more slowly than those with faster life histories (impala, kudu, wildebeest).

3. Small population sizes can fail to buffer rare species from large perturbations in environmental conditions, especially if density-dependent population thresholds must be met for growth rates to remain positive. Therefore, we expect that species with smaller starting populations (e.g., sable, roan, eland, black rhinoceros) will decline more quickly and recover more slowly than those with larger populations (e.g., impala, zebra, wildebeest).

4. Water dependence likely drives population responses to surface water sources during drought. Therefore, we expect that water-dependent ungulate populations far from rivers and waterholes will decrease in high drought years, and water-independent populations will either increase or have no response to river and waterhole-distance in drought years.

5. Grazers may depend more on a nutritious grass layer to offset forage reductions during drought. Therefore, we expect populations of grazing mammals to increase on the abundant plains of basaltic-derived soils during drought.

Finally, we can use our GJAM analysis to reveal how rare antelope respond to water sources during drought, and how the rare antelope group co-varies in response to the environment. We therefore pose two additional hypotheses:

6. Droughts may cause common herbivores (e.g., zebra) to cluster about surface water sources, leading to increased competition and predation risk for rare antelope (especially roan, which are known to prefer sparsely populated habitat, Estes 1991). Therefore, we predict that rare antelope population size will increase

with distance from waterholes, and that this increase will be greater in drought years (negative PDSI) than in non-drought years.

7. If rare antelope population declines of the late 1980s to early 1990s can be explained by similar responses by the group to environmental and climatic changes, then (1) sable, roan, tsessebe, and eland will be a distinct sub-group that show similar responses to environmental covariates and their interactions with drought, and (2) rare antelope populations will not co-vary as strongly with rivers or boreholes as those of the full set of ungulate populations.

Here, for the first time, we use thirty years of harmonized herbivore census data for fourteen species in the Kruger National Park, South Africa, to address questions of population and community responses to drought. First, we calculate population growth rates for all fourteen species, comparing trends during the 1983-1993 dry spell to the 2000-2010 drought recovery period. Then, we use a Generalized Joint Attribute Model to jointly model species responses to rainfall anomalies and surface water sources (rivers, artificial waterholes) under drought conditions (using the Palmer Drought Severity Index, PDSI) from 1982-2014.

2.2 Study area and species

2.2.1 The Kruger National Park

The Kruger National Park, covers about two million hectares of lowveld semi-arid savanna in the northeast corner of South Africa (31-32°E, 25.5-22.5°S), lying between the Drakensburg Great Escarpment to the west and the Mozambiquan coastal plain to the east. Most of the Kruger Park sits at 300m above sea level with a slight downward slope to the east, excepting three mountainous regions in the east (Lebombo), south (Malelane), and northwest (Punda Maria) (Venter et al. 2003) (Fig. 2.1).

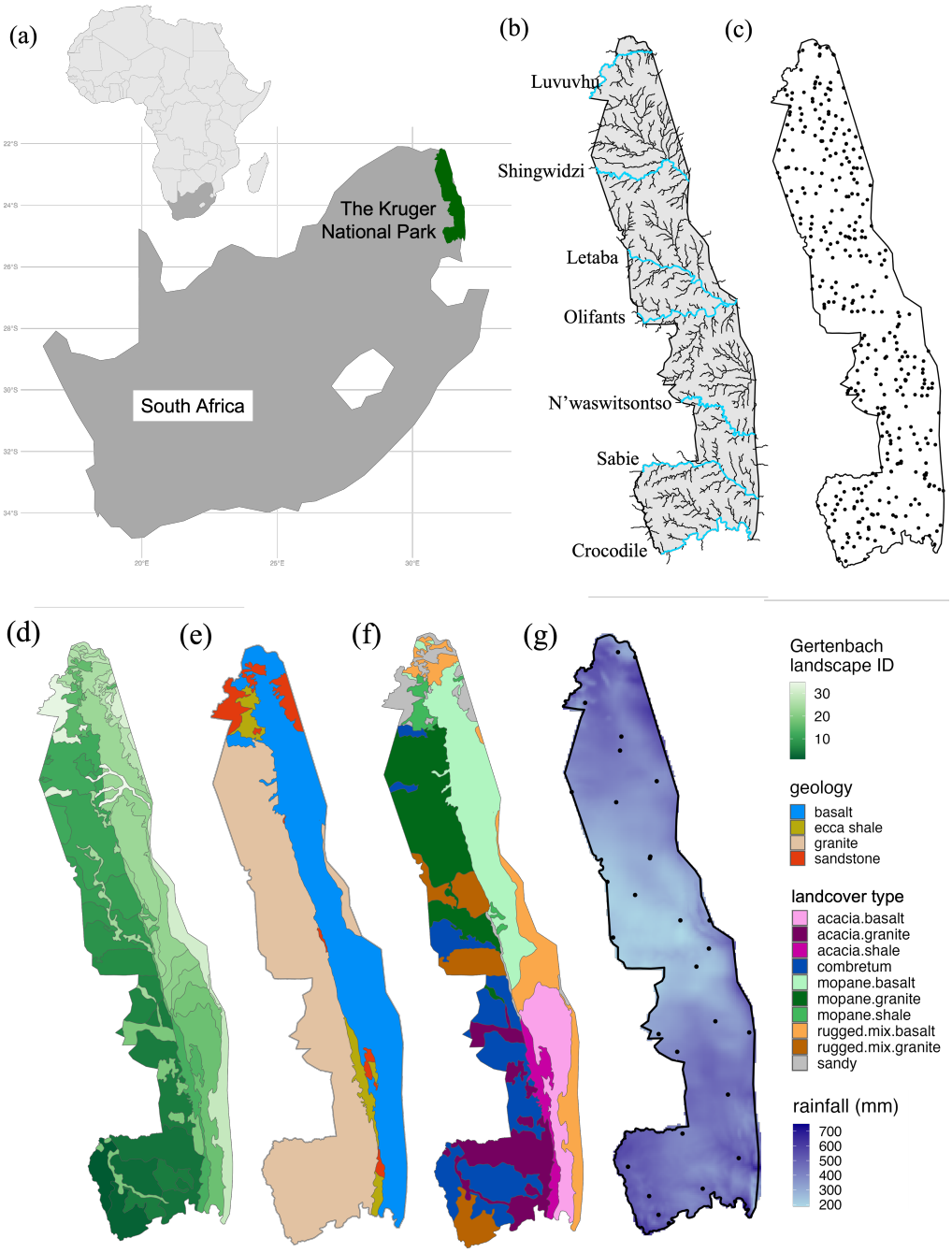

FIGURE 2.1**:** The Kruger National Park in South Africa (a); major rivers and tributaries (b), artificial waterholes (c), landcover classifications (d) and substrate types (e), the aggregate landcover-substrate classes used in this study (f), and a sample rainfall map for 1988 with 22 rainfall stations (g). ID values are not given for landcover classifications (d) as there are too many to feasibly distinguish by color, but more details can be found in Gertenbach 1983.

The Kruger Park's climate is semi-arid with hot, wet summers (November-April, maximum temperature 35°C) and cool, dry winters (May-October, minimum temperature 7°C). Rainfall follows a north-south gradient (300-500mm MAR in north; 500-700mm MAR in south) and arrives in short, intense storms during the wet summer. Major droughts occurred in 1982-83, 1991-92, and 2014-16, while 1999-2000 was one of the wettest rainfall years on record (Fig. 2.2).

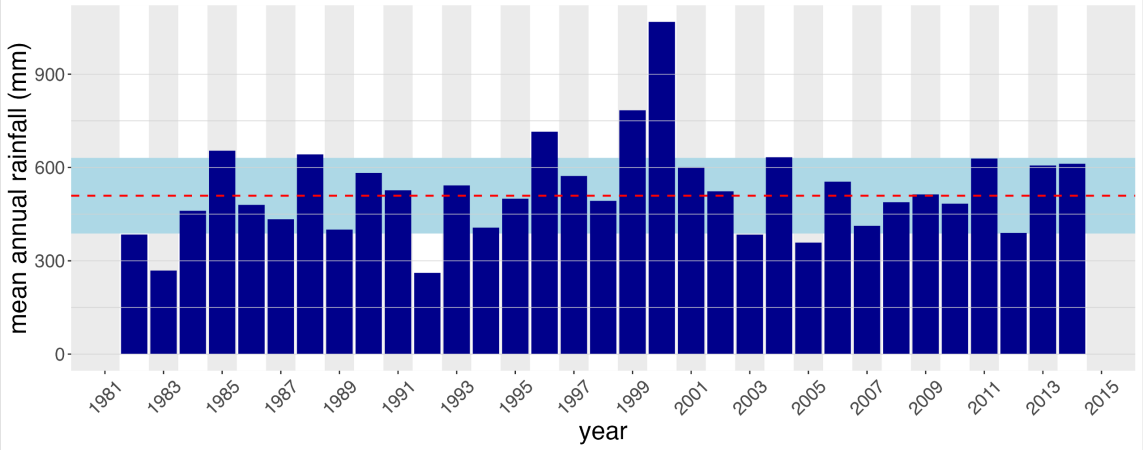

FIGURE 2.2**:** (a) Annual rainfall parkwide averages from 1982-2014, generated using rainfall surfaces from MacFadyen et al (2018). Each blue bar represents the total rainfall year, e.g., the bar for 2014 includes rainfall from July 2013-July 2014. The red dashed line indicates the average over the entire dataset and light blue band indicates plus/minus one SD from that mean. (b) Annual regional rainfall anomaly from each region's mean rainfall; colors correspond to a north-central-south split of Kruger Park. Note that 1983 and 1992 were particularly dry years, with the Kruger Park receiving less than 300mm of rainfall. In contrast, 1999 and 2000 were some of the wettest years on record, with rainfall in 2000 so high that we omitted it when calculating average rainfall.

Ecosystems within Kruger vary between open plains and closed forest, but the vast majority is mixed savanna. Geological substrate marks an east-west divide, with basaltic soils dominating the east and granites the west. Vegetation is heterogeneous, but generally follows substrate with more open savannas in the east and closed savannas in the west. 75% of the Kruger Park is savanna bushveld, a coexistence of grasses and trees without a closed canopy (Venter et al. 2003).

Volcanic basalt soils in the east of the Kruger Park lead to broad, flat plains, while

granitic soils in the west form undulating catenas, with ecca shales in between. This is also combined with rocky montane habitats and sandy Punda Maria soils, leading to a well-defined broad category of geological substrate and topology in our landcover aggregations. Vegetation types fall into three categories of dominant plant: *Colophospermum mopane, Vachellia* and *Senegalia spp.* (formerly *Acacia*), and *Combretum spp.* These three vegetative types fall into vegetative categories used to broadly characterize savannas along a moist-dystrophic (nutrient poor) to arid-eutrophic (nutrient rich) gradient, with Mimosaceae (including *Vachellia* and *Senegalia spp*) on the eutrophic end and Detarioideae (including *C. mopane*) on the dystrophic end; *Combretum spp.* fall in between these groups (Osborne et al 2018). The gradient between eutrophic and dystrophic soils can lead to broad changes in herbivore biomass and biodiversity (Osborne et al 2018).

The Kruger National Park has a long history of fencing. The southern, western, and parts of the northern boundary fences were completed in 1961. Mozambiquan authorities erected a partial eastern boundary fence in 1973, and this eastern fence was completed by the South African Government in 1974 as a result of political instability in Mozambique. The entire Kruger Park fence was completed in 1978 , completely disallowing migrations into and out of the Kruger Park for many large herbivores until 1994, when western fences were removed between the Kruger Park and private game reserves (Whyte 2001).

The major water features in the Kruger Park include five permanent rivers (the Luvuvhu, Letaba, Olifants, Sabie, and Crocodile) and several hundred artificial waterholes (Fig. 2.1b). The rivers flow from west to east and form the major natural sources of drinking water for animals during the dry season (May-August), with hectares of drylands in between (Smit et al. 2007). After the western boundary was completed in 1961, park management added more than 300 artificial waterholes to supplement water during the dry season, as migratory animals (especially wildebeest and zebra) could no

longer migrate out of the park towards dry season refugia (Gaylard et al. 2003, Pienaar 1985, Smit et al. 2007). More than half the artificial waterholes were closed in the park between 1994 and 1997 to return some regions of the park to a drier surface water state (Pienaar et al. 1997, Smit et al. 2007).

Finally, fires (which mostly occur in the dry winter months of June, July, and August) follow vegetation, with higher-intensity and more frequent fires striking the eastern basaltic plains, and less-frequent, lower-intensity fires in the western bushveld. These fire regimes help maintain the Kruger Park's distinctive vegetative structures and are carefully monitored and prescribed by park management, which over the years has used several fire management policies of different intervention levels (see Biggs and Potgieter 1999, van Wilgen et al. 2014).

2.2.2 Focal Species

Focal species are listed in Table 2.1 and consist of the 14 largest herbivores in the park. All species in this study are considered ungulates, hoofed mammals in either the order Perissodactyla (odd-toed ungulates; in this study, both rhinoceroses and zebra) or Artiodactyla (even-toed ungulates), except bush elephant (*Loxodonta africana*) which are members of Proboscidea. Data for species diet were provided through the work of Codron et al. 2007; water requirements through Kihwele et al. 2020; group sizes and feeding guilds through Hempson et al. 2015; sizes and gestation rates through Western 1979, Wilson and Hirst 1977 (Table 2.1).

For the purposes of this study, "rare antelope" include roan, tsessebe, and sable, as explained in the Introduction; however, we also add eland (*T. oryx*) to this list. Although eland have not traditionally been categorized with rare antelope in the Kruger NP, their population trends within Kruger are very similar to the trends of the three traditional "rare antelope" species.

Finally, elephant populations in the Kruger NP were heavily managed from 1961 to

Table 2.1: List of species, traits, and census datasets (TCC = Total Count Census; DIST=Distance Transects, MRG = Megaherbivore and Rare Game) for each of fourteen species. $\%C_4$ in the diet is given as a proxy of grass dependence, while % dung and urine moisture is a proxy of water dependence (high moisture = high dependence). Body mass estimates, gestation length, gut type (R = Ruminant, NR = Non-Ruminant), feeding guild, and herd size are also given (See Sec. 2.2.2 for trait data sources). Species marked with an asterisk (elephant and buffalo) were analyzed using bull and mixed-herd data separately; all other species were not split by sex.

Species	Common name	Body Mass (kg)	Feeding Guild	% Moist.	% C4	Gut type
*Loxodonta africana**	elephant	4100	mixed	72	NA	NR
*Syncerus caffer**	buffalo	600	grazer	58	88	R
Ceratotherium simum	white rhino	2100	grazer	NA	90	NR
Diceros bicornis	black rhino	1000	browser	77	9	NR
Hippotragus equinus	roan	260	grazer	NA	96	R
Hippotragus niger	sable	210	grazer	48	98	R
Damaliscus lunatus	tsessebe	130	grazer	32	94	R
Tragelaphus oryx	eland	500	browser	45	NA	R
Aepyceros melampus	impala	50	mixed	31	60	R
Giraffa camelopardis	giraffe	1100	browser	44	5	R
Equus quagga	zebra	280	grazer	62	92	NR
Connochaetes taurinus	wildebeest	220	grazer	42	90	R
Kobus ellipsiprymnus	waterbuck	210	grazer	60	90	R
Tragelaphus strepsiceros	kudu	200	browser	43	7	R

Species	Gestation (days)	Herd size	1990 count	TCC	DST	MRG
*Loxodonta africana**	660	30-150	11,547	x		x
*Syncerus caffer**	339	>150	42,716	x		x
Ceratotherium simum	504	5-15	2,154	x		x
Diceros bicornis	468	1-2	60	x		x
Hippotragus equinus	270	5-15	194	x	x	1995+
Hippotragus niger	270	5-15	2,210	x	x	2000+
Damaliscus lunatus	270	>150	761	x	x	2002+
Tragelaphus oryx	263	30-150	744	x	x	2003+
Aepyceros melampus	191	30-150	116,744	x	x	
Giraffa camelopardis	437	30-150	5,031	x	x	
Equus quagga	363	5-15	32,244	x	x	
Connochaetes taurinus	234	>150	14,253	x	x	
Kobus ellipsiprymnus	257	5-15	3,176	x	x	
Tragelaphus strepsiceros	210	5-15	6,044	x	x	

1995 in efforts to limit damage to large old-growth trees and increasing densities due to boundary fencing. Elephant populations were culled annually down to 6,000 to 8,500 individuals until culling ceased in 1994-95 (Whyte et al. 2003, Whyte 2001). Buffalo were also culled in 1991 and 1992 to limit the spread of bovine tuberculosis (Rodwell et al. 2001). Because of broad elephant culling, although we include survey information in both analyses in this paper, conclusions made about elephant populations' responses to climate variables must consider these years of heavy management.

2.2.3 Species traits

In size, species range from medium-sized impala (*Aepyceros melampus*) at 50kg to the largest land mammal, the African bush elephant (*Loxodonta africana*) at 4,100kg. Size becomes important to many species in that smaller individuals (1) often prefer quality over quantity of forage, and (2) have a lower body mass to surface area ration, making passive heat radiation a more efficient thermoregulation strategy. Larger animals may struggle to offset heat loads, and often prefer to maximize quantity of forage intake over quality, given that the efficiency of nutrient extraction in the gut again diminishes with size (Bell 1971, Jarman 1974, Owen-Smith 1989).

Species can be divided by water needs, from obligate daily drinkers ("water dependent") to species needing to drink only every few days, or not at all ("water independent"). Water dependent individuals often gather around surface water, such as rivers or artificial waterholes, during the dry season (Lamprey 1963, Western 1975). Data for water dependence in this chapter come from a 2020 study by Kihwele and colleagues, which inferred water dependence on six functional traits, including dung moisture content and urine osmolality; high moisture content in excreta can be used as a proxy for high water dependence (Table 2.1, Kihwele et al. 2020).

Ten herbivores in this dataset are ruminants, which use separate stomach chambers to re-digest plant matter multiple times, extracting the most nutrients possible

while breaking down fiber (Hempson et al. 2015). Non-ruminants, such as zebra (*Equus quagga*), bush elephant, and both rhinoceros species (white *Ceratotherium simum* and black *Diceros bicornis*), instead complete digestion in the hindgut, extracting fewer nutrients but able to eat more quantity of forage without resting to ruminate.

Dietary requirements can also be separated into three broad categories: grazers (grass-eaters), browsers (tree- and forb-eaters), and mixed feeders (those that often eat both). Most ungulates in this study fall somewhere along a spectrum from browser to grazer, so here we use data from a 2007 study by Codron and colleagues which, for each species, measured the percentage of fiber content that contains C_4 species. As most savanna grasses are C_4, a high percentage of C_4 indicates high grass in the diet (Codron et al. 2007).

Group size varies among species (Hempson et al. 2015). Most form groups of 5-15 or 30-150 individuals, while black rhinoceros are only found singly or in pairs. Wildebeest (*C. taurinus*) and tsessebe (*D. lunatus*) often form groups larger than 150. Buffalo herds can span from fifty to 1,000 (Estes 1991, Hempson et al. 2015, Kingdon 2015). These large groups can cause observers to either over- or under-estimating group size or to double-count herds themselves (which may span across census blocks).

2.3 Materials

2.3.1 Regions of Interest

The Kruger National Park can be divided into 35 landscapes, each defined as "an area with a recurrent pattern of plant communities with their associated fauna and abiotic habitat" (Coetzee 1983, in Gertenbach 1983). A comprehensive work by Gertenbach (1983) provides detailed descriptions of each landscape type.

For our GJAM analysis, all count and effort values were aggregated to 166 regions of interest (Fig. 2.3) that follow the 35 Gertenbach landscape types (2.1d). These were then further divided by a 5km buffer around rivers, due to some landcover types spanning

Table 2.2: Geological parent material descriptions and substrate categories in the Kruger National Park. See Fig. 2.1e for a map of these geological substrate categories in the Kruger Park.

Parent Material Description	Category	Park Location
Alkaline (nephelinite) lavas; Andesite with subordinate tuff; Olivine-poor basalts; Olivine-rich basalts, subordinate alkali-basalts and shoshonites; Rhyolite, dacite (Lebombo Stage)	basalt	east
Shale with coal seams, mudstone, grit (Ecca Series)	ecca shale	center seam
Diabase Granite, gneiss, migmatite, amphibolite, schist, and undifferentianted metamor; Granophyre; Olivine gabbro	granite	west
Alluvium; Conglomerate, marl, sandstone (Malvernia Beds); Fine grained sandstone, mudstone, chert (Cave Sandstone and Red Bed Stages); Red and yellow sand (Aeoliam); Sandstone, quartzite, with intercalated andesite	sandstone	center seam; north

too large a latitudinal (and therefore, rainfall) gradient. The riverine split further allows us to consider the importance of surface water for animals far from rivers as well as the north-south rainfall gradient.

2.3.2 Geological Substrates

Maps of soil substrate material in the Kruger Park were provided by SANParks. We then aggregated the eleven parent materials into four major categories: basalts (east), granites (west), ecca shales (center seam between east and west), and sandstones (some center seam, mostly north in the Punda Maria region) (Fig. 2.1c, Table 2.2). Our analysis here focuses on the east-west basalt-granite divide, as these geological substrates cover the majority of the park.

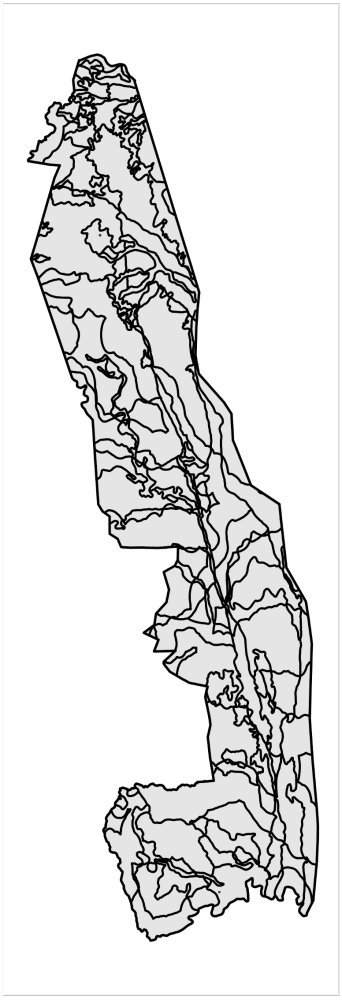

FIGURE 2.3**:** 166 regions of interest, determined based on the shapes given by the 35 distinct Kruger landcover types given by Gertenbach (1983) (Fig. 2.1 and separated by a 5km buffer zone around major rivers (Fig. 2.1b), to break up long vertical shapes.

2.3.3 Rainfall

Rainfall values for 1982-2014 were interpolated by MacFadyen et al (2018) across the Kruger Park monthly using rainfall station data from 22 stations, estimates from the Climate Hazards group Infrared Precipitation with Stations dataset CHIRPS, Funk et al 2015), and other locational factors such as distance from Indian Ocean (See 2.1g for an example rainfall interpolation map for 1988, as well as rainfall station locations).

2.3.4 Artificial waterholes

Artificial waterhole maps were collected from data provided by Scientific Services. For the population climate response analysis, for each region in Fig. 3 we generated a ran-

dom sample of 500 points within each of 166 regions, calculated each point's distance from nearest artificial waterhole, and averaged all 500 distances to obtain one value for the region. These data also include open and closure dates, which are particularly important after the 1994-1996 closure of over half of waterholes; therefore, the "average distance from waterhole" covariate used in our analysis of population responses is updated every year to reflect only open waterholes.

Other methods considered include a measure of "waterholes per hectare" for each region, however many regions had no waterholes, or may have a waterhole just inside a neighboring region; this measure was chosen to better assess the access to water across each region.

2.3.5 Rivers

River data were provided by the WWF HydroSHEDS Free Flowing Rivers Network, which uses SRTM elevation data to map free-flowing rivers at a resolution of 15 arc-seconds (Grill et al. 2019). For population climate response analysis, we used the same method as above, generating 500 random points in each of 166 regions in Fig. 3 and measuring the average distance-from-river.

Other methods considered include a raw measure of "length of river in region"; however, because many of these region boundaries are defined by rivers, this measure would have omitted rivers that were just over the border, or erroneously counted a large river-bound region with no rivers within as "high concentration" given the length of the perimeter.

2.3.6 Herbivore Census Data

Data for all censuses were collected in the May-August dry season to maximize visibility and the clustering of individuals around drainage lines and water sources. For some species, males, females and calves were counted separately; however, for all but

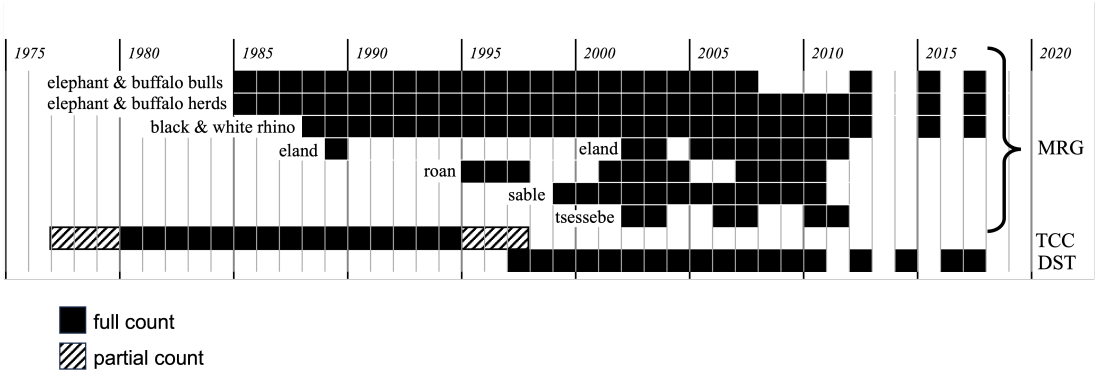

FIGURE 2.4**:** Timeline of data collection for all major surveys in the Kruger Park: Total Count Census (TCC), Distance Transects (DST), and Megaherbivore and Rare Game (MRG). Hashed lines indicate a partial census was conducted. Species labels indicate when each species was introduced for the MRG.

elephant and buffalo, we aggregated all census counts together, ignoring sex. Elephant and buffalo data were consistently counted separately for bulls and mixed herds, and there is evidence that these groupings have significant ecological differences, mostly due to physical size (male elephant can be twice as large as females) (Smit et al. 2007) and herd size (male elephant and buffalo usually congregate in small groups of 1-10, while mixed herds can be as large as 350 and 1000, respectively (Hempson et al. 2015) so these groups remained separated for our analyses.

All data collected indicated species, location (GPS and census block or transect ID), sex if possible, number of individuals, and year. Data were processed to remove obvious miscounts (e.g. in 1990, the total buffalo count was 13 in TCC, an obvious year with missing data or no effort) to ensure the most stable data from year to year. See Table 2.1 for a summary of data sources for each species in this study, and Fig. 2.4 for a timeline summary of dataset coverage. All census data were provided by SANParks Scientific Services.

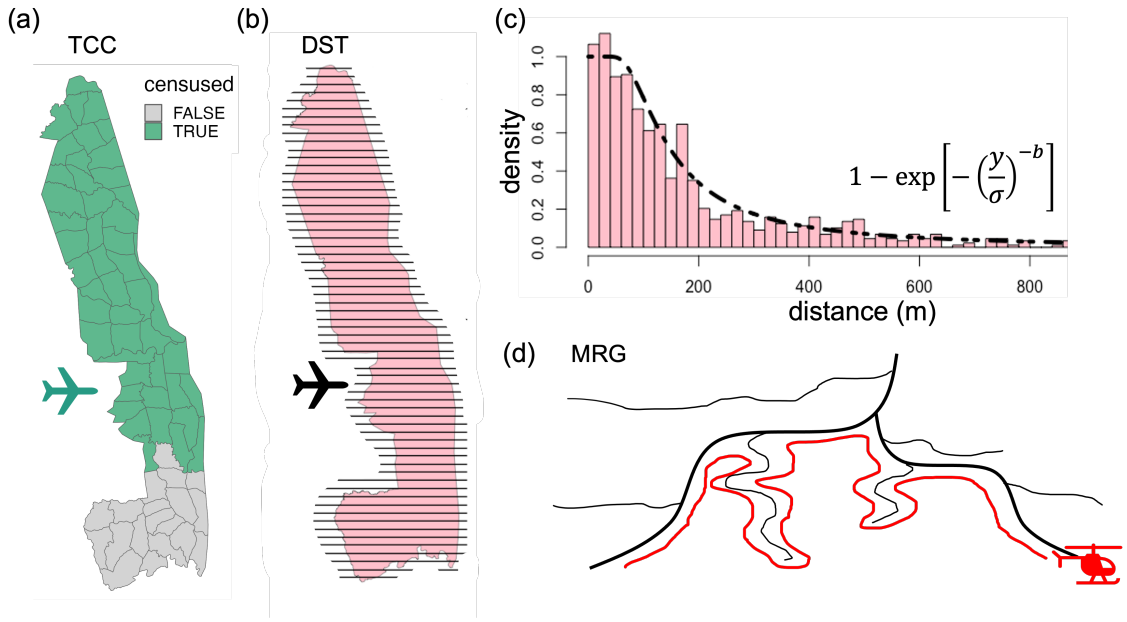

FIGURE 2.5**:** (a) Coverage for the Total Count Census. Each segment of the park is a "census block" which was flown contiguously over consecutive days. All census blocks were not flown in all years; in this example, the south was omitted from the 1995 census. (b) Coverage for the Distance Transect census. Transects were flown laterally at different intensities of coverage; in this example, sampling intensity was at 15% for the 1998 census (Kruger et al. 2008). (c) An example Distance density curve superimposed over a histogram of individual sighting density over distance-from-aircraft, in meters). Note that smaller distances are more well represented, as an observer is more likely to see individuals close to the aircraft than further away. We fit these data to a hazard-rate function (given above the histogram), which is consistently high close to the aircraft before falling off rapidly. A species that is difficult to detect (small, nocturnal) would have a steeper decline than one that is easier to detect (large, gregarious). (d) Example helicopter flight path (adapted from Whyte 2001). Black lines represent rivers and tributaries ("drainage lines"), while red is a hypothetical helicopter path.

Total Count Census (TCC): 1977-1997

Large mammals in Kruger National Park were irregularly censused from 1965-1975. However, systematic annual aerial censuses started in 1977. From 1977-1997, parallel transects (400m each side) were flown across 66 census blocks in the park (Fig. 2.5), with full coverage from 1985 to 1993. From 1977-1984, areas in the far north with sparse population coverage were not censused, and from 1994 to 1997 the south was only flown once (Fig. 2.5). While many mammal species were surveyed during this time,

in this study we only cover the fourteen largest mammalian herbivores in the Kruger Park (Table 2.1, Fig. 2.4).

Transects were flown via fixed-wing aircraft with four observers, two per side. In earlier years, abundance and location of each species were recorded on paper maps, but after 1994 the use of handheld Garmin GPS was introduced to improve efficiency and location accuracy (Viljoen and Retiff 1994).

Sources of observational bias for the TCC counts include undercounting of large groups, missing solitary animals or small groups, and undercounting or missing groups entirely due to habitat preferences (e.g., groups in dense shrub or forest may be missed) (Redfern et al. 2002). Additionally, while individual observers may have bias in their count ability, specific rules for environmental conditions and methods were enacted to attempt to minimize observer, environmental (e.g., rain or smoke) and method biases (Viljoen and Retiff 1994, Viljoen 1989). Although counts were originally recorded individually by observer, current data available has already been processed and does not include observer identity.

Distance Sampling Census (DST): 1998-2017

In 1998, Scientific Services shifted to a Distance sampling method as a part of their new Strategic Adaptive Management plan (Braack et al. 1997, Kruger et al. 2008, van Wilgen and Biggs 2011), in which lateral, evenly spaced strip transects are flown across a lower percentage of park area than the TCC. Distance sampling reduces the overall area covered, thereby saving time and fuel costs.

In addition to abundance and location, observers note the distance-from-aircraft for each group observed. Because the human ability to detect an animal from an aircraft naturally declines over distance (animals far away are hard to see), observations naturally follow a decaying "detection curve" (Fig. 2.5c), with the frequency of observations shrinking as distance grows. With this information, Distance sampling allows for a

good estimate of species density, especially for common species, and controls for some of the bias inherent in the TCC (e.g., DST considers that detection at long distances declines) (Barry and Welsh 2001, Kruger et al. 2008, Miller et al. 2019).

From 1998-2017, surveyors flew lateral transects across the width of the park; each observation included species, herd size, and distance from aircraft (Kruger et al. 2008). From 1998-2000, lateral transect lines were flown covering 15% of the park's area; from 2001-2004, 22% of the park was covered; from 2005 onward, 28% (See example Fig. 2.5a). As in the TCC, DST used fixed-wing aircraft with four observers, and took place during the dry season (May-August) each year.

According to a review of the method (Kruger et al. 2008), some key Distance estimation assumptions were violated (that all animals on the transect line are detected, all animals detected are in original locations), and this method likely underestimates the abundance of rare species such as roan or tsessebe; however, samples were adequately precise for more common species such as zebra and impala (Kruger et al. 2008). For this reason, although we provide density estimates for all species, we recommend care when using densities for rare antelope (eland, tsessebe, sable, roan) and low-density black rhino, as they may have been undercounted.

Megaherbivore and Rare Game Census (MRG) 1985-2017

Concurrently with the TCC and DST surveys, the MRG (1985-2017) specifically focused on buffalo, elephant, black rhino, and white rhino (Joubert 1983, Whyte 2001). As concerns grew about rare antelopes' population decline, roan, tsessebe, eland and sable antelope were added to the MRG at later points starting in the 2000s (Table 2.1, Fig. 2.4). Like the fixed-wing surveys, the helicopter survey also included four observers (two per side) but took less time to complete (22 days on average). For this reason, MRG surveys were conducted in the last two weeks of August and the first two weeks of September each year, rather than during the entire May-August dry season. Flight paths generally

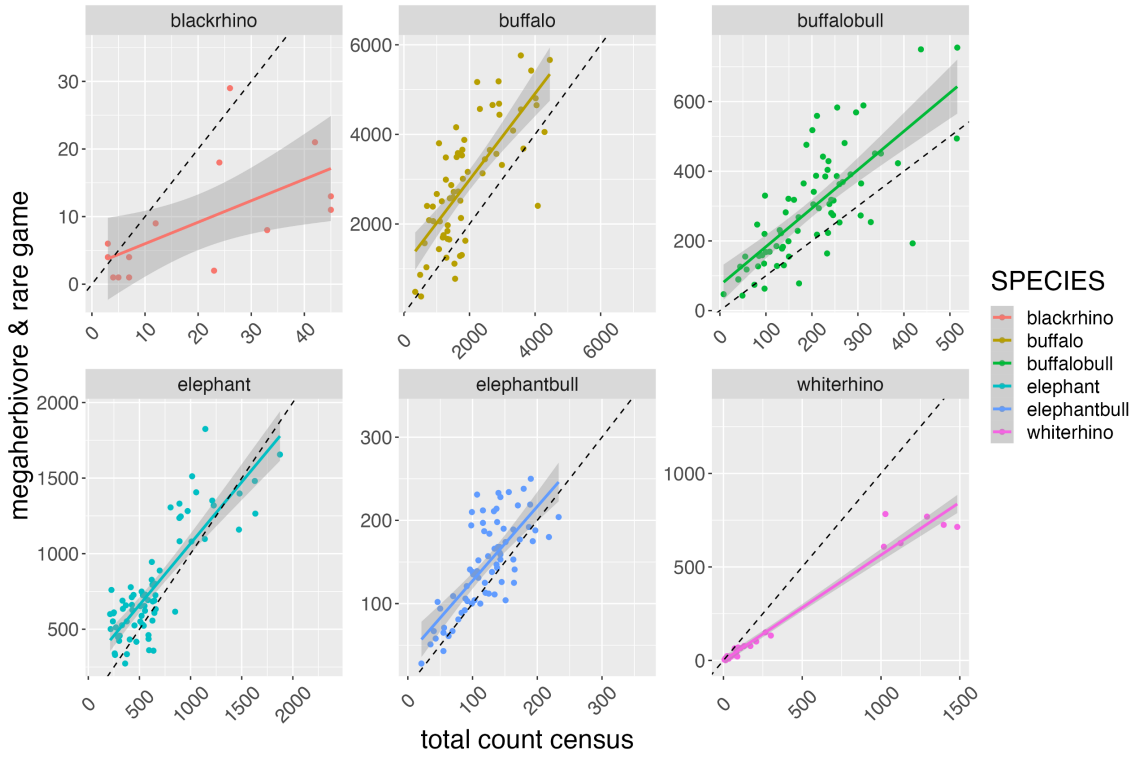

FIGURE 2.6**:** Comparison of total count census (TCC) with megaherbivore and rare game census (MRG) numbers in years that overlap. The black dashed line indicates 1:1 ratio of MRG to TCC. Most species are undercounted in TCC compared to values in MRG, except for white and black rhinoceros.

were at 150m and a speed of 100 knots, and tracked drainage lines (See example Fig. 2.5d), around which herbivores cluster in the dry season (Smit et al. 2007, Whyte 2001).

The MRG census is considered to be more accurate than either DST or TCC for several reasons. Focusing on a few key species allows for observer attention to be more focused than a fifteen-or-greater species census. The helicopter is able to maneuver close to herds, causing animals to break into smaller, more easily counted groups. Helicopters allow for better forward visibility and can hover, staying low over each group and allowing for more accurate counting and recounting. Surveying at the same time every year minimizes year-to-year bias. Finally, a helicopter is able to maneuver along drainage lines, where most species congregate during the dry season, so confidence in a full count of individuals in a region is higher; in addition, following drainage lines

Table 2.3: Calculations for effective survey effort (area in hectares) for each region R in Fig. 2.3. For TCC effective effort is equivalent to total area surveyed in hectares (Fig. 2.5a). For DST, Distance curves were calculated for each species S, and the proportion of total regional area that is allotted as the effort in hectares for each R, S is given as the effective width of transect surveyed (the area under the Distance curve (Fig. 2.5b), greater for more easily spotted species, lesser for more cryptic species) multiplied by the length of transects flown (Fig. 2.5c) through the region (Eqn. 2.2) For MRG, we calculated a species-specific constant k as the average ratio of MRG totals to TCC totals for each species, when available. (Fig. 2.5d)

	effective area calculation for region R
Total Count (TCC)	total hectares × proportion of R surveyed
Distance Sampling (DST)	length of transects flown × sum under Distance curve for each species S
Megaherbivore and Rare Game (MRG)	total hectares × species-specific constant

allows the helicopter pilot to function as an observer, as they may not need to strictly follow a lateral transect, instead following the easily recognizable visual features of the landscape (Whyte 2001).

2.4 Methods

2.4.1 Data Harmonization

The basis of our data harmonization method for census data involved effective survey effort, which was calculated for each census, year, and species, based on known attributes of each survey. For this study, effort is measured as hectares surveyed.

For TCC, survey effort is calculated as total regional area flown. Some census blocks were not flown every year (Fig. 2.4, Table 2.3); in these years and regions, survey effort is reduced to reflect actual area flown. Species count data was aggregated over each region for each year.

For DST, survey effort is given for each region r by the total transect length L_r multiplied by the survey width W (the distance of reliable species detection from aircraft). Transect placement and density changed by year (y) (Fig. 2.5b, Table 2.3); therefore, we calculated L_{ry} by summing the length of all transect segments over each region in

each year. In a Distance-sampling scheme, survey width W changes by species (s) detectability, often determined by size, cryptic nature, and habitat choice. We calculated W_s for each species based on the spread of count density with distance-from aircraft. This was done for each species by pooling survey counts and distances across all survey years, then using the R package Distance (Miller et al. 2019) to fit a detection function to the frequency of detection at each distance (Fig. 2.5c). In general, animals far from the aircraft are hard to detect, so counts are more frequent at short distances. We then integrated the detection function (here, we chose a hazard-rate function) across the maximum survey width (400m) to calculate W_s in meters:

$$W_s = \int_0^{400} \left(1 - \exp\left[\left(\frac{m}{\sigma_s}\right)^{-b_s}\right]\right) dm \tag{2.1}$$

where b_s and σ_s are species-specific fitted parameters for the hazard-rate detection function. Animals that are hard to detect have few counts at large distances, and therefore a small value of W_s and a smaller value for survey effort:

$$E_{s,r,y} = L_{r,y} \times W_s \tag{2.2}$$

One weakness of this method is that fitting a detection function requires species abundances above a low threshold (>60 counts) in order to properly model detection. To address this, the Distance package uses aggregated data from similar common species to estimate detection curves for rare species such as eland, tsessebe, roan, and black rhino (Miller et al. 2019).

Finally, to estimate effort for the MRG surveys, we must account for the increased effort in MRG compared to TCC. Because MRG surveys were flown across drainage lines (Fig. 2.5, Table 2.3) and not on straight, evenly spaced transects, MRG counts were generally larger than TCC or DST counts. This could either be due to double-counting (animals move between flight paths and are counted twice) or more accurate counting

Table 2.4: Estimated species-specific constants for calculating MRG effort for each species, given as the ratio of MRG counts to TCC counts, on average. Most species had positive ratios (i.e., more MRG than TCC counts), except black and white rhino, which were consistently undercounted in MRG compared to TCC. Rare antelope had almost no overlap between MRG and TCC, so the overcount-undercount ratio could not be assessed and no offset was added.

species	constant
buffalo (herd)	1.65
buffalo (bull)	1.64
elephant (herd)	1.35
elephant (bull)	1.25
roan	1
sable	1
eland	1
tsessebe	1
black rhino	0.61
white rhino	0.6

(drainage line flight paths allow multiple opportunities to sight cryptic animals). To account for these differences, we ran a linear regression between TCC and MRG counts for each species (Fig. 2.6, Table 2.4) to obtain a species-specific constant by which we augmented the total regional area covered.

For buffalo and elephant herds and bulls, MRG consistently returned higher abundance values than TCC, as expected. However, for populations of black and white rhinoceros, the TCC consistently returned higher abundance than MRG; see the Discussion for more on this discrepancy. Finally, because there were few years where rare antelope were counted in both TCC and MRG survey values (only 1995-1997 for roan), we chose a species-specific constant of 1.0. This harmonization technique for MRG has some uncertainty that is discussed in detail in the Discussion.

2.4.2 Population growth rates during drought decline and recovery

For our first analysis on herbivore population responses to drought (Question 1), per-capita population growth rates were calculated and compared for an era of drought-

induced population decline N_1 = (1984-1994) and an era of above-average rainfall and recovery N_2 = (2000-2010) across the entire park. We calculated growth rates $r(s,y)$, where $w(s,y)$ is the population density for species s in year y:

$$r(s,y) = \log\left(\frac{w(s,y+1)}{w(s,y)}\right) \tag{2.3}$$

and calculated the mean for both the decline and recovery intervals:

$$\hat{r}_{N_i} = \frac{1}{n}\sum_{y \in N_i} r(s,y) \tag{2.4}$$

We then modeled the average growth rate during the recovery period as a function of size, gestation rate, and water and grass dependence to address Hypotheses 1-4.

2.4.3 Drought impacts through distance from water source

For our analysis of drought interactions with landscape features, we used GJAM to jointly model the response of each species S for each region-year to each environmental covariate Q, with residual covariance Σ. Environmental covariates include: PDSI, rainfall anomaly, distance from waterholes, and distance from rivers, as well as an interaction with PDSI for each other covariate. Finally, although each species' preferred habitat is well known, we account for any covariance coming from preferred habitat by including landscape type in our model.

Our GJAM model is given as follows:

$$\mathbf{w}_i | \mathbf{x}_i, \mathbf{y}_i \sim MVN(\boldsymbol{\mu}_i, \boldsymbol{\Sigma}), \tag{2.5}$$

where $\mathbf{w}_i$ are the responses, given counts per effort $\mathbf{y}_i$ and the length-Q design vector $\mathbf{x_i}$, which contains environmental covariate values. The mean vector $\boldsymbol{\mu}_i = \mathbf{B}'\mathbf{x}_i$ contains the $Q \times S$ matrix of coefficients $\mathbf{B}$ and design vector $\mathbf{x}_i$. $\boldsymbol{\Sigma}$ is an $S \times S$ covariance matrix.

Most covariates were uncorrelated (waterholes-rainfall 0.02; rivers-rainfall 0.00, rivers-waterholes 0.05, PDSI-waterholes 0.04, PDSI-rivers 0.00), except rainfall anomaly and PDSI (correlation = 0.68). This correlation was predictable, as rainfall is a measure included in calculating PDSI; however, because rainfall anomaly from the mean is a regional measure of rainfall relative to the mean for that region, it can be a useful measure of rainfall refugia during drought years.

2.4.4 Community sensitivity to climate covariates

Because GJAM models species jointly, it also provides a species covariance matrix (Σ). This matrix can be used to calculate a matrix of community sensitivity ($\mathbf{f}$) to environmental covariates using a matrix of fitted beta coefficients ($\mathbf{B}$) for environmental covariates:

$$\mathbf{f} = \text{diag}(\mathbf{B}\boldsymbol{\Sigma}^{-1}\mathbf{B}') \tag{2.6}$$

Sensitivity vector $\mathbf{f}$ can be used to understand how sensitive community responses are to the environment, as well as subgroups (such as rare antelope) by only using the covariance matrix for select species. Sensitivity is a joint measure of species covariance and the variance of the environment; both must be large in order for sensitivity to be high.

In addition to sensitivity, we can also calculate a matrix of the environmental component of species covariance ($\mathbf{E}$) with the following:

$$\mathbf{E} = \mathbf{B}'\mathbf{V}\mathbf{B} \tag{2.7}$$

where $\mathbf{V}$ is a matrix of variance in the predictor variables, and B is the matrix of fitted beta coefficients for predictors. The $\mathbf{E}$ matrix represents similarity between species' responses to covariates, with similar species having similar columns in $\mathbf{B}$ (Clark et al.

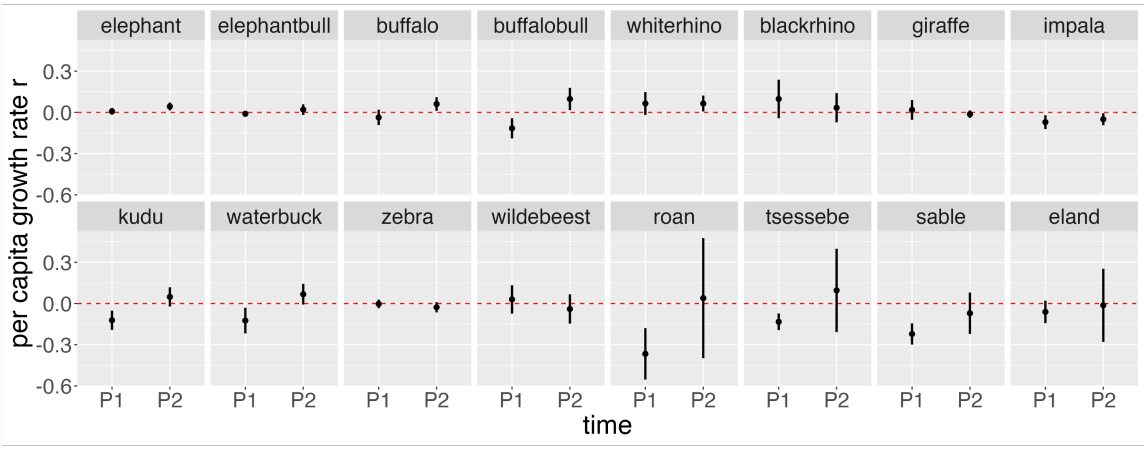

FIGURE 2.7**:** *Per capita* growth rates by species during decline period P1 (1984-1994) and recovery period P2 (2000-2010). Note that rare antelope are all grouped in the bottom right four figures. Only two species had a positive population growth rate during the decline period: white and black rhino, likely due to re-introduction efforts before the turn of the century. Kudu, waterbuck, and buffalo all faced significant, rapid recovery, while elephant and impala growth rates were slower to recover. Zebra, wildebeest, and giraffe growth rates fell further during this period. Rare antelope growth rates all improved, but none were significantly positive even during the recovery period. See Table 8 for mean r and standard error values, as well as interpretations.

2017). Thus, with **E** and **f**, we can gain further understanding than we would through simple beta-fitted coefficients of species' relationships with their environment and with other species.

2.5 Results

Here, we found that long-term drought decline and recovery rates were not dependent on herbivore size, gestation rates, water dependence, or grass dependence, but that small population sizes declined more quickly and struggled to recover after drought periods. We also found that large grass-dependent species such as buffalo and elephant relied heavily on waterholes during drought years, and that rare antelope rely on waterholes more than anticipated and formed a unique group based on responses and sensitivity to environmental covariates.

Population growth rates (Fig. 2.7) were averaged over ten years and a large area,

and therefore are noisy. Low population counts can increase noise in calculating year-to-year growth rates, as an increase of one individual at a small population is more meaningful than in a large population. Although some species growth rates do cross zero, these can still be meaningful—noisy growth rates indicate a population in flux, without a steady growth trend. It is therefore still useful to discuss even noisy trends in the context of population stability.

2.5.1 H1: Grass and water dependence did not determine drought period declines

In Hypothesis 1, we expected that grass- and water-dependent species would decline more during the drought period than mixed feeders or grazers. In general, our results did not strongly support this expectation (Fig. 2.7, Table 2.5). Some large and medium-sized grass-dependent species did decline during the drought period: buffalo, roan, tsessebe, sable, elephant, waterbuck. However, zebra, wildebeest, and white rhino, though grass-dependent, did not decline during the drought period. Furthermore, two species that are not grass-dependent – kudu (a browser) and impala (a small mixed feeder) – declined, despite their access to browse. Neither measure of grass dependence (%C4 in diet, $p = 0.55$, Fig. 2.8a) or water dependence (% moisture in dung/urine $p = 0.57$, Fig. 2.8b) was statistically significant in its impacts on population decline rates.

2.5.2 H2: Slow life history did not determine recovery rates

In Hypothesis 2, we expected that larger species with slow life histories would recover more slowly than smaller species or those with faster gestation rates. There is no evidence that either size ($p = 0.39$, Fig. 2.8c) or gestation rate ($p = 0.34$, Fig. 2.8d) predicted population growth rates during the post-drought recovery period.

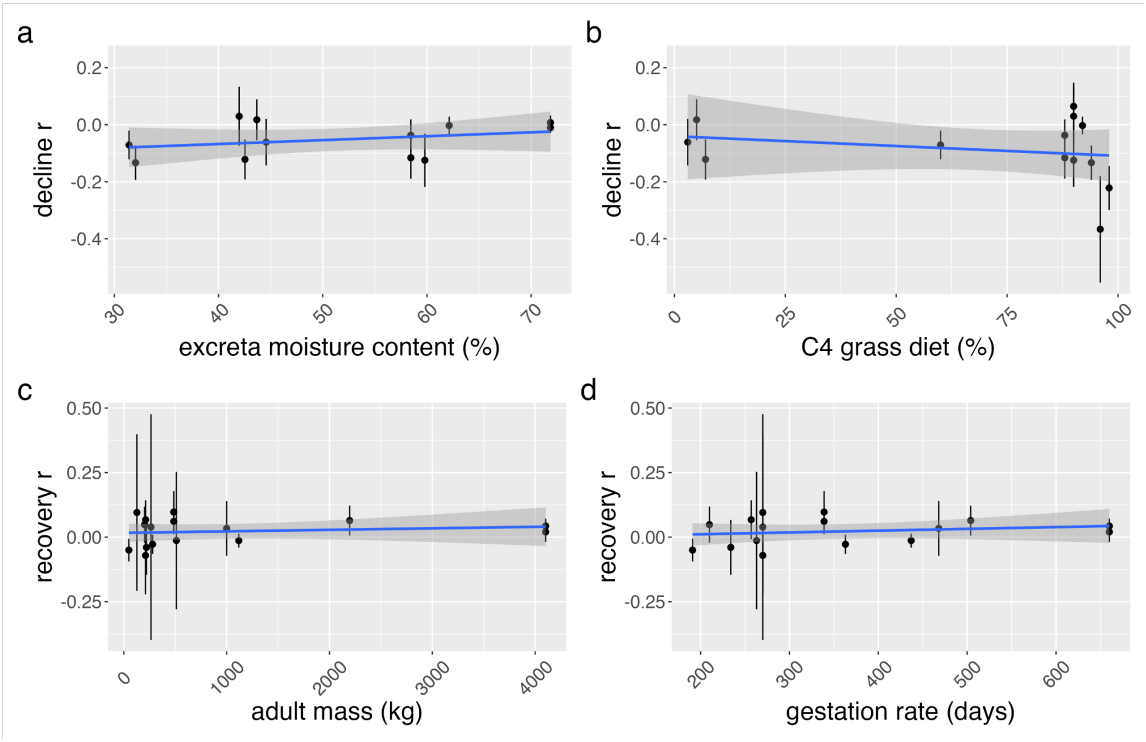

FIGURE 2.8**:** Decline period population growth rates (r) as a function of (a) dung and urine moisture content (a proxy for water dependence, $p = 0.24$, Kihwele et al. 2020) and (b) dietary % of C4 (a proxy for grass dependence, $p = 0.43$, Codron et al. 2007) Recovery period population growth rates as a function of (c) size ($p = 0.52$, Estes 1991) and (d) gestation rate ($p = 0.51$, Western 1979, Wilson and Hirst 1977). None of these covariates were statistically significant to species' growth rates during the drought recovery period (all $p \gg 0.05$)

2.5.3 H3: Small-population rare antelope declined quickly with ambiguous recovery

In Hypothesis 3, we expected that species with smaller initial populations would decline more quickly and recover more slowly than those with larger populations. In agreement with our predictions, some species with small initial populations (roan antelope, tsessebe, and sable antelope) all had very low per capita population growth rates (< -0.1) and highly variable recovery rates centered around zero (Fig. 2.7, Table 2.5). Black rhinoceros did not decline as much as expected, instead experiencing steady population growth during both the decline and recovery periods (similar to white rhino).

Table 2.5: Species-specific per capita growth rates, averaged across all regions of interest, in the decline period (1984-1994) & recovery period (2000-2010), with interpretations & general explanations for population trends. Trends are considered "slight" or "slow" if error bars cross zero but mean is noticeably not equal to zero. Trends are "fast" if error bars do not cross zero but the magnitude of the mean is less than 0.2. Trends are "rapid" if the magnitude of the mean is greater than 0.2. See Figure 2.7.

Species	Mean r ± s.e. in decline period	Mean r ± s.e. in recovery period	Interpretation
elephant	-0.004 ± 0.02	0.055 ± 0.02	little change in decline
elephant bull	-0.005 ± 0.02	0.03 ± 0.03	& slow recovery
buffalo	-0.045 ± 0.05	0.053 ± 0.04	slight decline & moderate recovery
buffalo bull	-0.109 ± 0.06	0.143 ± 0.06	fast decline & fast recovery
white rhino	0.056 ± 0.07	0.08 ± 0.05	no growth in decline &
black rhino	0.057 ± 0.12	0.065 ± 0.09	moderate growth in recovery
giraffe	0.01 ± 0.06	-0.012 ± 0.02	little change in decline or recovery
impala	-0.073 ± 0.04	-0.035 ± 0.04	decline, slow decline
kudu	-0.134 ± 0.06	0.052 ± 0.06	fast decline, fast recovery
waterbuck	-0.114 ± 0.08	0.037 ± 0.06	
zebra	-0.014 ± 0.02	-0.027 ± 0.03	little change in decline or recovery
wildebeest	0.022 ± 0.09	0.011 ± 0.08	
roan	-0.428 ± 0.15	0.039 ± 0.36	fast decline, ambiguous recovery
tsessebe	-0.149 ± 0.05	-0.004 ± 0.25	
sable	-0.235 ± 0.06	-0.01 ± 0.12	
eland	-0.056 ± 0.07	0.111 ± 0.2	

2.5.4 H4: Drought impacted herbivore populations far from water sources

In Hypothesis 4, we expected water-dependent grazers (Table 2.1) to be negatively affected by distance-from-water in drought years, and water-independent browsers and mixed feeders to have the opposite response. We found that buffalo mixed herds, elephant bulls, white rhino, and kudu concentrated around waterholes during drought years (Fig. 2.9b). Only impala and giraffe concentrated around rivers during drought, with all other species' responses not different from zero (Fig. 2.9d). Contrary to our expectations, no species concentrated about both sources of water during drought.

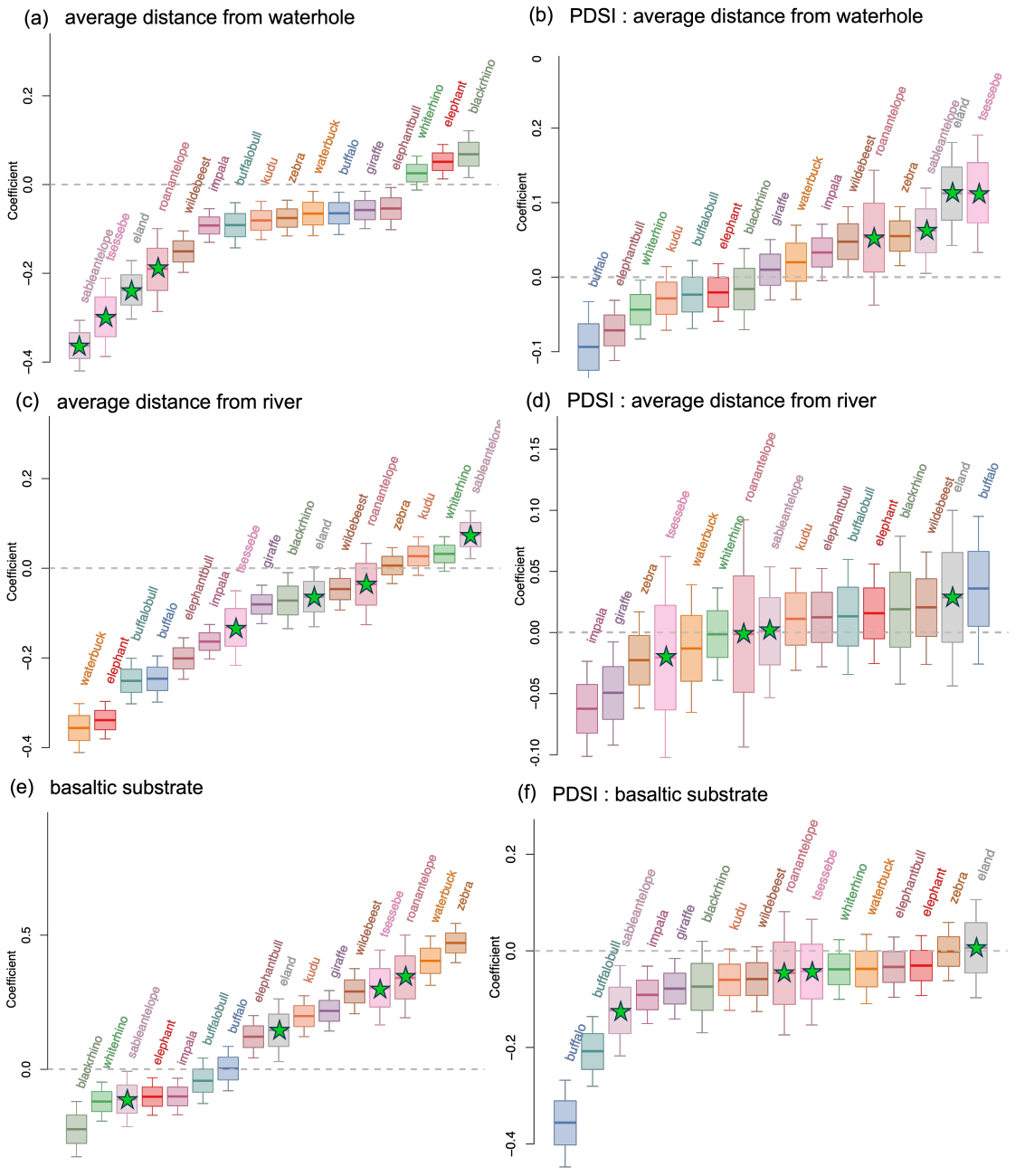

FIGURE 2.9**:** Species responses to regional average distance from waterholes (a), distance from rivers (c), and basaltic substrate (e), as well as these covariates' interactions with PDSI (b, d, f, respectively). Species with a positive coefficient for waterhole or river distance generally decrease in regions with more waterholes (a) or rivers (c). Positive values for PDSI : distance indicate a dry-year concentration in regions with more waterholes (b) or rivers (d). Species with a positive coefficient for basalts (e) generally have higher populations in basaltic regions. Negative values for PDSI : basalts (f) indicate a reliance on basalts in dry years. Recall that a negative PDSI indicates a dry year. Rare antelope are indicated with green stars.

2.5.5 *H5: Drought-year population increases on basalts partially followed dietary class*

In Hypothesis 5, we hypothesized that populations of grazing mammals would increase on basaltic-derived soils during drought, as these soils generally provide for a more nutritive and reliable grass layer. Our model results from GJAM (Fig. 2.9e) show that, as expected, grazing mammals such as waterbuck, zebra, wildebeest, roan, and tsessebe had high populations on the basalts in general; however, several species known to consume browse such as kudu, eland, and giraffe also preferred basalts. In addition, grazers such as buffalo, sable antelope, impala, and wildebeest all had significant increases during drought years on basalts, supporting our hypothesis (Fig. 2.9f). However, kudu, giraffe, and impala, all browsers or mixed-feeders, also had significant increases on basalts during drought, while known grazers such as zebra had no response to basalts during drought.

2.5.6 *H6: Rare antelope populations were higher in regions far from waterholes*

In Hypothesis 6, we expected that rare antelope population sizes would increase with distance from waterholes, and that this increase would be greater in drought years (negative PDSI) than non-drought years. Our results do not uphold this prediction: Rare antelope populations, in general, decrease with distance from waterhole (Fig. 2.9a), and the interaction between drought and distance was positive (Fig. 2.9b). This indicates that rare antelope populations were higher far from waterholes during wet years, and higher close to waterholes during dry years. For rivers, eland and tsessebe populations increased closer to rivers, while sable increased far from rivers; there was no evidence of an interaction with drought year for rare antelope.

2.5.7 *H7: Rare antelope formed a sub-group with distinct sensitivity to climate drivers*

In Hypothesis 7, we expected that rare antelope would form a distinct sub-group given similar responses to environmental covariates. To determine individual species' simi-

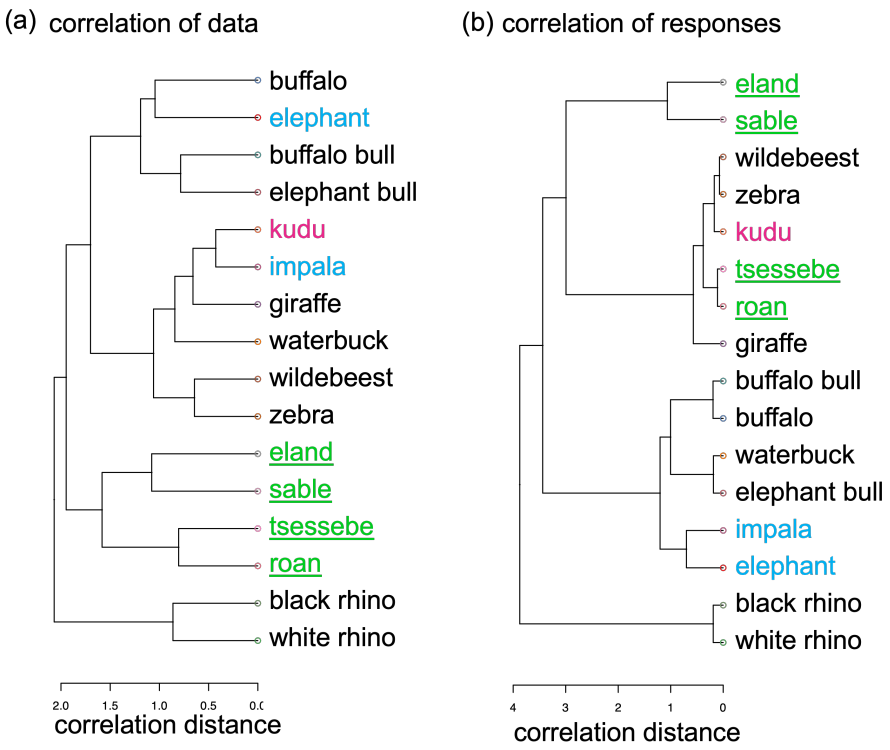

FIGURE 2.10**:** Correlations between species drawn from raw density values (a) and responses to covariates (b); (b) was derived from the **E** matrix in Eqn. 2.7. Correlation distance is calculated for each species-species pair, with a shorter distance indicating higher correlation between two species. Note that, while correlations in the data are relatively predictive of species responses, some species do reshuffle in their responses to covariates: E.g., elephant and impala (blue), both mixed feeders, were highly correlated in their responses, while kudu (pink) and impala were not, despite being correlated in their raw data. Rare antelope (green, underline) are closely correlated in the raw data but split into tsessebe and roan (correlated with kudu, zebra, and wildebeest) and eland and sable (not closely correlated with any other group).

larity to other species based on climate drivers, we compared values of vector **E** (Eqn 2.7) by calculating a correlation distance between all species pairs. These correlations are presented in tree form for visual comparison (Fig. 2.10), where short correlation distances indicate a high correlation between two species in raw data densities (Fig. 2.10a) or in their responses to environmental covariates (Fig. 2.10b). Rare antelope clustered as a group in their raw densities, but split into two distinct sub-groups in their responses to environmental covariates: roan-tsessebe, which were closely correlated with kudu,

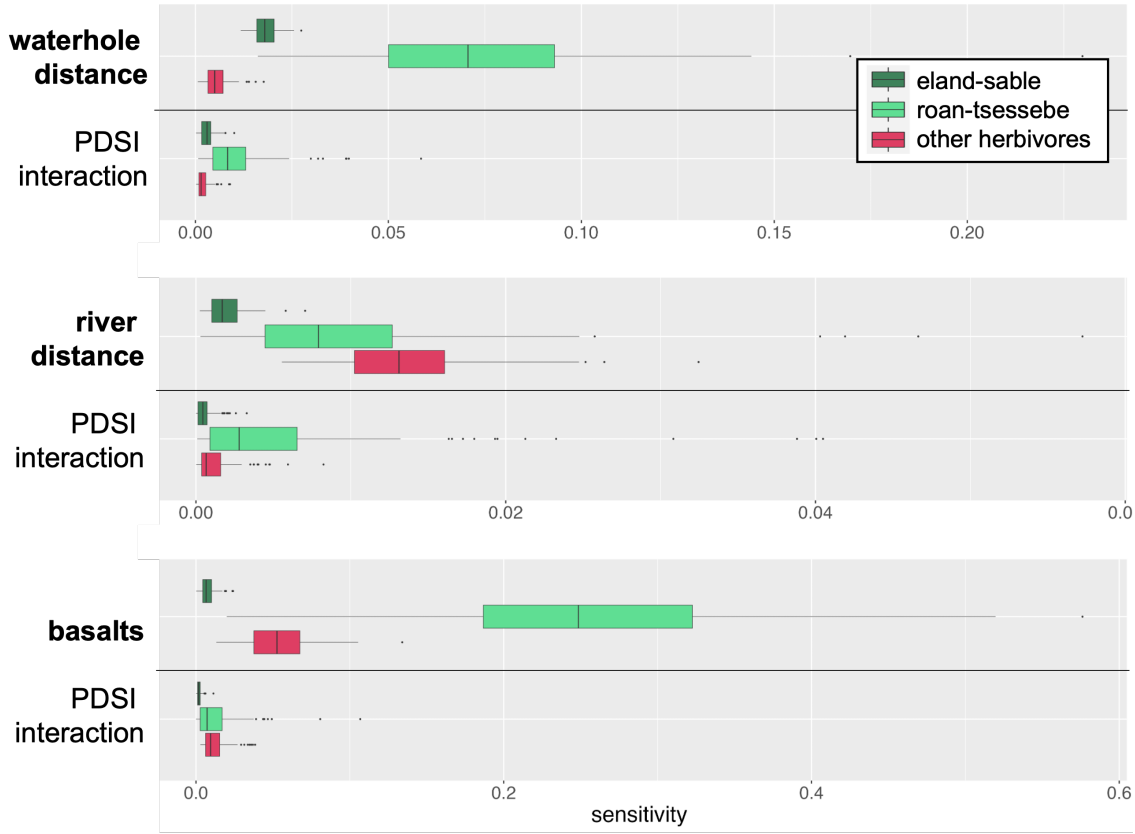

FIGURE 2.11**:** Rare antelope (greens) response sensitivities to climate covariates (Eqn. 2.6), compared to other, more common herbivore species (pink). In general, both rare antelope groupings are more sensitive to waterhole distance, and less sensitive to river distance, than other herbivores. Eland and sable (dark green), in turn, are less sensitive than roan and tsessebe (light green) to all covariates and PDSI interactions. The largest difference between the two rare groups is in their sensitivity to basalts, with roan-tsessebe sensitivity an order of magnitude larger than eland-sable.

zebra, wildebeest, and giraffe; and eland-sable, which were not closely correlated with any other species grouping.

Finally, we also predicted that the rare antelope group would be less sensitive to rivers or waterholes when compared to the other, more common herbivores. This was determined using sensitivity values from matrix **f** (Eqn 2.6). As a group, rare antelope were more sensitive to waterhole distance than the full suite of herbivores, and much less sensitive to river distance; however, the eland-sable pairing was generally less sensitive to environmental covariates than the roan-tsessebe pairing. The two rare ante-

lope pairings were most different in their sensitivity to basalts: roan-tsessebe sensitivity was an order of magnitude larger than eland-sable, with common herbivore sensitivity splitting the two (Fig. 2.11).

2.6 Discussion

This study aimed to provide a comprehensive long-term analysis of drought effects on herbivore populations in the Kruger Park. With a novel harmonization of three decades of herbivore census data, we showed that (1) herbivore size, gestation rates, water dependence, and grass dependence did not drive long-term drought decline and recovery rates. Instead, (2) small population sizes declined more quickly and struggled to recover after drought periods. We also used a Bayesian joint species analysis to show that (3) large grass-dependent species such as buffalo and elephant relied heavily on waterholes during drought years, and that (4) no species had identical responses to both waterholes and rivers, suggesting unique properties of both to support herbivore populations during drought. We also found that (5) grazers did not uniformly increase on basalts during drought years. Finally, for rare antelope in particular, we found that they (6) rely on waterholes in dry years but not in wet years, (7) formed two unique groups (eland-sable and roan-tsessebe) based on responses to environmental covariates, and (7) rare antelope were less sensitive to rivers and basalts than the entire suite of ungulates.

There is still much uncertainty in the harmonization of these three datasets. First, low-density species (roan, black rhinoceros, tsessebe, and eland) did not have sufficient abundance data in the Distance-sampled dataset to properly model species detection curves, and rare antelope (sable, tsessebe, roan, and eland) did not have sufficient overlap between MRG and TCC surveys to estimate the effective survey area offset represented by MRG. While the Distance package is able to pool common species'

data to estimate a general detection curve for rare species (Miller et al. 2019), and we have no evidence to assume that effort for rare antelope in MRG was not equal to TCC, these densities should be used with caution when comparing between dataset coverage years. Second, many of these datasets have unknown year-to-year biases in species of importance to the management of Kruger Park (e.g., rare antelope), which may have altered survey effort for those species (i.e., key species will be counted with more care). Finally, the method of comparing survey effort between TCC and MRG is simple, and is particularly concerning for rhinoceros: Rhino abundances are consistently smaller in MRG than TCC (Fig. 2.6), despite the increased sampling intensity of the former. This may be due to behavioral or habitat-choice differences at different times of the year, as TCC takes place from May-August (and southern census blocks are flown first), while MRG takes place in August-September. The difference could also be due to an imbalance of priorities: The MRG survey's initial intention was to survey buffalo and elephant numbers, with rhinoceros and rare game later added. During the period of overlap for rhinoceros in MRG and TCC (1988-1994), there was little concern for their populations, as poaching did not spike in earnest until the early 2010s (Ferreira et al. 2015) and the populations seemed to be doing well (Ferreira et al. 2011). Whether the discrepancy in effort is due to habitat, behavior, or management priority is unclear, and warrants further investigation.

No single species trait was associated with drought response. This was unexpected, as previous studies have found links between drought responses and grass dependence, water dependence, and size (Abraham et al. 2019, Staver et al. 2021, Veldhuis et al. 2019). When growth rates are grouped by decline and response trend, the pattern is a bit clearer (Table 2.6). Species insensitive to drought are either known for large migrations to access better forage during drought (zebra, wildebeest), or are large browsers able to access resources unobtainable by any other ungulate, perhaps making them less vulnerable to drought-driven competition (giraffe). It has previously been found

Table 2.6: Decline and recovery matrix for species in this study (Fig. 2.7). Rows indicate average growth rates during the decline period (1984-1994), while columns indicate average growth rates during the recovery period (2000-2010).

		Recovery		
		-	0	+
Decline	-	Decline throughout: **impala**	Do not recover: **roan, tsessebe**, **eland, sable**	Decline, then recover: **buffalo, kudu, waterbuck**
	0		Insensitive to drought: **zebra, wildebeest**, **giraffe**	Insensitive, but benefit following rains: **elephant**
	+			Increasing during drought **black and white rhino**

that grazers concentrate on the eastern basalts (Chirima et al. 2012), likely migrating to these rich grasslands to offset drought declines. Species that declined during the drought but recovered afterwards were either grass-reliant and so recovered with the vegetative layer (buffalo and waterbuck), or are known to be highly sensitive to annual rainfall rates (kudu, see Owen-Smith 1990). Impala population growth rates were only slightly different from zero. This result is initially puzzling, given predictions by several recent studies that small mixed-feeders should do well under drought (Abraham et al. 2019) . Impala, however, with their large population and diet-switching flexibility, could be prevented from massive post-drought increases by reaching the parkwide carrying capacity. Management also may have played a large role in population responses seen here: rhinoceros populations were subject to concerted population preservation efforts by management, likely confounding any trait influences on responses to drought. In addition, elephant culling, which was a staple of park management from the 1960s, ceased in 1994 (Whyte 2001). As this study's drought decline period spanned this culling period, it is likely that the artificially depressed elephant numbers are the main cause of neutral elephant population growth rates in the decline period. Finally, all four rare antelope species saw a distinct decline during drought and lack of recovery post-drought,

which confirms the decline patterns on which we based our rare antelope population analysis.

The noisiness of the population growth-rate anaylsis showcases the strengths of our GJAM joint distribution analysis of rare antelope. Despite the low population density of these antelope, we extracted key information about their ecology. We found that rare antelope responded as two separate groups to their environment. Given all four species' similar directionality in their responses to rivers, waterholes, basalts, and drought interactions (except sable's increase further from rivers; see Fig. 2.9), it is likely that sable and elands' lower sensitivity to all environmental covariates, and especially waterholes and basalts, drives the difference between the two groups (2.11). Although the smaller populations of tsessebe and roan may drive some of this pairing's greater sensitivity to their environment, the magnitude of sensitivity differences between the two pairings for waterholes and basalts suggest that this finding is not solely due to inter-annual noise at small population sizes.

Finally, we also found that rare antelope did not have the negative response to waterholes that we had predicted. Previous studies found that the presence of artificial waterholes caused declines in rare antelope numbers due to the influx of common grazers (Harrington et al. 1999), and so we expected to find the same. However, rare antelope populations increased in areas far from waterholes during wet years, and close to waterholes during dry years. This discrepancy may arise because, while rare antelope have been influenced in the past by waterhole crowding, none are water-independent animals; they all still need to access surface water. Because our dataset spanned many years since the waterhole closures of the mid-1990s, these results reveal that the waterholes remaining on the landscape may play a key role in rare antelope population recovery. These findings suggest that the surface water requirements of rare antelope outweigh the risk posed by crowded and predator-threatened waterholes.

2.7 Conclusion

Despite no statistical connection between traits and growth rates, our results point out clear groupings in decline and recovery trends for savanna herbivores. Rare antelope in particular have been a concern for Kruger management for many years. Our findings that rare antelope respond similarly to drought and surface water indicate that broad-scale management solutions, such as maintaining the remaining artificial waterholes, may be successful in restoring these populations. However, the roan-tsessebe and sable-eland divide warrants further research into the magnitude of these species' sensitivities to different environmental variables. These results have implications beyond the Kruger Park as well. The management of large wildlife communities is difficult, and its history is filled with well-meant but ultimately ecologically disastrous decisions, such as fire suppression and waterhole provision. However, a complete about-face on policy may sometimes be an over-correction. Here, we have shown that rare antelope, despite predictions to the contrary, now rely on waterholes, and do so more during drought than in high-rainfall years. In addition, our sensitivity analysis shows a reduced reliance on rivers compared to all ungulates in the study, indicating that waterholes are their preferred surface water source.

The story of rare antelope and waterholes has been told in many ways – positively in the 1960s and negatively in the 1990s. This study, then, adds a more balanced take: The proliferation of waterholes may have harmed rare antelope populations in the past, but in moderation may help these populations weather the drought conditions that will become more frequent under climate change.

3

Thermoregulatory strategy differentiation intensifies under higher temperatures for two African savanna ungulates

Margaret E. Swift, Robin Naidoo, Piet Beytell

3.1 Introduction

The heating and drying of African savannas under climate change will place mounting pressures on mammalian herbivore thermoregulation. Even if some mammals are able to manage the high predicted environmental heat loads (Engelbrecht et al. 2015) through the evaporation and replenishment of body fluids (Taylor 1970a,b), climate-driven desertification threatens to shrink the drinking water sources that support animals in semi-arid regions (Mirzabaev et al. 2019, Nkemelang et al. 2018). But these thermoregulatory challenges may not specifically drive detectable behavior changes. Climate change also threatens herbivores' food sources through the desiccation of grasses

(Wigley-Coetsee and Staver 2020) and increased vulnerability of woody plants to fire (Higgins et al. 2000). In addition, predators will shift their behaviors in response to increasing heat loads (Veldhuis et al 2020, Creel et al 2016), therefore reshaping the "landscape of fear" that ungulates must navigate (Laundre et al, Gallagher et al). Given these dietary and predatory restraints, it is not obvious that ungulate reliance on thermoregulatory strategies will be the dominant behavioral trend at higher temperatures. While many studies have investigated the individual thermoregulatory strategies of savanna ungulates (Boyers et al. 2021, Finch 1972, Schmidt-Nielsen et al. 1956, Taylor 1969), a comparative study of the extent to which ungulates rely on different thermoregulatory strategies at higher temperatures is missing.

If heat stress is a dominant limiting force on ungulate behavior under a warmer climate, then ungulate expression of thermoregulation strategies should intensify under hotter and drier conditions. For example, animals that depend on intake of surface water to thermoregulate ("water-dependent"; e.g., blue wildebeest *Connochaetes taurinus*, roan antelope *Hippotragus equinus*) may stay closer to water sources at high temperatures; those that don't rely on surface water ("water-independent", e.g., eland *Tragelaphus oryx*, gemsbok *Oryx gazella*) may instead increase their selection of water-rich foods (Taylor and Lyman 1967). Conversely, behaviors associated with other needs may take precedence. For example, increasing temperatures could limit ungulates nutritionally, as photosynthesis is often one of the first plant cell functions to be inhibited by heat stress (Mathur et al. 2014), and increased temperatures can lower grass digestibility through lignification and higher fiber content (Deinum and Dirven 1975, Van Soest 1996). Additionally, if predators maximize activity during cool night hours, herbivores may forego foraging during these times, instead moving these activities to the hottest parts of the day (Veldhuis et al 2020). If nutritional or safety needs become more important for survival and reproduction, then ungulates might exhibit behaviors that seem to oppose their thermoregulatory needs, such as increasing foraging time during hot days,

decreasing activity during cool hours when predators are active, or moving further from water sources in search of under-grazed rangelands.

The relationship between ungulate water dependence and thermoregulatory behavior is well understood in the literature (see Lamprey 1963, Western 1975, Maloiy and Hopcraft 1971, Veldhuis et al. 2019, Kihwele et al. 2020), but less is known about how these behaviors will change under the increasing temperatures and aridization of climate change. For example, recent studies comparing water-dependent wildebeest to water-independent gemsbok showed that wildebeest were more dependent on surface water than gemsbok, and that gemsbok increased nocturnal activity during a hot-wet season (Boyers 2018, Boyers et al. 2021). However, to date little research has focused on how species' dependence on different thermoregulatory strategies changes from low to high temperatures. As climate change interacts with other forms of anthropogenic global change, such as the proliferation of veterinary fencing (Jakes et al. 2018), roads (Meijer et al. 2018, Forman 2000), urbanization (Tian et al. 2022), and agriculture (Maitima et al. 2009), free-ranging savanna ungulate movements will become increasingly restricted. Therefore, an understanding of how thermoregulatory movement patterns and distributions are expected to change at higher temperatures will be key to preserving wild ungulate populations in the future.

Ungulates, like all mammals, must expend energy to maintain a constant internal temperature (Crompton et al. 1978) when environmental conditions fall outside of their "thermoneutral zone" (TNZ). The TNZ, a species-specific range of ambient temperatures in which an individual's heat loss and heat production are balanced without physiological exertion (Commission 2003), ranges from 36-40°C for most wild ungulates (Parker and Robbins 1985). The energy needed to maintain homeothermy outside of the TNZ is influenced by both internal and ambient conditions (see Porter and Gates 1969 for a review). Internal heat is generated by basal metabolism, exercise, hindgut digestion and, for ruminants, fermentation of tough fibers in the foregut (Kingma et al.

2012, Rutherford et al. 2019). Ambient conditions, including solar radiation, air temperature, relative humidity, and wind production, can change the rate of heat loss through the skin (Kingma et al. 2012). Although large mammals can and do thrive outside of their TNZ (Speakman and Król 2010), exceeding their upper thermal limits necessitates expenditure of water and energy, often through sweating and panting, to maintain homeothermy. If this water is not replenished, or if heat production outpaces heat loss, heat stress can cause delayed or compromised reproduction (Marai et al. 2007, Hansen 2009, Boni 2019), decreased growth rates (Hahn 1999), oxidative stress (Ganaie et al. 2013), impaired short- and long-term cognition (Soravia et al. 2021), and, eventually, organ failure and death (Orr 1955).

At high temperatures in arid conditions, maintaining homeothermy is a delicate balance between shedding heat and saving water. When ambient temperatures are cooler than body temperature, animals radiate heat from their skin. This process loses efficiency as temperatures and body size increase, however, necessitating other cooling methods (Owen-Smith 1989, Porter and Kearney 2009). Evaporation-based cooling (e.g., sweating, saliva spreading, panting) is effective but uses precious water (Finch 1972, Taylor 1977, Taylor et al. 1969). To avoid evaporative water loss, many arid-adapted mammals employ nasal panting, in which the nasal passage acts as a graduated thermal sink for heat and moisture control. As the animal inhales through the nose, the outside air borrows heat and moisture from the epithelial lining, cooling the mucosal membrane. On the exhale, graduated evaporation across the membrane releases heat and returns up to 60% of water to the nasal passage (Taylor 1977). In addition to recovering water, nasal panting is energy efficient, and therefore does not increase an individual's metabolic heat load. The increase in blood flow to the lungs during panting is paired with a decrease in non-respiratory muscle blood flow; in fact, the cardiovascular energy cost of this process is close to zero (Hales 1973, Robertshaw 2006, Taylor 1977). The cooling of nasal panting can be enhanced by increasing inhale-

exhale frequency; this would lead to hyperventilation if the entire lung's capacity were exchanged on every breath, but animals avoid this risk by keeping breaths shallow (Hales 1973, Taylor 1977). Thus, through nasal panting, an individual can benefit from the energy efficiency of passive evaporative cooling, and modulate that cooling potential, without the high water losses associated with sweating.

Non-evaporative cooling strategies can further mitigate water loss and reduce heat gain (Taylor 1970b, Terrien 2011). Herbivores with dietary flexibility such as impala (*Aepyceros melampus*) and savanna elephant (*Loxodonta africana*) switch from eating dry grasses to water-rich woody plants during drought (Abraham et al. 2019). Exploration and foraging increase exercise-induced heat loads (Boyers et al. 2019); therefore many herbivores, from temperate grasslands (Belovsky and Slade 1986) to arid savannas (Owen-Smith and Goodall 2014, Ruckstuhl and Neuhaus 2009) walk and forage less when temperatures or water demands are high (Owen-Smith 1996). To recover crucial foraging time given up during the day, many animals forage during the cool night hours; however, this strategy increases the risk of nocturnal predation (Cozzi et al. 2012, Crosmary et al. 2012, Fuller 2016).

Despite this array of water-saving and heat-minimizing behaviors, many African ungulates still require daily drinking water. The desiccation of waterholes and plants in the dry season therefore tethers water-dependent ungulates' ranges to permanent water sources when rain is sparse (Hempson et al. 2015, Kihwele et al. 2020, Veldhuis et al. 2019). Water-dependent species, such as zebra (*Equus quagga*), blue wildebeest (*C. taurinus*), and waterbuck (*Kobus ellipsiprymnus*), persist through the resource-poor dry season by concentrating around permanent rivers and waterholes; their ranges then expand in the wet season (Lamprey 1963, Smit et al. 2007, Weir and Davison 1965, Western 1975). The dry-season clustering around water sources mitigates dehydration, but also increases competition for resources as herbivores over-forage or trample nearby grasses and forbs (Owen-Smith 1998). It also increases predation because lion,

hyena, and leopard are drawn to the high concentration of prey at dry-season water sources (Cain et al. 2012, Crosmary et al. 2012, Hayward and Hayward 2012). In the coming decades, under more severe and frequent droughts, ephemeral surface water in southern Africa may dry more quickly and fill more slowly (Bates et al. 2008, Nkemelang et al. 2018). This could lead ungulates in arid and semi-arid habitats to cluster more intensely around a smaller number of permanent rivers and waterholes, thereby decreasing water-dependent herbivores' effectiveness as environmental engineers and exacerbating the competition and predation costs of concentration.

Given the threat of climate change on African ecosystems, it is critical to understand how ungulate thermoregulation will respond to the subsequent increase in temperature and aridification (Fuller et al. 2021). In this study, we investigate temperature-induced trends in three common heat regulation behaviors exhibited by ungulates: a *Surface Water Strategy* (SWS) of remaining close to water sources during times of thermal stress, a *Microclimate Selection Strategy* of prioritizing selection of cooler microclimates, and an *Activity Budget Strategy* (ABS) of increasing daytime resting and rumination (moving foraging to night hours) to minimize heat gain. We model the change in thermoregulatory strategy under higher temperatures of two ungulate species at opposite ends of the water-dependence spectrum: water-dependent roan antelope (*Hippotragus equinus*), known to rely on SWS, and water-independent gemsbok (*Oryx gazella*), known to rely on both ABS and MSS. We used two years of temperature and location data from GPS-enabled collars fitted on both species in the semi-arid savanna of Khaudum National Park, Namibia.

If heat stress is the key limiting factor for ungulate behavior at higher temperatures, then we expect to see the following indicators of thermoregulatory strategy "intensification":

1. **Surface Water Strategy (SWS):** During the dry season and at higher temperatures, (a) distance from permanent surface water will be smaller and (b) seasonal surface water density will be greater.

2. **Microclimate Selection Strategy (MSS):** Above the TNZ (35°C), the difference between collar temperatures and ambient temperatures will be smaller at high temperatures than at low temperatures.

3. **Activity Budget Strategy (ABS):** The average proportion of individuals ruminating in the day will be greater during the dry season than the wet season. Daily rumination will increase, and nightly rumination will decrease, at higher temperatures.

4. We expect both species to exhibit some reliance on each strategy listed above. However, we expect that the magnitude of these "intensification" markers will be greater in **roan for SWS**, and in **gemsbok for ABS and MSS**.

SWS expression is intensified if, at high temperatures, there is a statistically significant decrease in distance from permanent surface water, and an accompanying increase in the seasonal surface water density within 300m.

MSS expression is intensified if, on hot days, the difference between maximum daily collar temperatures and the ambient temperature (measured by ERA5 reanalysis) is smaller than on average days. MSS expression is measured by a point value rather than a regional estimate (SWS) or temporal estimate (ABS). Therefore, we can restrict the MSS analysis to only ambient temperatures above 35°C, the point at which both species begin to exit their thermoneutral zone (TNZ).

Finally, ABS expression is intensified if the magnitude of daytime rumination increases, and the magnitude of nighttime rumination decreases, on hotter days. The indicator for ABS intensification (activity state proportions), unlike that of MSS (tem-

perature) and SWS (distance from water), cannot be measured directly from collar temperature or location. To extract an activity state for each GPS point, we use a Hidden Markov Model (HMM) to categorize states from distributions of step lengths and turning angles. Each GPS point is then assigned one of three activity states based on the categorized distributions: ruminating (resting and digesting food; categorized as short steps with many zeros), foraging (feeding in one area; short or medium-length steps and frequent turns), or exploring (traveling between habitats; long, directed steps with few turns).

It is clear that climate change will have an outsized impact on southern Africa and its many unique ecosystems (Engelbrecht et al. 2015). Southern African savannas in particular are one of the last refuges of Pleistocene megafauna, which are integral to savanna functioning. If ungulate thermoregulatory strategy intensifies under higher experienced temperatures, as we expect, then we can use our findings to better understand future changes in these animals' behavior and distribution on the savanna. If these strategies do not intensify, then further investigation will be needed into how other behavioral limitations are expected to shift under anthropogenic climate change.

3.2 Study area and species

3.2.1 Study area

Khaudum National Park (18.76S, 20.73E) covers about 385,000ha of the Kavango East region in northeast Namibia, northwest of the Okavango Delta. Formed as a game reserve in 1989, the park contains two rest camps, a small dirt airstrip, and welcomes only about 3000 visitors annually (Ministry of Environment 2020), leaving animal populations relatively undisturbed by traffic and tourist activity. Khaudum is bordered to the west by small-scale farms and to the east by a veterinary border fence with Botswana. To the north are two communal land conservancies (George Mukoya and Muduva Nyangana) with two more (Nyae Nyae and N#a-Jaqna) bordering the park to the south. The north

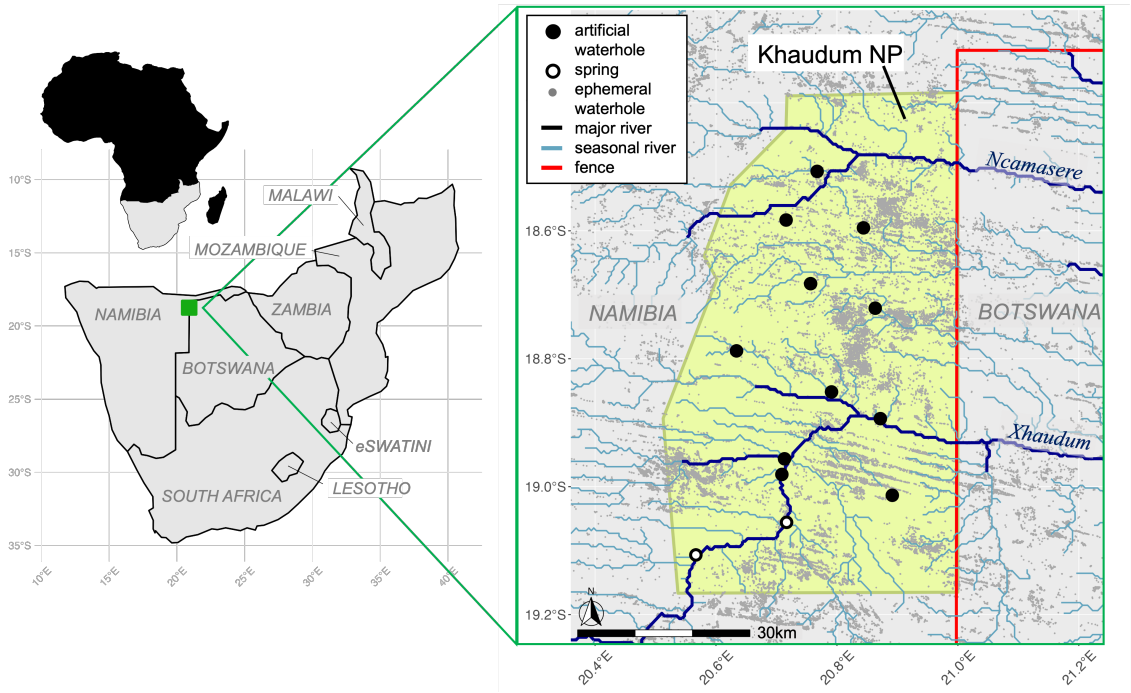

FIGURE 3.1**:** Khaudum National Park surface water sources. Natural ephemeral waterholes lie along ancient streambeds called *omiramba* (gray; see diagonal lines in the southeast). Perennial major rivers (dark blue; Xhaudum and Ncamasere), seasonal minor rivers (light blue) and eleven artificial waterholes (black dots), which consist of year-round water supplied via dam or pump. Two natural springs (white dots) are also permanent fixtures of the Khaudum hydroscape.

of the park is dominated by sandy, dystrophic soils and broadleaf savanna woodlands. To the south, calcrete and quartzite-derived soils sport acacia broadleaf shrubland, occasionally mixed with teak woodland (*Baikea plurijuga*) where sands run deeper (Ministry of Environment 2013, 2020)

Khaudum NP is semi-arid, receiving 400-500mm of rainfall annually, most falling from November to April during the summer wet season (min 20°C, max 40°C).

The rest of the year is cool and dry from May-August (min 3°C, max 35°C); at the end of winter temperatures rise again, often above 40°C in October. Elevations range from 1,080m above sea level in the north to 1,150m above sea level in the southwest.

Many ephemeral waterholes cover Khaudum NP, and are sources of drinking water in the wet season but shrink or disappear entirely in the dry season. Often, these

waterholes form in ancient riverbeds called *omiramba* (singular *omuramba*). These distinctive landscape features are important east-west migration pathways, especially for elephant, and dominate the park's southeastern quarter (Fig 3.1).

There are thirteen permanent waterholes in Khaudum NP: two natural springs and eleven artificial waterholes, the latter maintained by the Namibian Ministry of Environment, Forestry, and Tourism (MEFT) (Fig. 3.1). Each artificial waterhole is supplied with water through either a dam or a borehole system. Permanent waterholes are often used by water-dependent mammals, notably elephant, zebra, blue wildebeest, and roan antelope, and are hotspots of over-foraging and predator activity (Owen-Smith 1996). Although the MEFT maintains existing artificial waterholes, current management plans do not intend to add more to the park (Ministry of Environment 2020).

Two major permanent rivers flow through Khaudum NP, the Ncamasere and the Chadom (Fig. 3.1), but 1,042km of seasonal rivers also flow through the park. Rivers in the park often flow on a NW-SE diagonal (Fig. 3.1), mirrored by dry ephemeral riverbeds (*omiramba*) that result from wind and water erosion and deposition. These pans are small and often hold pools of water that fill with the wet season rains and contract during the dry season, making them difficult to detect (Schaffer-Smith et al. 2022).

3.2.2 Focal Species

This study explores the heat regulation strategies of two related ungulates, the water-dependent roan antelope (*Hippotragus equinus*) and water-independent gemsbok (*Oryx gazella*). Roan antelope are large grazers (220-300kg; 1.4m shoulder height; Estes 1991, Kingdon 2015) that rely on high hydration (23L/100kg/day) to regulate heat loads, a water requirement that cannot be met through forage alone (Kasiringua et al. 2017, Taylor 1969, van Rooyen 2002). Roan are therefore dependent on surface water, especially in the dry season, and must drink daily (Estes 1991). Gemsbok, a slightly smaller grazer (180-220kg; 1.25m shoulder height; Estes 1991, Kingdon 2015) also in the

tribe Hippotragini, require little water (as little as 10L/100kg/day), almost all of which can be gained through forage (Taylor 1970b). On a semi-arid savanna with little reliable surface water, gemsbok have adapted to tolerate body temperatures of up to 45°C and selectively prioritize brain cooling (Taylor et al. 1969), allowing them to minimize panting and associated energy expenditures (Estes 1991, Taylor 1970b). Both species employ nasal panting, and will also sweat if well hydrated and at high temperatures experimentally (>35°C), but in semi-arid field conditions this strategy is not preferred (Holland 2015, Taylor 1970b, but see Taylor 1977 for discussion on the metabolic costs of panting vs. sweating). Gemsbok, also in the tribe Hippotragini, require little water (as little as 10L/100kg/day), almost all of which can be gained through forage (Taylor 1970b). On a semi-arid savanna with little reliable surface water, gemsbok have adapted to tolerate body temperatures of up to 45°C and selectively prioritize brain cooling (Taylor et al. 1969), allowing them to minimize panting and associated energy expenditures (Estes 1991, Taylor 1970b). Both species employ nasal panting, and will also sweat if well hydrated and at high temperatures experimentally (>35°C), but in semi-arid field conditions this strategy is not preferred (Holland 2015, Taylor 1970b, but see Taylor 1977 for discussion on the metabolic costs of panting vs. sweating).

Both species congregate in small to medium-sized breeding herds, gemsbok around 5 individuals and roan around 20 (Table 3.1, Fig. 3.2). Because breeding herds have markedly different behavior from solitary males, our study focuses on female roan and gemsbok as representatives of their general populations' behaviors.

3.3 Materials

3.3.1 GPS telemetry data

GPS telemetry data were gathered using sixteen satellite- and GPS-enabled collars (GSSAT) manufactured by Africa Wildlife Tracking and deployed on eight females from each species (Table 3.1). Collars recorded location in three dimensions (latitude, longi-

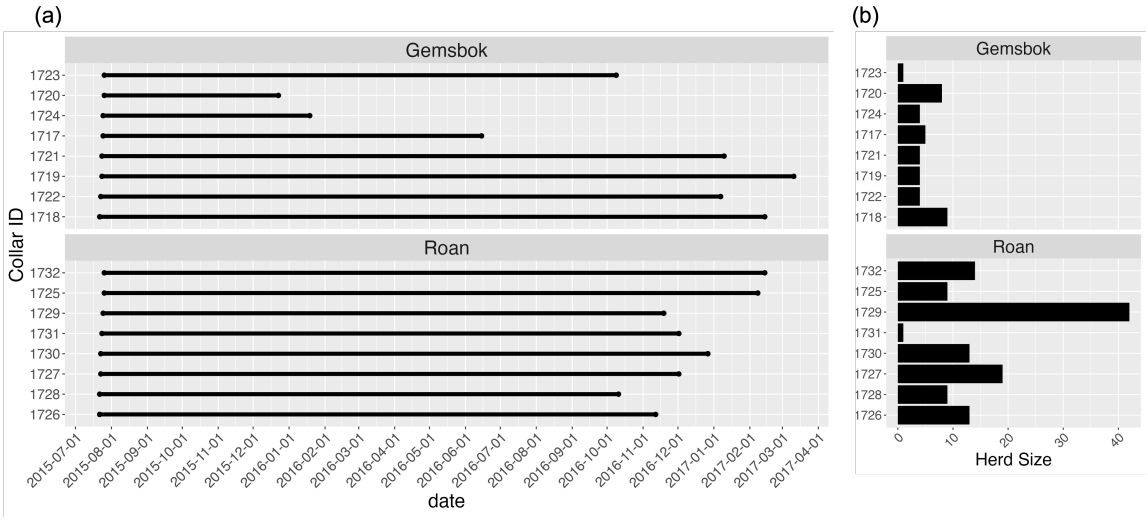

FIGURE 3.2**:** (a) Timeline of collar placement and removal for each individual in our study (8 roan and 8 gemsbok, all female). Most collars lasted at least one year. (b) Herd sizes for each individual female in our study. Most individuals were part of breeding herds, making their locations a better representation of the population as a whole than solitary males. On average, roan (mean=17.6) congregated in larger herds than gemsbok (mean=4.8). See Table 3.1 a tabular version of these data.

tude, altitude), as well as temperature, every hour. All collars were deployed in July 2015; data collection proceeded for different lengths of time for each collar, with the longest duration extending to March 2017. Collars that did not malfunction early yielded an average of 11,646 fixes per individual (Table 3.1). To offset behavioral changes due to collaring stress at the outset, or mechanical failure of collars before removal, here we omit the first and last five fixes from each collar. Finally, at the end of their functional lives, some GPS collars began to intermittently skip data fixes; therefore, we track missed fixes and omit all data after 15 missed.

3.3.2 Microclimate temperature data

Temperature readings in this study are measured at the individual level by Africa Wildlife Tracking GPS collars. Temperature data from GPS collars are often used as a proxy for ambient temperature (Ericsson et al. 2015), but we stress here that the temperature readings from these collars must be understood as the experienced mi-

Table 3.1: GPS collars were deployed in late July 2015, and all but four were active for two years. All collared individuals were female. Herd size varied between and among species, although gemsbok generally resided in smaller herds (about 5 for gemsbok, 18 for roan). See Figure 2 for a visualization of these data on a timeline.

Collar	Species	Date Deployed	Date Stopped	Number of fixes	Herd size	Ended early?
1717	Gemsbok	2015-07-25	2016-06-15	5,345	5	X
1718	Gemsbok	2015-07-22	2017-02-14	12,172	9	
1719	Gemsbok	2015-07-24	2017-03-11	12,824	4	
1720	Gemsbok	2015-07-26	2015-12-23	2,996	8	X
1721	Gemsbok	2015-07-24	2017-01-10	11,876	4	
1722	Gemsbok	2015-07-23	2017-01-07	11,321	4	
1723	Gemsbok	2015-07-26	2016-06-09	6,007	1	X
1724	Gemsbok	2015-07-25	2016-01-19	3,837	4	X
1725	Roan	2015-07-26	2017-02-08	12,496	9	
1726	Roan	2015-07-22	2016-11-12	11,310	13	
1727	Roan	2015-07-23	2016-12-02	14,881	19	
1728	Roan	2015-07-22	2016-10-11	13,558	9	
1729	Roan	2015-07-25	2016-11-19	11,029	42	
1730	Roan	2015-07-23	2016-12-27	12,264	13	
1731	Roan	2015-07-24	2016-12-02	11,560	1	
1732	Roan	2015-07-26	2017-02-14	12,725	14	

croclimate temperature of the individual. Although a study of moose temperature data in Sweden (Ericsson et al. 2015) found a strong correlation between collar and ambient temperatures, the magnitude of offset between the two varied by season; in addition, temperature ranges in Sweden are much colder than in Namibia, so these findings may not be comparable to our study.

To validate our microclimate temperature data, we use ERA5 reanalysis data from the European Centre for Medium-Range Weather Forecasts (ECMWF), a reanalysis product that predicts hourly temperatures at a 31km resolution. As a reanalysis product, ERA5 has some biases (including major cold-temperature biases for 2000-2006), but has been validated against weather station observational data across a variety of ecosystems, including the mountainous regions of Turkey (Yilmaz 2023), arid and semi-arid regions of Uzbekistan (Rakhmatova et al. 2021), and across North America (Tarek

et al. 2020). These validations are generally at an aggregate scale (monthly or yearly), however, and validation of hourly data such as in this dataset is not readily available. For this reason, although we use ERA5 data to validate that the collar microclimate dataset represents reasonable estimates of the ambient temperatures that individuals are experiencing, we rely on collar temperature data in our models of distance-from-water, microclimate selection and activity budget management (Sec. 3.4.4)

3.3.3 Surface water sources

Two major sources of surface water are considered for this analysis: Seasonal surface water (rivers and seasonal waterholes) and permanent surface water (the eleven artificial waterholes and two natural springs noted in Fig. 3.1).

Seasonal surface water data were supplied by Schaffer-Smith and coauthors' (Schaffer-Smith et al. 2022) mapping of >2 million seasonal waterholes in the Kavango-Zambezi region. Surface water was delineated for 18 2- and 3-month time blocks from 2017-2020 using an Automated Water Extraction Index (AWEI) on 10m resolution Sentinel-2 data. These data are the best available for mapping small waterholes in the KAZA region, as other commonly-used datasets such as WWF HydroSHEDS (Grill et al. 2019) and the Pekel surface water dataset (Pekel et al. 2016) are too coarse (15 arc-seconds and 30m, respectively) to map small seasonal waterholes.

For this study, we split the waterholes dataset into "wet" and "dry" season average fill level (number of pixels) and locations. For each season, we then retained water sources that were "filled" (at least one pixel) for at least 60% of the dataset, using only surface water sources that were likely to be filled during our study period. For each GPS collar point, we calculated the density of water (number of "filled" pixels) within 300m of the individual.

Artificial waterhole and natural spring location data were provided by the Namibian Ministry of Environment, Forestry, and Tourism.

3.3.4 Vegetation data

Vegetation productivity, measured using the Enhanced Vegetation Index, was sourced from Landsat 8 32-day composites of L1T orthorectified scenes, at top-of-atmosphere reflectance, using Google EarthEngine (Gorelick et al. 2017). EVI is more sensitive to canopy variations than the Normalized Difference Vegetation Index (NDVI), as it includes a canopy background adjustment measure and uses the blue band to correct for aerosol interference on red wavelengths (Huete et al. 2002). For each GPS telemetry fix in the dataset, we took the temporally closest composite to the fix and extracted the median EVI within a 300m buffer. Although the focus of this study is not on the vegetative layer, inclusion of EVI is important when considering where animals generally spend their time, and improved our models (See Eqn. 3.4.3 below; on average AIC improved by 15,000 for roan and 500 for gemsbok when EVI was included).

3.4 Methods

3.4.1 Daily heat categories

Raw collar microclimate temperatures were used for the SWS analysis because each GPS collar fix can be associated with a temperature and a distance. For ABS and MSS, however, activity states and microclimate temperatures are aggregated across individuals and hours to gain population-wide daily responses. Thus, for meaningful conclusions to be drawn, we aggregated ERA5 temperature data to a daily scale as well.

We assigned a daily heat category (DHC) for each date of the study based on the maximum ERA5 ambient parkwide temperature on that day. The average daily temperature peak was 31.6°C and the standard deviation was 4.2°C. Any day with a maximum temperature lower than one standard deviation below the mean (threshold = 27.4°C) was categorized as “mild”; those with maximum temperatures greater than one standard deviation above the mean (35.8°C) were categorized as “hot”; and days with a

maximum temperature within one standard deviation of the mean on either side (i.e., between 27.4°C and 35.8°C) were categorized as "average".

3.4.2 Hidden Markov Model for defining activity states

Activity states were determined with a Hidden Markov Model (HMM) using the momentuHMM package in R (McClintock and Michelot 2018). HMMs simultaneously model a hidden, state-dependent process (the unknown behavior or physical state of an animal, e.g. a state of hunger) and observations (known measurements with biases, e.g. an animal is seen feeding) of those behaviors or states (McClintock et al. 2020, Zucchini et al. 2016). HMMs follow the assumption of the Markov property, that the current state (at time t) is conditioned solely on the previous state (at time $t-1$); the Markov property implies that the time between state-switching follows a geometric distribution. HMMs also contain a conditional independence property, that the distribution of an observation (at time t) is determined solely by the current active state (at time t). The momentuHMM package uses a recursive algorithm (also known as a "forward algorithm") to consider all possible states that could have generated the current time series, then uses maximum likelihood estimation to generate the most likely distribution of parameters governing each state. The program then uses a Viterbi algorithm to assign each GPS fix a likely state, given estimated parameters (Zucchini et al. 2016).

For our HMM, we defined three distinct activity states: ruminating, foraging, and exploring, using a Gamma distribution for step lengths and a Von Mises distribution for turning angles. Ruminating was defined by very short (often 0m) steps from one fix to the next and an even distribution of turning angles (mean step size 83m in 1 hour, Von Mises zero-angle concentration $K = 0.51$). Both gemsbok and roan are ruminants and set aside large portions of their day to rest and digest their food; for simplicity, the ruminating category encompassed both. Foraging occurred at short and medium step lengths (mean step 177m) with less frequent bouts of straight lines (zero-angle

$K = 0.29$) as the animal wandered back and forth in search of food. Exploration was defined by continuous, directed movement; exploring animals took much longer steps than in other states (mean 524m) and had the highest concentration of straight-line paths ($K = 1.82$).

3.4.3 Surface Water Strategy reliance

To determine the strength of each species' reliance on SWS, we calculated the average density of seasonal surface water and the distance of individuals from permanent surface water. Seasonal surface water sources (>1 million) were much more numerous than the permanent water sources (13 total), therefore necessitating these two different methods of measuring water dependence. We then determined the magnitude of the change in that distance (1) between the wet and the dry season and (2) at different collar temperatures. SWS reliance was indicated for seasonal water by an *increase* in water density during the dry season or at higher temperatures. SWS reliance was indicated for permanent water by a *decrease* in distance from permanent surface water during the dry season or at higher temperatures,

Seasonal differences in distance from permanent surface water were compared using a t-test ($\alpha = 0.05$) for each species' distance from each water source in the wet and the dry season. To determine the strength of the effect size, we used a Cohen's d to compare samples (Cohen 1988).

To address the effects of temperature on water reliance, we modeled each measure (density y_1 and distance y_2) as a function of season (S), microclimate temperature (T), and EVI (E), as well as an interaction between season and the other covariates:

$$y_i = \beta_{0i} + \beta_{1i} S + \beta_{2i} T + \beta_{3i} ST + \beta_{4i} E \tag{3.1}$$

3.4.4 *Microclimate Selection Strategy reliance*

To understand the seasonal and species-specific differences between experienced microclimate and ambient temperatures, we compared collar temperature data to hourly modeled ERA5 temperature data. We ran linear regression of collar temperature (T_{collar}) as a function of season (N), species (S), and ERA5 temperature (T_{ERA5}):

$$T_{collar} = \beta_0 + \beta_1 N + \beta_2 S + \beta_3 T_{ERA5} + \beta_4 T_{ERA5} S + \beta_5 T_{ERA5} N \tag{3.2}$$

To determine the strength of each species' reliance on MSS, we then calculated the difference between measured collar temperature and ERA5 reanalysis ambient temperature for each GPS fix. For points with an ambient temperature above 35°C (the edge of ungulates' average thermoneutral zone, TNZ), we We then compared these values across season, species, and daily heat category (DHC). On hotter ambient-temperature days, a decrease or no change in the maximum temperature indicated a reliance on MSS. Because the variances across these categories were not equal (a key assumption to use an ANOVA) via a Levene test for variance equality, we used a non-parametric Kruskal-Wallis test to compare means within species and season ($\alpha = 0.05$).

3.4.5 *Activity Budget Strategy reliance*

To determine the strength of each species' reliance on ABS, we assigned each GPS point an activity class of ruminating, foraging, or exploring (using HMM), and compared these ranges across season, species, and daily heat category (DHC). A reliance on ABS was indicated by the following as individuals experienced higher ambient temperatures: (1) an increase in the proportion of individuals ruminating in the daytime, and (2) a decrease in the proportion of individuals ruminating at night.

We compared activity budgets between diurnal (about 04:00-17:00) and nocturnal (about 19:00-03:00) hours (calculated using the suncalc package, Thieurmel and El-

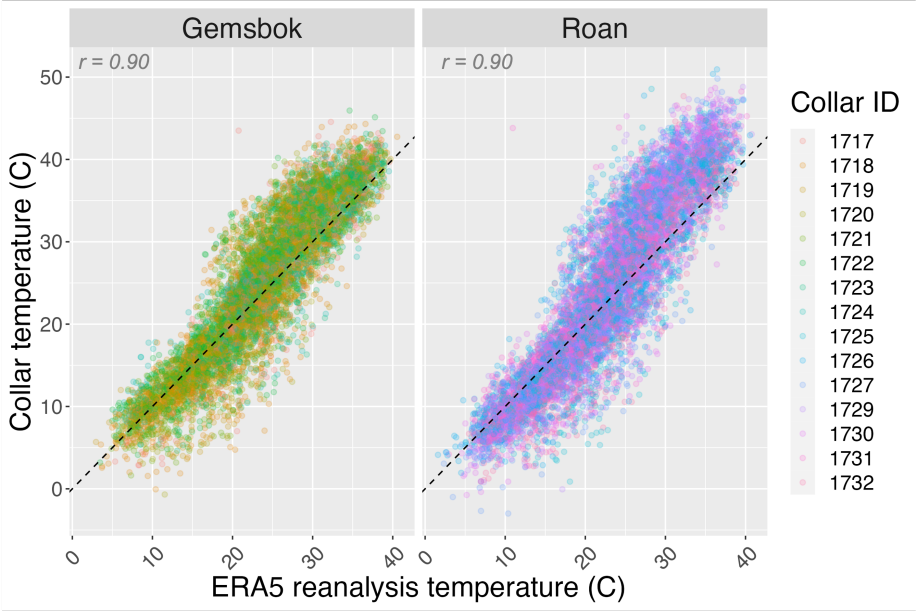

FIGURE 3.3**:** Comparison of ERA5 reanalysis product with individual collar temperature data, by species. Correlation for both roan and gemsbok collar temperature data with ERA5 temperatures is $r = 0.90$.

marhraoui 2019) because the sample size for dawn and dusk hours (2,872 GPS fixes at dawn and 8,130 at dusk) was much smaller than for day and night (78,435 GPS fixes in the day, 66,034 at night). We used a χ^2 test of proportionality (d.f.=4) to compare proportions within the same season-species-time of day, and a Cramér's V value to determine the effect size of the difference between "mild" and "hot" DHC rumination.

Table 3.2: Full effects for Eqn 3.2, with collar temperature regressed against season, species, and ambient (ERA5 reanalysis) temperature. Collar temperature increased at a higher rate for roan than gemsbok and in the dry than the wet season. In addition, the dry season and roan had more negative intercepts than the wet season and gemsbok, indicating that collar temperatures were generally lower in the dry season (winter) than the wet season, and for roan than gemsbok.

	wet	dry
roan	$-3.74 + 1.25 T_{ERA5}$	$-4.90 + 1.28 T_{ERA5}$
gemsbok	$-0.11 + 1.08 T_{ERA5}$	$-1.27 + 1.11 T_{ERA5}$

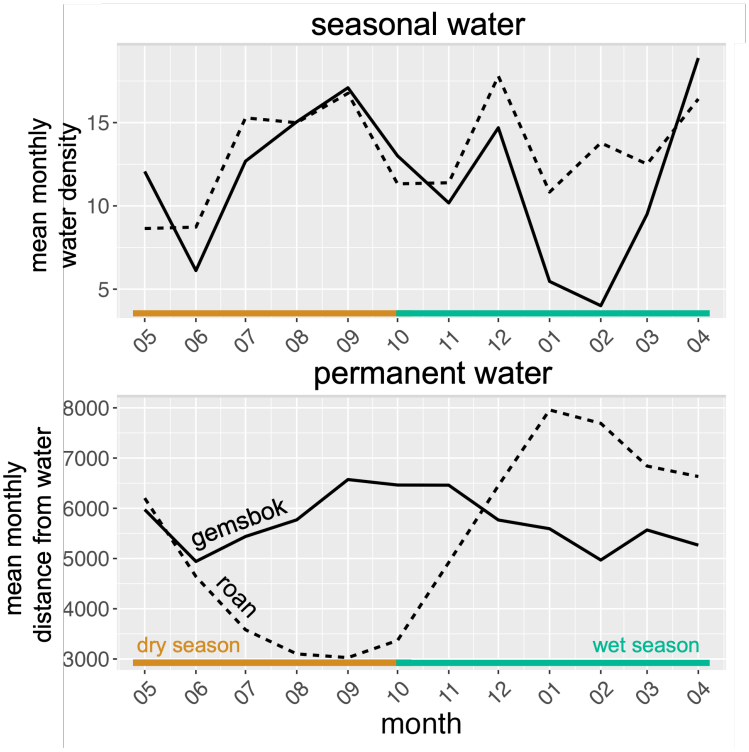

FIGURE 3.4: Seasonal waterhole density (pixels per 300m radius) and distance from permanent surface water, monthly by species. Seasonal differences for seasonal surface water density (top) are negligible. Roan (dashed line) are closer to permanent surface water in the dry season (brown) and farther in the wet season (green). Gemsbok (solid line) do not change their average distance from permanent surface water seasonally (Table 3.3).

3.5 Results

3.5.1 Validation of microclimate temperature data with ERA5

Hourly microclimate temperatures for both roan and gemsbok were highly correlated with the ERA5 reanalysis estimates ($r = 0.90$ for both species) (Fig. 3.3). Our model for collar temperature data regressed against ERA5 temperature, interacting with season and species (Eqn 3.2), found that collar temperature increased at a higher rate (given ERA5 ambient temperatures) for roan than gemsbok and in the dry than the wet season (Tab. 3.2). In addition, the dry season and roan had more negative intercepts than the wet season and gemsbok, indicating that collar temperatures (given ERA5 ambient temperatures) were generally lower in the dry season (winter) than the wet season (summer), and for roan than gemsbok (Tab. 3.2).

Finally, after the first year of the study, collar 1728 (a roan female) collar temperature correlation with ERA5 dropped to $r = 0.4$, with recorded temperatures often around

Table 3.3: Average natural water density (left column) and distance from permanent waterholes (right column), by species and season. Water density is given as the mean number of "filled" pixels within 300m of an individual. All differences between seasonal means were statistically significant ($p < 0.05$, asterisk and bold); however, the only difference with a large effect size is the wet-dry seasonal difference in roan distance from permanent waterholes. See Fig. 3.4.5.

	Mean natural water density $\pm$ 1 SD	Mean distance (m) $\pm$ 1 SD from permanent waterholes
Gemsbok		
dry season	10.3 $\pm$ 25	6,000 $\pm$ 2,670
wet season	14.3 $\pm$ 28	6,020 $\pm$ 2,520
wet-dry diff.	4.0	-20
p-value	$\ll$ **0.01***	**0.017***
Cohen's d	-0.15	-0.01
effect size	negligible	negligible
Roan antelope		
dry season	12.7 $\pm$ 28	3,560 $\pm$ 2,600
wet season	13.9 $\pm$ 29	7,000 $\pm$ 4,300
wet-dry diff.	1.2	3,500
p-value	$\ll$ **0.01***	$\ll$ **0.01***
Cohen's d	-0.04	0.96
effect size	negligible	large

60°C, 10°C hotter than co-occurring collar temperatures. Therefore, temperature data after June 2016 for collar 1728 were removed from the study.

3.5.2 Surface Water Strategy reliance

As expected, roan were on average closer to permanent water sources as the dry season progressed (Table 3.3), and farther from these water sources with the onset of the wet season. This follows a known expand-contract pattern in water-dependent ungulate ranges (Lamprey 1963, Weir and Davison 1965, Western 1975).

The average wet season distance of roan from permanent waterholes (7,000m) was about 1.3km further than this species' average daily distance walked (5,690m), and was 3.5km further from permanent waterholes than in the dry season ($p \ll 0.01$) (Table 3.3). Gemsbok followed this pattern as well but, while a 20m difference in the dry season

Table 3.4: Results for model 3.4.3, where natural surface water density (rivers and seasonal waterholes) and distance from permanent surface water (artificial waterholes and natural springs) is regressed by season, microclimate temperature, season x temp, and EVI. All covariates were statistically significant (bold, asterisk) except the wet season for gemsbok (rivers, permanent waterholes) and roan (rivers)

	species	value type	intercept	temp (°C)	wet season	temp× wet	EVI
seasonal water	Gemsbok	β-value	23	0.05	-0.58	-0.13	-37
		p-value		$\ll$ **0.01**∗	0.41	$\ll$ **0.01**∗	$\ll$ **0.01**∗
		Gemsbok were in regions with more water at ↑ temperatures, and less water in the wet season and at ↑ EVI.					
	Roan	β-value	23	0.02	-1.5	0.006	-33
		p-value		**0.05**∗	**0.01**∗	0.7	$\ll$ **0.01**∗
		Roan were in regions with more water at ↑ temperatures, and less water in the wet season and at ↑ EVI.					
permanent water	Gemsbok	β-value	6,100	26	68	-8.3	-2,480
		p-value		$\ll$ **0.01**∗	0.33	$\ll$ **0.01**∗	$\ll$ **0.01**∗
		Gemsbok were **farther** at ↑ temps, were **farther** in the dry season, were **closer** at ↑ EVI & when temps ↑ during the wet.					
	Roan	β-value	4,930	-35	4,130	-18	-1,760
		p-value		$\ll$ **0.01**∗	$\ll$ **0.01**∗	$\ll$ **0.01**∗	$\ll$ **0.01**∗
		Roan were **closer** at ↑ temps, were **closer** in the dry season, and were **closer** at ↑ EVI & when temps ↑ during the wet.					

is statistically significant ($p < 0.05$), it is not biologically relevant. Both species had negligible seasonal differences in seasonal surface water density.

When comparing the effect size of wet-to-dry seasonal differences in distance from water sources, Cohen's d values were small or negligible for all measures except one: Roan difference in wet-to-dry season distance from permanent surface water had a Cohen's d value of 0.96, which is considered a large effect. See Table 3.3 for seasonal water densities, permanent water distances, p-values, and effect sizes.

Finally, at high temperatures, gemsbok and roan both were located in regions with slightly more seasonal surface water ($p \ll 0.01$ and $p = 0.05$, respectively) (Table 3.4). For permanent surface water, however, species diverged in their responses. At high temperatures and during the dry season, roan were closer to permanent surface water

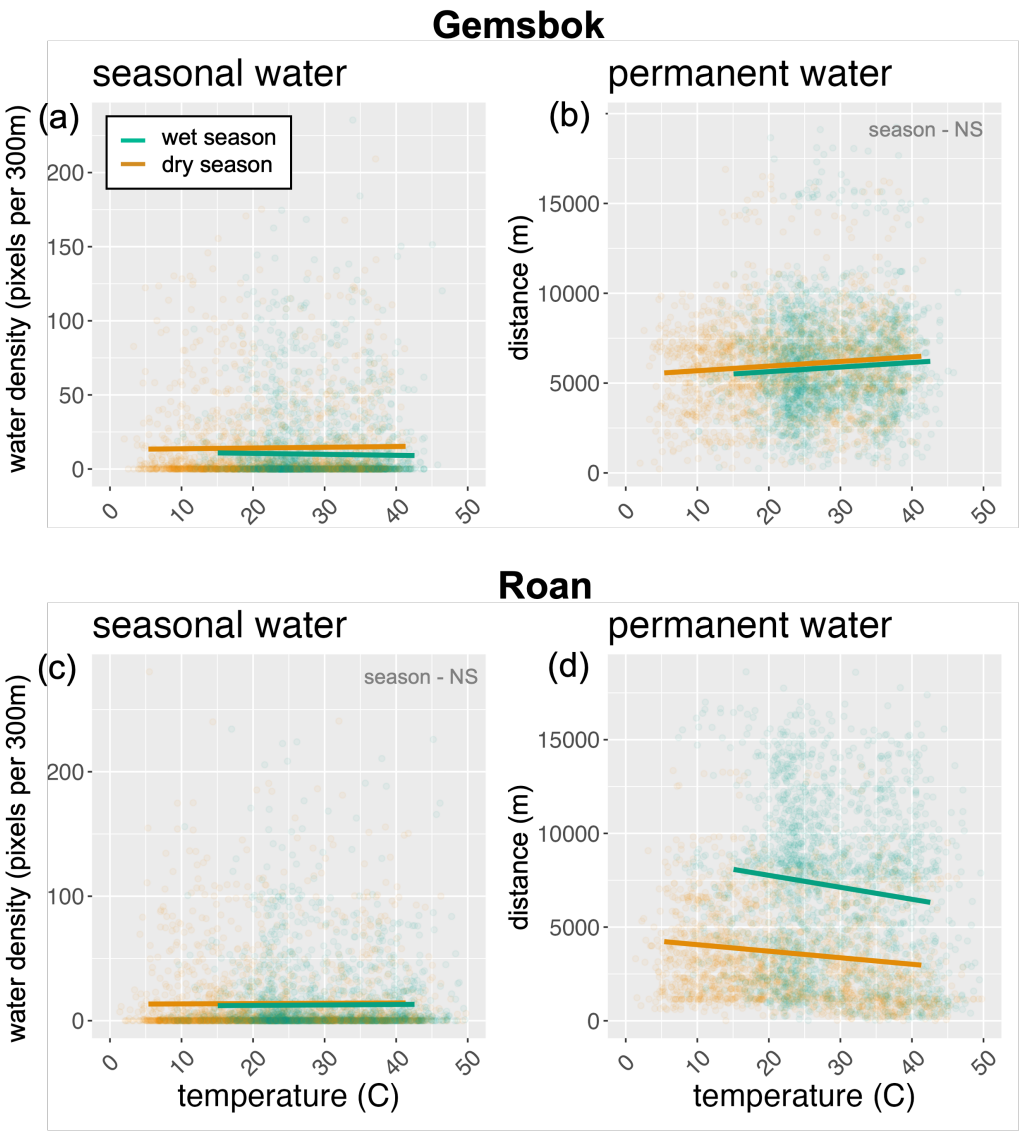

FIGURE 3.5**:** Seasonal water density, and distance from permanent water, by species, predicted by a multinomial logistic regression of season, temperature, season × temperature, and EVI (Eqn 3.4.3, Table 3.4). Covariates are statistically significant ($p \ll 0.01$) unless otherwise noted. Individuals of both species are located in regions with slightly more seasonal surface water at high temperatures. Gemsbok are farther from permanent water at high temperatures, while roan are closer.

($p \ll 0.01$) (Fig. 3.5d); however, gemsbok were *farther* from permanent surface water at high temperatures ($p \ll 0.01$) (Fig. 3.5b), with little seasonal difference.

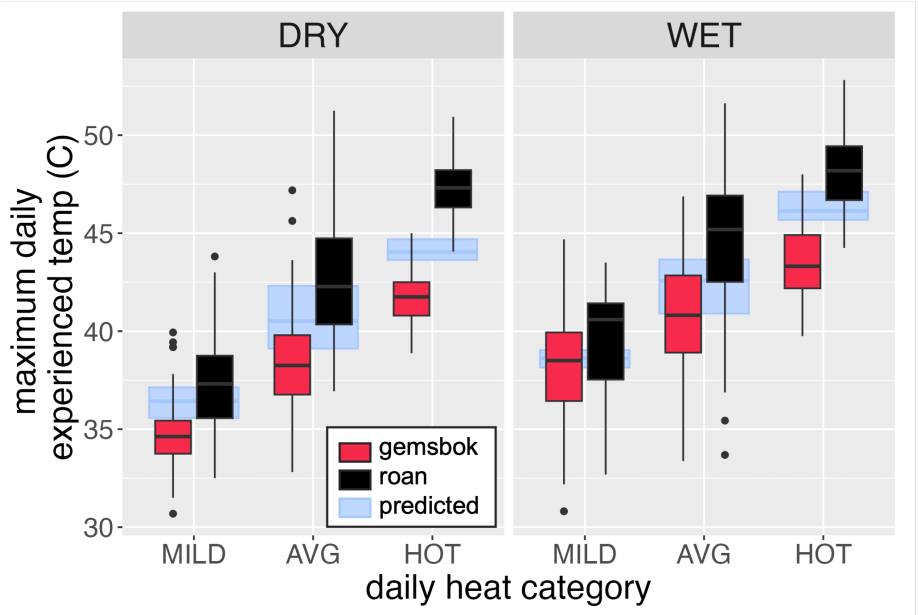

FIGURE 3.6**:** Maximum daily experienced temperature for each species during mild, average, and hot daily heat categories. For each individual, the maximum collar temperature was calculated and separated by daily heat category. The blue box represents the total predicted maximum collar temperature by a linear regression, with ERA5 reanalysis temperature and season (not species) as covariates. Species was not included in prediction to emphasize specific differences from the overall predicted maximum collar temperature.

Table 3.5: Average hourly microclimate temperatures experienced by gemsbok are 0.3 lower than roan in the dry season ($p \ll 0.01$) and 0.2 lower in the wet season ($p \ll 0.01$). These values increase to 0.98°C in the dry season and 0.82°C in the wet season (both $p \ll 0.01$) during the day (about 04:00-17:00). All species differences are statistically significant for all seasons (bold, asterisk), but effect sizes are statistically negligible.

	All values		Daytime values	
	Dry season	Wet season	Dry season	Wet Season
Gemsbok T range (°C)	8.5 – 37.7	18.8 – 38.9	8.2 – 38.6	19.9 – 39.8
Roan T range (°C)	7.6 – 40.1	17.6 – 41.5	17.6 – 41.5	19.3 – 42.4
mean difference (°C)	0.3	0.2	0.98	0.82
p-value	$\ll$ **0.01**$*$	$\ll$ **0.01**$*$	$\ll$ **0.01**$*$	$\ll$ **0.01**$*$
Cohen's d	0.02	0.03	0.07	0.09
effect size	negligible	negligible	negligible	negligible

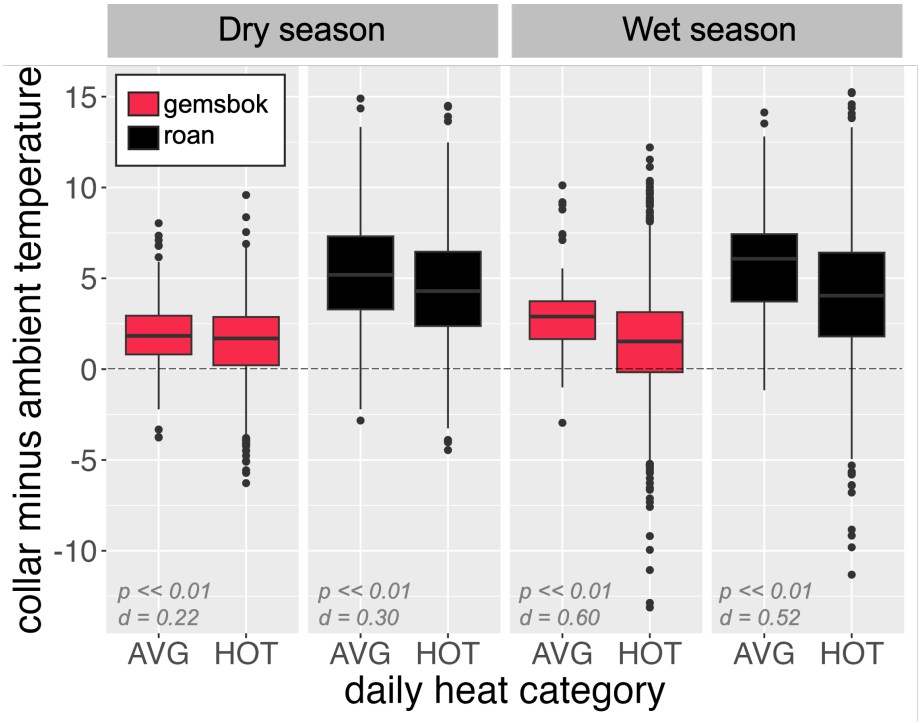

FIGURE 3.7**:** Difference between collar and ambient temperatures during average and hot daily heat categories. All values were significantly smaller ($p \ll 0.01$) during hot days than average days, but the effect size for this difference was larger in the wet season.

3.5.3 Microclimate Management Strategy reliance

On average, gemsbok experienced microclimate temperatures that were lower than those of roan. In addition, especially on hot days in both seasons, gemsbok microclimate temperatures were lower than those predicted by ambient (ERA5) temperatures and season (Fig. 3.5.2).

Both species experienced a smaller collar-to-ambient temperature difference on hot days than average days (no mild days had collar temperatures 35>°C) (Fig. 3.5.2). The effect size during the dry season was small, and medium for the wet season (Table 3.5), indicating increased reliance on MSS during the wet season, which was not expected. These differences were greater for roan than for gemsbok, reflecting a lower overall microclimate temperature for gemsbok than for roan.

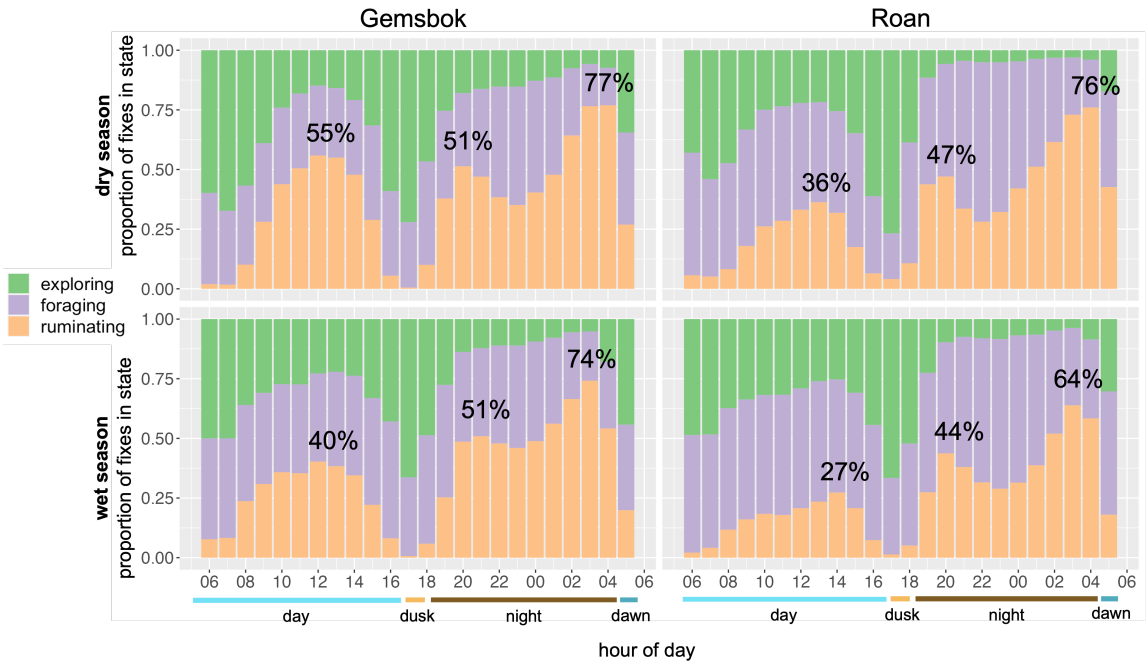

FIGURE 3.8**:** Proportion of GPS collar fixes that corresponded to each activity state (green exploring, purple foraging, orange ruminating/resting) by season, binned by the hour of the day. Rumination peaked at 12:00, 21:00, and 03:00; the black text indicates the percent of ruminating fixes. The 12:00 rumination peak increases in the dry season for both species, but is more distinct and higher-peaked for gemsbok.

3.5.4 Activity Budget Strategy reliance

When comparing experienced microclimate temperatures across species and seasons, gemsbok experienced a 0.2°C cooler microclimate than roan during the wet season ($p < 0.01$), and a 0.3°C cooler microclimate in the dry season ($p \ll 0.01$) (Fig. 3.3, Table 3.4). However, the effect size of this difference was statistically negligible (Cohen's $d = 0.02$ in the dry season, 0.03 in the wet). When comparing just across daytime hours, the difference in experienced microclimate temperature was 0.98 in the dry season and 0.82 in the wet season (both $p \ll 0.01$). Although this result was also statistically negligible (Cohen's $d = 0.07$ in the dry season, 0.09 in the wet), the difference of 1°C in experienced temperature may be biologically relevant, as small increases in temperature can have a large influence on thermoregulation strategy and efficiency.

Table 3.6: Activity budget allocations of the percentage of GPS fixes in each activity state (foraging-F, exploring-E, and ruminating-R) during three peak rumination times of the day (03:00, 12:00, 20:00) in the dry season and the wet season, by species. Seasonal differences are compared using a χ^2 test of proportionality. All seasonal differences in activity budget during peak rumination times are statistically significant ($p < 0.05$, bold, asterisk) except for gemsbok at the 03:00 rumination peak. See Fig. 3.8 for a visualization of these data.

Gemsbok

	Dry season			Wet season			Seasonal differences		
Peak time	% F	% E	% R	% F	% E	% R	p-value	Cramér's V	effect size
03:00	18	6	77	21	5	74	0.12	0.03	small
12:00	29	15	56	37	23	40	$\ll$ **0.01***	0.16	medium
20:00	31	18	51	38	14	49	$\ll$ **0.01***	0.08	small

Roan

	Dry season			Wet season			Seasonal differences		
Peak time	% F	% E	% R	% F	% E	% R	p-value	Cramér's V	effect size
03:00	24	3	73	32	4	64	$\ll$ **0.01***	0.10	medium
12:00	45	22	33	50	29	21	$\ll$ **0.01***	0.14	medium
20:00	47	6	47	55	7	38	$\ll$ **0.01***	0.08	medium

Hourly activity budgets generated by the HMM highlighted three main rumination periods throughout the day: 03:00, 12:00, and 20:00 (Fig. 3.8a, Table 3.6). The proportion of each population in the ruminating state was highest at 03:00 (gemsbok: 77% dry and 74% wet; roan: 76% dry and 64% wet), and both species' peaks were greater during the dry season ($p \ll 0.01$) (Table 3.6). Gemsbok rumination proportion is generally greater than that of roan, especially during the 12:00 peak (19 points greater in the dry season and 13 in the wet, $p \ll 0.01$), and the 12:00 peak increase from wet to dry season is larger for gemsbok (40% to 55%) than roan (27% to 36%) (Fig. 3.8, Table 3.6).

Exploration peaked at dusk for both gemsbok (72% in the dry season, 66% in the wet) and roan (77% in the dry, 67% in the wet). During this peak time, foraging values fell for gemsbok (27% in the dry, 33% in the wet) and roan (19% in the dry, 32% in the wet) and rumination fell to 1-4% for both species in both seasons (Fig. 3.8b)

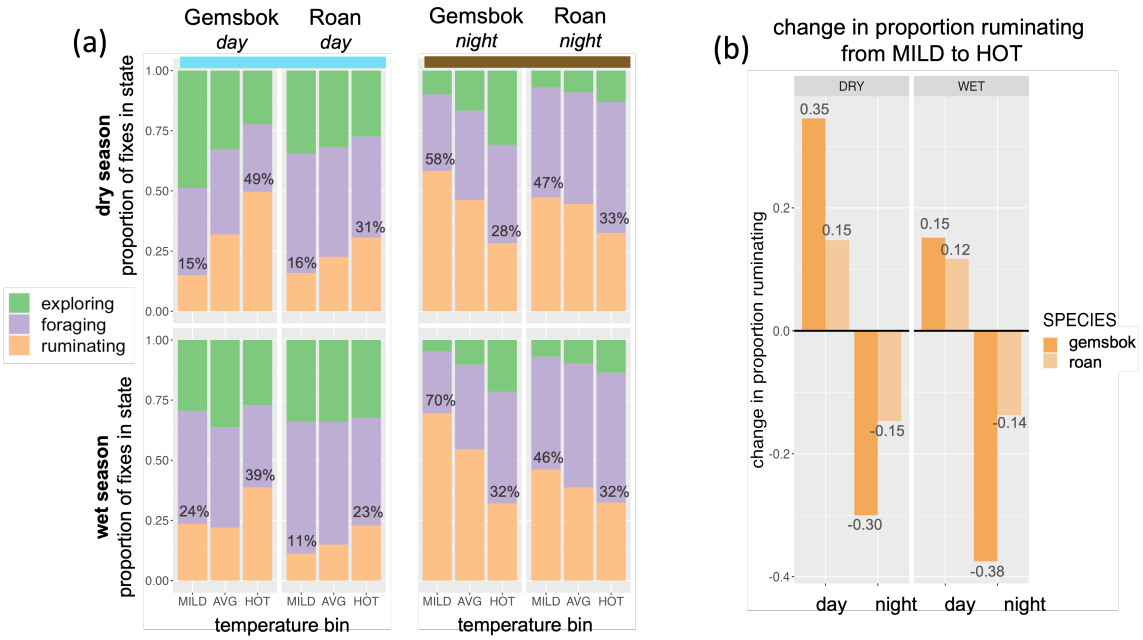

FIGURE 3.9**:** (a) Proportion of GPS collar fixes that corresponded to each activity state (green *exploring*, purple *foraging*, orange *ruminating*) by maximum daily heat category (DHC; <27.4°C "mild", 27.4°C to 35.8°C "average", >35.8°C "hot") by time of day and season. Both species tend to increase their daily rumination on hotter days and decrease nighttime rumination to compensate (rumination for mild and hot days are indicated). All differences are statistically significant ($p \ll 0.01$), but the effect size (measured by Cramér's V) is greater for gemsbok than for roan (Table 3.7) (b) A visualization of the effect sizes for (a), given as the change in the proportion of fixes in ruminating state from "mild" to "hot" DHC. The absolute change in allocation of rumination between mild and hot days is greater for gemsbok than roan, and this difference is magnified in the dry season.

For both roan and gemsbok, the differences in daily activity budgets across seasons and daily peak experienced temperatures were statistically significant (all $p \ll 0.01$); however, the effect size of these differences in average activity state proportion were small (Cramer's $V = 0.04$ for oryx across seasons and 0.017 across temperatures; 0.07 for roan across seasons and 0.018 across temperatures). While hourly activity budgets varied (Fig. 3.8), the overall allocation of activity to ruminating, exploring, and foraging remained similar (27% exploring, 36% foraging, 37% ruminating for gemsbok; 25% exploring, 47% foraging, 28% ruminating) regardless of season or an increase in DHC.

Table 3.7: Change in the proportion of fixes in ruminating state from "mild" to "hot" days, for both roan and gemsbok, in the dry and wet season, given during the day and at night. Although all differences are statistically significant ($p < 0.05$, bold, asterisk), the absolute change in allocation of rumination between mild and hot days is greater for gemsbok than roan. This difference is positive in the day (higher rumination on "hot" days) and negative at night (less rumination on "hot" days), and is magnified in the dry season (greater absolute difference between "mild" and "hot" in the dry season than in the wet). See Fig. 3.9 for visualization.

Gemsbok

	Dry season		Wet season	
	Day	Night	Day	Night
change in rumination proportion	0.35	-0.30	0.15	-0.38
p-value	$\ll$ **0.01***	$\ll$ **0.01***	$\ll$ **0.01***	$\ll$ **0.01***
Cramér's V	0.18	0.16	0.12	0.17
effect size	large	large	medium	large

Roan

	Dry season		Wet season	
	Day	Night	Day	Night
change in rumination proportion	0.15	-0.15	0.12	-0.14
p-value	$\ll$ **0.01***	$\ll$ **0.01***	$\ll$ **0.01***	$\ll$ **0.01***
Cramér's V	0.08	0.07	0.07	0.06
effect size	medium	medium	medium	medium

Higher DHC ("hot" days) were associated with a higher daytime rumination and lower nighttime rumination for both species (Fig. 3.9). This increase was much greater for gemsbok (dry season: 15% to 49%, $V = 0.18$; wet season: 24% to 39%, $V = 0.12$) than for roan (dry season: 16% to 31%, $V = 0.08$; wet season: 11% to 23%, $V = 0.07$) (Fig. 3.9b, Table 3.7). These increases in daytime rumination were accompanied by similar decreases in nighttime rumination for both gemsbok (in the dry season 58% to 28% and $V = 0.16$; wet season 70% to 32% and $V = 0.17$) and roan (dry season: 47% to 33% and $V = 0.07$; wet season: 46% to 32% and $V = 0.06$) (Fig. 3.9b, Table 3.7). Again, gemsbok exhibited a much stronger response to higher experienced temperatures, especially in the dry season, which can be seen visually looking at the dark orange bars in Fig. 3.9b, or by comparing values of Cramér's V in Table 3.7.

3.6 Discussion

Our findings show that, while both species relied to some extent on all three strategies, (1) roan relied more on the Surface Water Strategy and gemsbok more on the Activity Budget Strategy and Microclimate Selection Strategies, and that (2) these specific dependencies intensified under higher temperatures.

Many ungulates in arid regions, including sable antelope (*Hippotragus niger*, Owen-Smith and Goodall 2014) and greater kudu (*Tragelaphus strepsiceros*, Owen-Smith 1996), are known to increase daily rest at higher temperatures; both roan and gemsbok in this analysis follow this strategy. However, gemsbok clearly rely more heavily than roan on reallocating time towards resting and rumination, and away from exploration and foraging, apparently as a means of managing heat stress (Fig. 3.8). When conditions are drier, gemsbok increase their already-high amount of midday rumination (Fig. 3.8), and on hot days they spend more of their night foraging and exploring, again shifting rumination to midday (Fig. 3.9a). By restructuring their day to minimize heat gain, gemsbok can better utilize their high tolerance for increased body temperatures without increasing water intake. Gemsbok can therefore afford to stay away from crowded and predator-dense permanent waterholes (Table 2, Fig. 3.4.5c), taking advantage of less congested rangeland. However, to maintain their heat and water balance, gemsbok may suffer from this strategy either a loss of overall foraging and exploration, or an increase in nighttime predation risk due to more nocturnal activity.

Reliance on the microclimate selection strategy (MSS) was particularly surprising on the seasonal scale. Although gemsbok generally had a lower maximum microclimate temperature than roan, both species experienced a greater drop in collar-to-ambient temperature differences during hotter days in the wet season. This indicates that, during the wet season, both species relied more heavily on MSS than in the dry season. In particular, gemsbok rely on MSS during the wet season and as temperatures increase.

This could have implications for future gemsbok management: In regions with little shade or wind, gemsbok may not be able to rely on MSS during hot, dry weather.

Although their activity budgets did change to reflect higher heat loads, roan depended heavily on surface water access, especially through permanent waterholes. During the dry season and under hotter temperatures, they restricted their range to within a day's walk of these waterholes, even though they are often hotspots for water and forage competition (Owen-Smith 1996) and predation (Hayward and Hayward 2012). This wet-to-dry increase of 3,500m (compared to just 40m for gemsbok, Table 2) indicates that the start of the wet season loosens a strict limitation on roan landscape use. That roan dependence on permanent waterholes increases in hotter and drier conditions has twofold implications for the species' climate responses: First, that future heating and aridification may drive roan to remain closer to sparse water resources during the dry season, increasing competition for resources and predation risks; second, that the forage restriction of climate-change induced droughts may be compounded by a longer dry season (cite), further reducing the landscape's ability to sustain large populations of roan. Finally, while these findings indicate a strong reliance on permanent waterholes, we cannot extend this analysis to more natural regions with no augmented water supply, such as the nearby Okavango Delta.

The future restriction of roan to overcrowded permanent waterholes with poor forage quality and higher predation is cause for concern, beyond the loss for Khaudum's biodiversity. Roan antelope are very sparsely populated throughout their range in southern Africa, as this species takes advantage of poorer-quality habitat than other grazers of its size (Estes 1991). If their thermoregulation (and therefore hydration) needs increase in the coming years, roan may lose their ability to function in their low-quality terrain niche on the African savanna. In addition, many other species are dependent on water access to adequately maintain homeothermy.

This study not only quantifies the observed behavioral differences between wa-

ter dependent and independent ungulates at the landscape scale but illuminates how these strategies change with rising temperatures along a daily and seasonal gradient. As anthropogenic climate change approaches 1.5°C of warming, savanna ungulates will experience higher heat stress; we show here that these climatic changes will have differential effects on animals that follow divergent heat-management strategies, possibly favoring water-independent species such as gemsbok and harming water-dependent species such as roan. Water-dependent ungulates may be more restricted around permanent waterholes in the future, while for water-independent ungulates, a clever management of the timing of daily activities may lead to more access to the resources of unused rangeland.

4

Ungulate seasonal range expansion drives responses to fencing on a southern African savanna

Margaret E. Swift, Robin Naidoo, Piet Beytell

4.1 Introduction

The proliferation of wildlife fencing is one of the greatest human impacts on mammalian herbivores today. Fences are a ubiquitous feature of grassland and savanna ecosystems across the globe, and in many areas their extent exceed roads by an order of magnitude (Jakes et al. 2018). In southern Africa, thousands of miles of veterinary fences have been erected primarily to prevent the spread of disease between wildlife and livestock (Gadd 2012). The unintended consequences of these fences, however, are significant – over the past 70 years, hundreds of thousands of wild ungulates have died from fence entanglement or migration restrictions (Ferguson and Hanks 2010, Gadd 2012, Osofsky 2019). These losses show that fence crossing is costly, but must be neces-

sary for some individuals. But which ones, and why? Recent studies have found that sex (Naidoo et al. 2022), age (Segar and Keane 2020), and migratory behavior (Hering et al. 2022a,b) drive differences in ungulate fence-encounter responses and crossing rates. Seasonal range expansion in non-migratory populations could also influence fence responses, but this trait has yet to be studied. Species that expand their ranges in the wet season often do so to access more forage or ephemeral pools of rainwater; this drive may cause them to encounter and cross fences more often. On the other hand, crossing a fence is an energetically costly activity (Hering et al. 2022a), one which might not be undertaken by species that do not seasonally change their ranges. The inclusion of seasonal range expansion to our knowledge of why individuals attempt to cross fences will further aid in predictions of ungulate behavior under future climate and fencing scenarios.

While not new, *fence ecology* is emerging as a field that aims to address the relative lack of attention on fences worldwide, compared to other linear features such as roads and power lines (Jakes et al. 2018; see Hoare 1992, McKillop and Sibly 1988, Taylor and Martin 1987 for early fencing work). Fence ecology frameworks have called for more research into the ecological effects of fences on ecosystems, populations, and individuals (Jakes et al. 2018, McInturff et al. 2020). Meanwhile, authors in the related field of *movement ecology* have also recently called on researchers to study the interface between large herbivores, seasonal movement, and environmental change, including fencing (Owen-Smith et al. 2020). As fencing proliferates across rangeland ecosystems, the question of how fencing impacts ecological functioning from individuals to communities will only grow more pressing.

In southern Africa, recent work answering the fence ecology call has focused on the effects of fence encounters across species, sex, age, and migratory ability, especially in regions fragmented by veterinary fencing. For example, a study of three antelope species (greater kudu, eland, and springbok; *Tragelaphus strepsiceros, T. oryx,* and *Anti-*

dorcas marsupialis, respectively) in Etosha NP, Namibia, found that a veterinary fence with elephant-created gaps ("semipermeable" in the sense that it is crossable in places, but still generally restricts movements) imposed energetic costs on crossing, and that fence encounters were most common for eland, a social and nomadic species (Hering et al. 2022a,b). In another study, the veterinary border fence between Namibia and Botswana was differentially permeable to bush elephant (*Loxodonta africana*) depending on sex: Solitary bulls crossed in 29% of close (<25m) fence encounters, while females in breeding herds never crossed, possibly due to the hazards of fence-crossings to juveniles (Naidoo et al. 2022). Beyond Africa, differential permeability has been shown in a community of pronghorn antelope (*Antilocapra americana*) and mule deer (*Odocoileus hemonius*) in Wisconsin, USA, where pronghorn encountered and crossed fences twice as often as mule deer, and increased their fence crossing 1.5 times in the summer compared to the winter (Xu et al. 2021). Another study in the American Prairie Reserve, USA, found that permeability was greatest for females and juvenile groups (Segar and Keane 2020). These studies show that individual traits such as sex, age, and migratory status can greatly affect an animal's ability or willingness to cross a fence. However, questions remain for how these findings apply to other similar species, or how range expansion adds to this trait equation.

Veterinary fencing has a long history in southern Africa, especially in Namibia, Zimbabwe, and Botswana, the latter of which contains over 5,000km of cattle fencing inside its 3,700m of national borders (Gadd 2012). These countries introduced veterinary cordon fencing in the mid-20th century to prevent wildlife-to-livestock transfer of Foot-and-Mouth Disease (FMD), Contagious Bovine Pleuropneumonia (CBPP), and other diseases that can infect livestock and in turn threaten herders' livelihoods and human health (Gadd 2012, Taylor and Martin 1987). The presence of FMD or CBPP in a region can preclude participation in lucrative international beef markets (Gadd 2012, Thomson et al. 2013) and costs global economies, public health systems, and livestock agri-

culture billions of dollars per year (McLeod et al. 2016, Osofsky 2019). Restricting movements with cattle fences or double-cordon electric fencing between outbreak zones allows pastoralists in disease-free rangelands to sell their beef without lengthy quarantine restrictions (Taylor and Martin 1987, Thomson et al. 2013). These tangible benefits of veterinary fencing are not easily ignored.

The same structures that protect herders and livestock from disease and its financial consequences also reshuffle existing ecological relationships where they are erected (McInturff et al. 2020). Ungulates caught in fencing may die due to injury, predation, or starvation (Harrington and Conover 2006, Mbaiwa and Mbaiwa 2006). Predation pressures rise near fences as well: Lion (*Panthera leo*) densities can increase inside fenced areas (Creel et al. 2013) and some predators corner prey against fences (Dupuis-Desormeaux et al. 2016). Interactions with fencing can interrupt or relocate ungulate activities, for example by reducing feeding time and daily movement in Przewalski's gazelle (*Procapra przewalskii*) (You et al. 2013), or by increasing bush elephant foraging intensity in areas far from fences (Vanak et al. 2010).

Fences also impact wildlife beyond their physical structures, most notably by preventing movement between fragmented habitat patches (Wilcox and Murphy 1985). Fragmented landscapes are often lower in biodiversity than large, contiguous ones, as these smaller areas can sustain fewer species (He and Legendre 1996, McIntyre 1995, although see Anderson 1999) and have higher rates of extinction (Soulé et al. 1979, although see Fahrig 2003 for a comparison of habitat break-up vs habitat loss). Fence fragmentation prevents access to surface water sources that sustain populations in the dry season (Whyte and Joubert 1987), and artificial waterholes added by land managers to mitigate these restrictions may limit biodiversity (Loarie et al. 2009, Shannon et al. 2009) and increase predation of low-density ungulates (Harrington et al. 1999, Owen-Smith 1996, Smuts 1978). Many great African migrations, such as those of bush elephant (*Loxodonta africana* Naidoo et al. 2022) and zebra (*Equus quagga*, Bartlam-

Brooks et al. 2011, Kauffman et al. 2021), have been restricted or prevented by fence fragmentation, removing a source of nutrient cycling (McNaughton 1990, Subalusky et al. 2017) and reducing the savanna's carrying capacity for large, migratory ungulates (Ben-Shahar 1993). Finally, fragmentation can lead to genetic isolation (Wang and Bradburd 2014, Woodroffe et al. 2014), increasing population vulnerability to disturbance (Caughley 1994, Evans et al. 2017, Griffiths et al. 2020), climate change (Ehlers et al. 2008, Hughes and Stachowicz 2004), and local extirpation (Frankham 2005, Soulé et al. 1979).

When faced with a fence, animals may respond in several ways. Animals may spend time tracing along the fence in search of a place to cross (Nandintsetseg et al 2019), become trapped (Harrington and Conover 2006, Mbaiwa and Mbaiwa 2006), or bounce quickly away from the fence (Vanak et al. 2010). Animals also cross fences, either by using an existing gap, jumping, burrowing or, in the case of larger animals such as elephant, by creating their own gaps in the fence (Hoare 1992, Naidoo et al. 2022). These crossing tactics may interact; for example, savanna elephant (*L. africana*) use their strength to power through fencing, opening barriers for opportunists to slip through (Jori et al. 2011). Fence crossing is of particular interest as it represents an incomplete restriction on movement, and has been particularly well-studied using camera traps (Burkholder et al. 2018, Wilkinson et al. 2021), GPS tracking data (Xu et al. 2021), and fence-design experiments (Palmer et al. 1985). Fence crossing can be energetically costly as the animal works to jump over or burrow under the fence (Hering et al. 2022a), but these costs may be offset by better access to water or forage on the other side (Dupuis-Desormeaux et al. 2016, Wilkinson et al. 2021).

Fences are well known to halt or reduce great migrations (Kauffman et al. 2021), but local movement patterns may also affect ungulate fence encounter behaviors and crossing rates. During the wet season, ungulates dependent on daily drinking water ("water-dependent") often expand their ranges, traveling further from their dry season

range to access more surface water and fresh forage (Lamprey 1963, McNaughton 1990, Western 1975). For example, water-dependent grazers blue wildebeest (*Connochaetes taurinus*) and plains zebra (*E. quagga*) in the Kruger NP, South Africa have been shown to be located, on average, over 1km closer to water sources during the dry season than the wet (Smit et al. 2007). Ungulates that depend less on surface water ("water-independent") often do not follow this expansion-contraction trend (Smit et al. 2007, Western 1975).

Because of this seasonal range expansion, we hypothesize that water-dependent species may be more motivated than water-independent species to overcome fencing barriers that block them from accessing wet-season resources. Alternately, range-expanders may find the costs of crossing too high, and instead bounce off the barrier and expand their wet-season ranges more on one side of the fence to compensate. Although the general importance of water-dependence for predicting range expansion is well established, it is unknown whether and how the behavior of water-dependent species differs from that of water-independent species when encountering fences, and whether the benefits of crossing outweigh the costs.

To answer these questions, we use four years (2013-2017) of GPS collar tracking data from 16 water-dependent roan antelope (*Hippotragus equinus*) and 16 water-independent gemsbok (*Oryx gazella*) along the fenced Namibia-Botswana border. With the following key questions and expectations, we aim to answer a larger question for fence and movement ecology, namely, *How do an ungulate's seasonal needs determine its response to a barrier that imposes costs to crossing?*

1. *Response:* If range expansion needs motivate water-dependent ungulates to cross fences, then we expect that (a) ranges will be larger in the wet season than the dry for roan, but not for gemsbok, that (b) roan fence encounters will occur more often in the wet season than the dry, and that (c) roan will encounter and cross

the BCF more often than gemsbok.

2. *Costs:* If fence crossings impose a noticeable cost on individuals, we expect a significant loss of foraging and ruminating time (both of which are necessary for energy acquisition) and an accompanying increase in exploration (and energy-intensive activity) prior to fence crossing.

3. *Benefits:* If individuals cross the fence to access better or more abundant resources, then we expect that individuals will choose post-crossing locations with (a) higher vegetative productivity, and (b) with more access to surface water sources, than their pre-crossing location.

To our knowledge, this paper is the first to compare fence encounters and crossings of two resident (non-migratory) ungulates at either end of the water dependence spectrum. As such, this study will add a new seasonal behavior angle to the burgeoning field of fence ecology. In addition, this paper aims to provide expectations of fence permeability based on seasonal movement traits for those that build and maintain wildlife fences in southern Africa.

4.2 Study site and species

4.2.1 Study Area: Kavango East, Namibia and Ngamiland, Botswana

We collected ungulate movement data from 2013 to 2017 across northwestern Botswana (Ngamiland region) and northeastern Namibia (Kavango East region; Fig. 4.1). This region is part of the larger Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA), a multinational, multi-use conservation area effort to preserve African savanna communities. All focal animals were fitted with GPS-enabled collars in Khaudum National Park, Namibia (18.76S, 20.73E), a 385,000 ha conservation area situated northwest of the Okavango Delta directly on the Namibian side of the border. Khaudum is

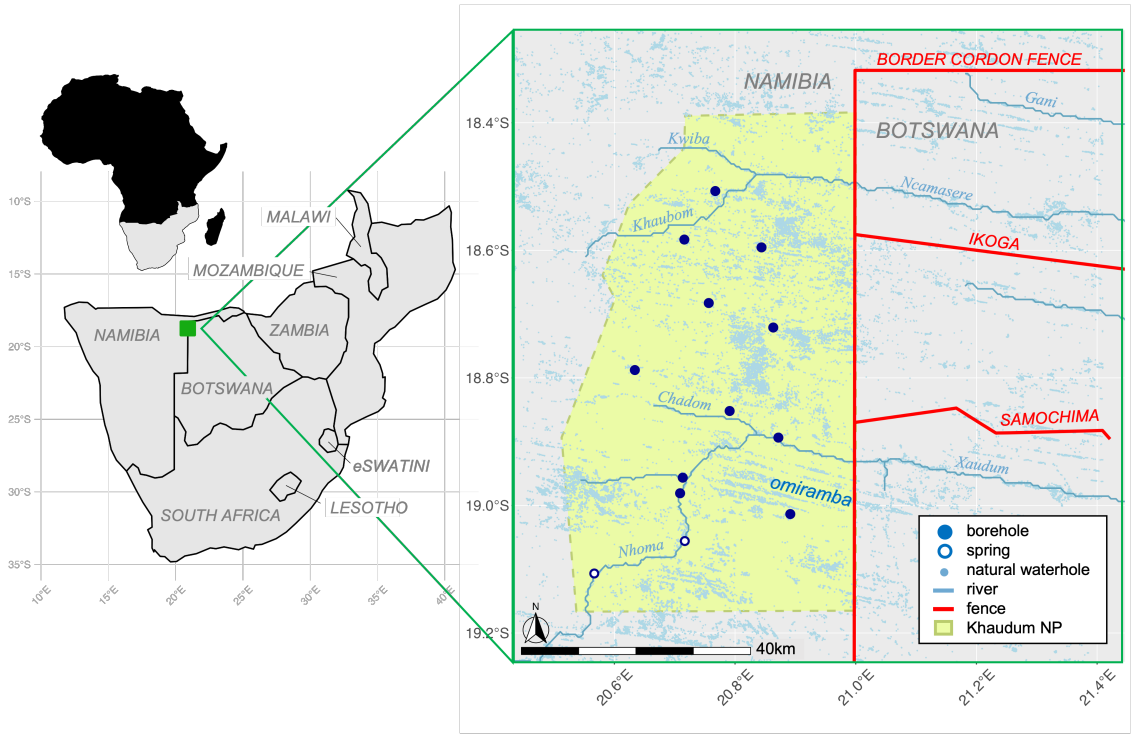

FIGURE 4.1**:** Study area: Khaudum National Park (light green) and surrounding areas. Red lines indicate electrified veterinary fencing erected to slow wildlife-livestock disease transfer. Major rivers and waterholes are labeled in light blue (Schaffer-Smith et al. 2022). Artificial waterholes (dark blue dots) and springs (white dots) are provided in Khaudum to supplement sparse surface water during the dry season.

flanked to the west by small-scale farms and to the east by several Herero pastoralist communities that use the territory for livestock herding (McGahey 2011). Community-run conservancies border the north (George Mukoya and Muduva Nyangana) and the south (Nyae Nyae and N#a-Jaqna) of Khaudum; these conservancies are primarily inhabited by Ju|'hoansi, Khwe, and !Xun herders and farmers (Dieckmann et al. 2014). The region receives nearly all its 400-500 mm of annual rainfall during the wet season from November to April and virtually no precipitation during the remainder of the year. Topographically, the area is flat, with a lowest elevation of 1,080m above sea level in the north and a highest elevation of 1,150m in the southwest.

The Border Cordon Fence (BCF) on the border between Namibia and Botswana (Fig. 4.1, Fig. 4.2) is a series of three parallel fences running north to south (Fig. 4.2b). It was

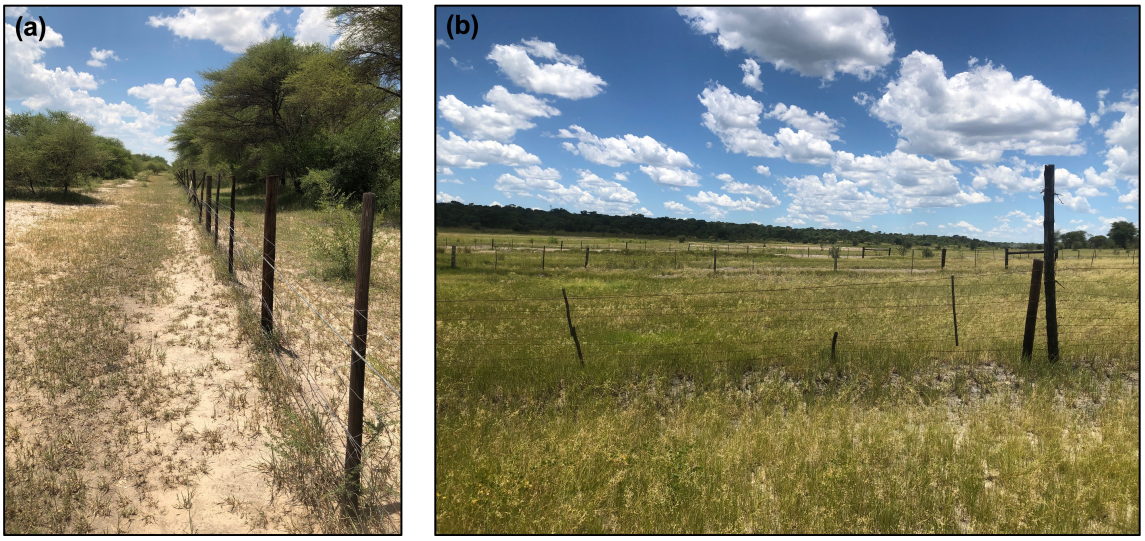

FIGURE 4.2**:** Photographs of the Border Cordon Fence. (a) shows one section in good repair. (b) shows all three fences along an open plain. ©Robin Naidoo, 2023.

erected in 1954 primarily to prevent transfer of Foot-and-Mouth Disease, Contagious Bovine Pleuropneumonia (CBPP), and other illnesses from wildlife to livestock (Consultants 2000). It was one electrified, but is no longer, and some portions on the Namibian side are in disrepair. While the BCF may be sufficient to limit buffalo and other large mammals from crossing, male elephant frequently cross the fence into Botswana (almost 30% of encounters led to crossings, Naidoo et al. 2022), leaving holes that can be exploited by other animals.

In addition, one third of the western park boundary (beyond which lie small-scale farms) is bounded by cattle or domestic fencing, and two other CBPP fences (Ikoga and Samochima, Fig. 4.1) run laterally across Botswana's Ngamiland region (Consultants 2000, McGahey 2011). Although these fences are important for wildlife movements, this study focuses on the BCF, so encounters and crossings are not given for CBPP or cattle fences.

Despite the region's proximity to the Okavango Delta, a large permanent water source that flushes during the dry season, fences effectively cut off Khaudum and the neighboring Ngamiland district of Botswana from the Delta. Wildlife must therefore

rely on the two major rivers (Ncamasere and Xhaudum), two natural springs, 1,042km of seasonal rivers, and many shallow seasonal pans called *omiramba* (a Herero term; singular *omiramba*) within the region to meet their water needs (Fig. 4.1). In addition to natural water sources, the Namibian Ministry of Environment, Forestry and Tourism maintains eleven artificial waterholes, but these are far from the BCF and are not included.

4.2.2 Focal species

Both roan and gemsbok are medium-sized antelope in the tribe Hippotragini that are not capable of jumping to clear a 2m fence (Lindsey et al. 2012, van Rooyen 2002). Roan antelope weigh from 220-300kg and stand 1.4m at the shoulder, while gemsbok weigh 160-220kg and stand about 1.25m. Both species are listed as Least Concern by the IUCN Red List, and while gemsbok populations are stable (about 373,000 individuals), roan are declining (50,000-60,000 mature adults) (Group 2017, 2020).

Roan antelope commonly prefer regions with low density of competing herbivores and predators. They avoid close-canopied woodlands and are often abundant on moist or dystrophic savannas (with relatively infertile soils) (Havemann et al. 2016, Joubert 1976, Kingdon 2015). They are known to follow the expansion-contraction pattern of wet season dispersal (Joubert 1976), outlined in the Introduction. They drink regularly, graze heavily, and browse on occasion. Herds of 5-35 individuals often form from females with young and a single male who excludes others. Home ranges range from 2 to $100 km^2$ in size (Havemann et al. 2016). Herds rarely interact. Roan gestation of a single calf is about 280 days. Although breeding can occur at any time of year, calves are not often born in the dry season (Estes 1991).

Gemsbok are often found in the Kalahari, but in areas at the edge of their range, such as Khaudm NP, they tend to inhabit wooded grasslands and shrublands (Estes 1991, Kingdon 2015). They often use habitats that are only visited by other grazers

in the wet season (Estes 1991). Gemsbok are grazers that, like roan, opportunistically feed on browse when grass is not available. Gemsbok herds often include both males and females, unlike most other antelope, and home ranges can vary from 4 to 400km^2 (Kingdon 2015). Gestation of a single calf lasts 264 days and breeding is not seasonal.

Gemsbok and roan antelope represent two ends of a water requirement spectrum. Gemsbok are a classic arid-adapted species, needing only 3L/day of water per 100kg of mass to maintain homeostasis; most of this water is acquired through grazing, some browsing, and watery fruits such as cucumber and melon (Estes 1991). Roan require up to 10L/day of water per 100kg, a much higher water requirement that cannot be met through forage alone (Estes 1991). Roan therefore rely heavily on surface water resources especially in the dry season to meet their hydration needs.

4.3 Materials

4.3.1 GPS collar telemetry data

GPS telemetry data were gathered using 33 satellite-enabled collars manufactured by Africa Wildlife Tracking. Animals were fitted with collars in two two-year bouts, with GPS location points ("fixes") captured every five hours from 2013 to 2015 and every one hour from 2015 to 2017 (Table 4.1). Seven collars were deployed on roan from 25-26 Aug 2013 and nine (two roan, seven gemsbok) from 14-18 October 2014; these collars lasted until May-September 2015 and August 2016, respectively, and recorded data every five hours. The second batch of collars (eight female gemsbok, eight female roan) recorded data every hour, and were all deployed in July 2015, with the roan collars lasting until early 2017 and gemsbok collars ending a year prior.

Collars recorded temperature, altitude, and time at every GPS fix for an average of 3,170 fixes per individual for the five-hour collars and 11,294 fixes for the one-hour collars (when ignoring those that malfunctioned or were removed early). Two individuals from the first batch were re-collared in the third; their individual ID was carried over

Table 4.1: GPS collar information for all individuals in this study. Individuals marked F.E. encountered the BCF at least once. Individual 1021 and 1115 were re-collared in 2015 with one-hour fixrate collars 1728 and 1727, respectively; total number of fixes for these two are an aggregate of the old and new collars.

Collar	Species	Sex	Deploy Date	Stop Date	# fixes	Herd size	F.E.	Re-collar
975	Roan	F	2013-10-15	2015-07-27	3,368	40+	X	
976	Roan	F	2013-08-25	2015-08-19	3,650	13		
977	Roan	F	2013-08-25	2015-09-05	3,699	10	X	
1020	Roan	F	2013-08-25	2015-09-19	2,855	11		
1021	Roan	F	2013-08-26	2015-06-11	–	9		1728
1022	Roan	F	2013-08-26	2015-05-14	3,002	34		
1115	Roan	F	2013-10-18	2015-07-23	–	14		1727
1509	Roan	M	2014-10-14	2016-08-28	3,260	1		
1510	Roan	M	2014-10-14	2016-08-27	3,219	Herd	X	
1511	Roan	M	2014-10-14	2015-07-20	1,293	1	X	
1515	Gemsbok	F	2014-10-14	2016-06-06	2,539	Herd		
1516	Gemsbok	F	2014-10-14	2016-08-27	3,151	Herd	X	
1517	Gemsbok	F	2014-10-14	2016-02-13	2,151	Herd	X	
1518	Gemsbok	F	2014-10-14	2016-08-28	3,219	Herd	X	
1519	Gemsbok	F	2014-10-14	2015-02-18	566	Herd		
1521	Gemsbok	M	2014-10-14	2016-08-26	3,385	Herd	X	
1717	Gemsbok	F	2015-07-25	2016-06-15	5,345	5		
1718	Gemsbok	F	2015-07-22	2017-02-14	12,172	9		
1719	Gemsbok	F	2015-07-24	2017-03-11	12,824	4		
1720	Gemsbok	F	2015-07-26	2015-12-23	2,996	8		
1721	Gemsbok	F	2015-07-24	2017-01-10	11,876	4		
1722	Gemsbok	F	2015-07-23	2017-01-07	11,321	4		
1723	Gemsbok	F	2015-07-26	2016-06-09	6,007	1		
1724	Gemsbok	F	2015-07-25	2016-01-19	3,837	4	X	
1725	Roan	F	2015-07-26	2017-02-08	12,496	9		
1726	Roan	F	2015-07-22	2016-11-12	11,310	13		
1727	Roan	F	2015-07-23	2016-12-02	14,881	19		1115
1728	Roan	F	2015-07-22	2016-10-11	13,558	9		1021
1729	Roan	F	2015-07-25	2016-11-19	11,029	42	X	
1730	Roan	F	2015-07-23	2016-12-27	12,264	13		
1731	Roan	F	2015-07-24	2016-12-02	11,560	22	X	
1732	Roan	F	2015-07-26	2017-02-14	12,725	14		

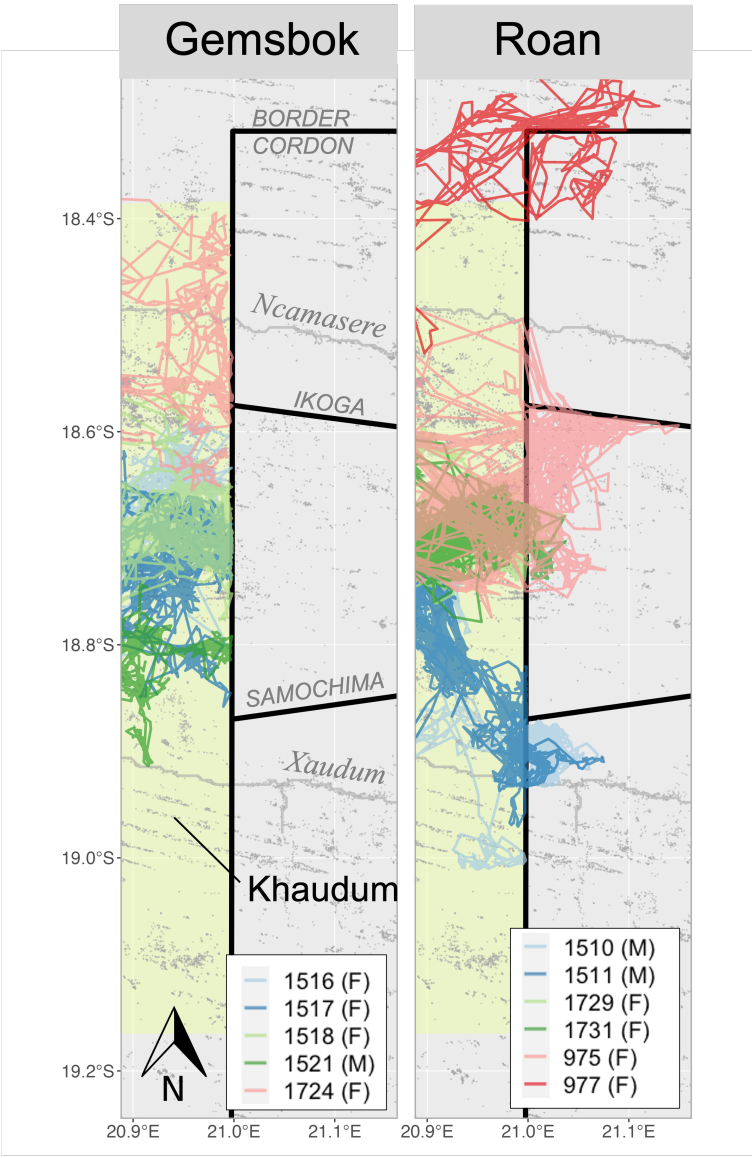

FIGURE 4.3**:** Map of fence encounters by species and individual. Gemsbok (left) never cross the fence, although they do encounter it. Roan (right) cross the fence many times at multiple crossing points.

for this analysis. For our analyses, we only used data from the five gemsbok (4 female, 1 male) and six roan (4 female, 2 male) that encountered the fence (Fig. 4.3, Table 4.1).

We removed the first and last five fixes from each dataset to account for behavioral changes due to collaring stress and end-of-life battery failure errors. To eliminate slowing fix rates when a collar battery began malfunctioning at the end of the battery's life,

we calculated a cumulative sum of the number of missing fixes in data collection; after fifteen cumulative gaps, the collar was labeled “malfunctioning” and we ignored data after this point.

4.3.2 Surface water data

Surface water was mapped using data from Schaffer-Smith and coauthors’ (2022) delineation of >2 million seasonal waterholes and rivers in the Kavango-Zambezi (KAZA) transfrontier conservation area, using an Automated Water Extraction Index (AWEI) on Sentinel-2 data at 10m resolution. These data are the best available for mapping small waterholes in the KAZA region. Commonly-used datasets such as HydroSHEDS are too coarse (15 arc-seconds) to map small seasonal waterholes, and only use a digital elevation model (DEM) from SRTM data to map free-flowing rivers, not small basins (Grill et al. 2019). Another common dataset, by Pekel et al. 2016, maps presence, occurrence, and seasonality of water sources using Landsat data; however, this too is at a coarser scale (30m) than is necessary to define small, seasonal waterholes.

Because our antelope collar data (2013-2017) do not temporally overlap with the Sentinel-2 derived waterhole dataset (2017-2020), we retained waterholes that were "filled" (at least one pixel flagged as water) for at least 60% of the dataset, to represent waterholes reasonably available during our study period; then, we split the waterhole map into dry season (May-October) and wet season (November-April). For each GPS point, we then extracted the total waterhole density (measured by the number of pixels marked as "water") in the appropriate season within a 300m buffer, the approximate mean step length for both antelope.

4.3.3 Vegetation data

Vegetation productivity, measured using the Enhanced Vegetation Index, was sourced from Landsat 8 32-day composites (once a month) of L1T orthorectified scenes (at 30m

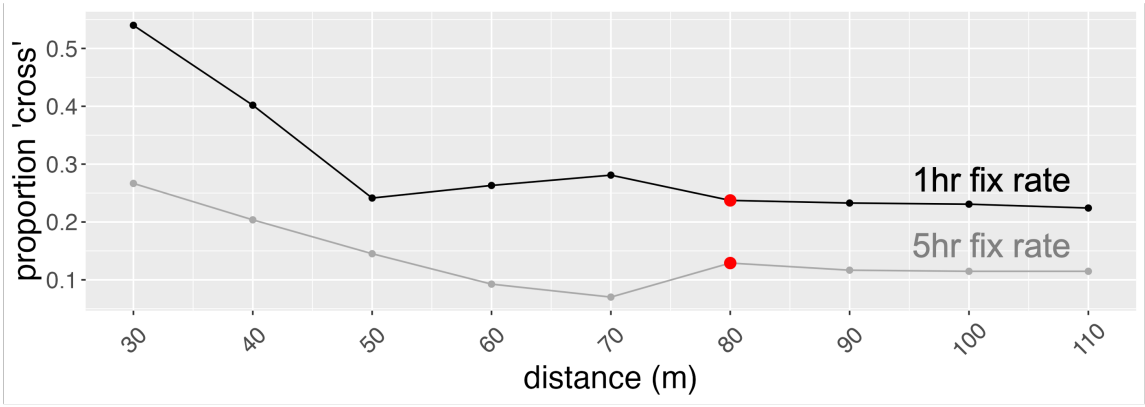

FIGURE 4.4**:** Proportion of fence encounters labeled "cross" at different levels of the distance parameter, for both the one-hour GPS fix rate dataset (black) and the five-hour dataset (gray). All points that fall within this buffer distance from the fence are considered encounters. We compared the percentage of "cross" encounters, and chose a distance at which the percentage leveled off (80m, red point), as suggested by the 'BaBA' package authors (Xu et al. 2021).

resolution), at top-of-atmosphere reflectance, using Google EarthEngine (Gorelick et al. 2017). EVI is more sensitive to canopy variations than the Normalized Difference Vegetation Index (NDVI), as it includes a canopy background adjustment measure and uses the blue band to correct for aerosol interference on red wavelengths (Huete et al. 2002). For each GPS telemetry fix, we took the temporally closest monthly Landsat 32-day composite to the fix and extracted the median EVI within a 300m buffer around the GPS fix.

4.4 Methods

4.4.1 Data Analysis

Determining fence encounter behaviors

We characterized fence encounter behaviors using a Barrier Behavior Analysis ("BaBA", Xu and Herrmann 2023, Xu et al. 2021). BaBA is a spatial and temporally explicit approach to categorize animal behaviors upon approaching a physical barrier, in this case the BCF. The BaBA method creates a buffer around the BCF and defines an encounter

Table 4.2: Types of fence encounter with accompanying descriptions. For a visual depicting all six crossing types, see Fig. 4.5

Type	Description
cross	Individual crosses all fences and ends on the other side
jag	Individual crosses one fence but quickly returns, ending on the same side
bounce	Individual approaches the fence and quickly moves away without crossing
trapped	Individual remains near fence for > 24hrs without crossing
trace	Individual walks along fence for >10h without crossing
average	Individual approaches fence but behavior does not change (not a bounce, trapped, or trace) and individual does not cross

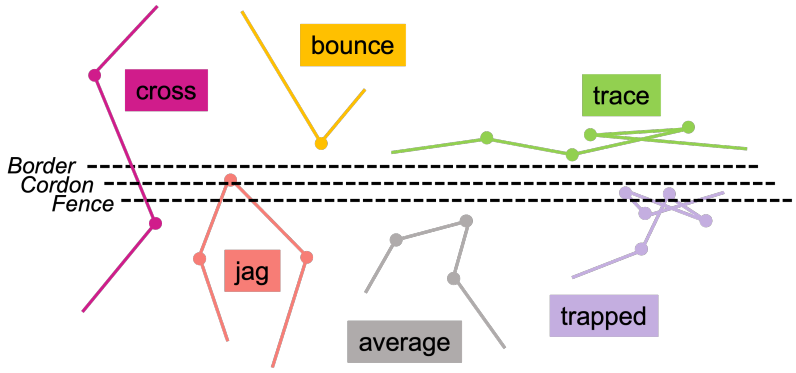

FIGURE 4.5**:** Fence encounter behavior types: A *cross* is a full crossing of the BCF, while a *jag* is a partial crossing with a quick return to the starting side. Animals may also *bounce* away from the fence upon encounter, *trace* along it, or continue with *average* behavior. Only one roan and one gemsbok encounter were labeled as *trapped* in this study, with GPS locations near the fence encounter area for >24 hours. Figure adapted from Xu et al. 2021. See Table 4.2 for a full description of fence encounters.

as any point when an animal's movement path intersects with a d-meter buffer around the barrier. Each encounter is categorized based on the amount of time spent near the barrier, the angle of approach and departure, the straightness of the overall path, and whether the individual crossed from one side to the other (Xu et al. 2021). We tested buffer distances d from 10 to 120m as suggested by Xu et al (Xu et al. 2021) and found that the proportion of encounters that resulted in a cross leveled off to about 20% at $d = 80m$ (Fig. 4.4); given that no crosses were observed for gemsbok, we used 80m as our buffer distance for both species.

To describe fence encounter types, we used a modified version of the encounter

type categorization used by Xu et al. 2021 (Fig. 4.5, Table 4.2). An encounter was labeled a *cross* if the individual's start and end points were on opposite sides of the BCF, and a *jag* if they returned to their starting side soon after crossing; this separated the long-term crossings of roan from the short-term jags of gemsbok across only a portion of the BCF (see Fig. 4.3). A *bounce* occurred when individuals approached the fence and quickly left without crossing, while a *trace* indicated prolonged contact and movement across the fence line without crossing (this encompasses both "trace" and "back-and-forth" from Xu et al. 2021). An animal was considered *trapped* if they remained in the same location near a fence for more than 24 hours without crossing. Lastly, an *average* movement was any fence encounter not classified as *bounce, jag, cross, trace,* or *trapped*.

Determining species ranges

Although 33 individuals were fitted with GPS collars for this study, only eleven encountered the fence at any point (Table 4.1, Fig. 4.3). The remaining 22 individuals with no fence encounters were used to obtain an estimate of home range size without fence interference effects. In addition, to minimize introduced noise from solitary males, which frequently foray far from their home ranges, we only calculated seasonal home ranges for females (9 roan and 9 gemsbok), which often travel in breeding herds and therefore represent the general home range for a larger portion of the population.

We calculated each individual's seasonal space use for each year using a k-nearest neighbor convex hull (k-NNCH), which gives an estimate of physical area traversed by an individual. k-NNCH, developed by Getz and Wilmers 2004, creates a convex hull (minimum convex polygon) for each point and its $k-1$ nearest neighboring points, which are then combined via a union of all individual convex hulls. This provides an estimate of home range that can account for linear boundary features, holes in the range, and irregularly shaped ranges, as well as providing estimates of high- and low-density

space use and core regions (Getz and Wilmers 2004). We implemented the k-NNCH method using the 'adehabitatHR' package (Calenge and Fortmann-Roe 2023) in R (R Core Team 2022, R version 4.3.1) for each individual-season-year (e.g., antelope 1510, wet season 2016). We used a subsample of collar data to visually determine the optimal k number of nearest-neighbors for which to implement k-NNCH, and chose a k of 25 as this number encapsulated all data points while still allowing gaps where no points are present.

Determining activity budgets for individuals

Activity budgets were determined with a Hidden Markov Model (HMM) using the momentuHMM package in R (McClintock and Michelot 2018) (See Section 3.4.2 for a more thorough review of HMMs and their use for modeling activities using these data). HMMs model a hidden process (the unknown behavior or physical state of an animal) from independent observations (known measurements with biases) of that behavior or state. We defined three separate activity states for each GPS point in our HMM: ruminating, foraging, and exploring. Both species in this study are ruminants and set aside large portions of their day to rest and digest their food; the "ruminating" category encompasses both "ruminating" and "resting" activities, as they are indistinguishable from these data. Ruminating is defined by very short (often 0m) steps from one fix to the next and an even distribution of turning angles (10% concentration of 0-degree angles). Foraging occurs at short and medium step lengths (mean step 481m) with more frequent bouts of straight lines (20% zero concentration) as the animal searches for food in a local area. Exploring animals take much longer steps (mean 1233m in 5 hours) and have the highest concentration of zero-angles (24%) as exploration indicates a continuous, directed movement.

4.4.2 Hypothesis testing

Response: Comparing roan and gemsbok seasonal ranges

We expected that for roan but not gemsbok, wet season range areas should be larger than dry season range areas. To test this expectation, we ran a Generalized Linear Mixed Model (GLMM) separately for each species, with each individual-season range area (A_{is}) as the dependent variable. Each year was taken as a replicate, with season (S) as the independent variable and a random effect (α_i) for collar ID (Table 4.3):

$$A_{is} = \beta_0 + \beta_S S + \alpha_i \tag{4.1}$$

Response: Comparing inter-specific and seasonal encounter and crossing rates

If roan seasonal expansion drives fence crossings, we expected a greater number of fence encounters per GPS fix, and crossings per encounter, for roan than for gemsbok. In addition, roan encounters and crossings should occur more often in the wet season, while gemsbok should show no seasonal difference in encounter or crossing number.

To test these predictions, we used a subset of collar data from individuals who encountered a fence at least once (6 roan and 5 oryx) and calculated the ratio of fence encounters to total number of fixes, and the ratio of crossings to the number of encounters, for each individual. We then used a χ^2 test ($\alpha = 0.05$) to compare the average fix-to-encounter and encounter-to-crossing rates between species. Finally, we used another χ^2 test ($\alpha = 0.05$) to compare wet and dry-season numbers of encounters and crossings for roan and gemsbok. See Table 4.3 for statistical test details.

Costs: Comparing activity budgets before and after a crossing

Energetic costs were measured as a decrease in energy-gaining activities such as ruminating and foraging directly before a crossing, in favor of energy-spending activities such as exploration. We expected that the proportion of time in the exploring state will

Table 4.3: Hypothesis testing for hypotheses given at the end of the Introduction. Expected result relationships and locations are given.

Question	Model or test	variable or formula	Expected Result
Are there costs to fence crossing?	χ^2	pre- and post- encounter activity budgets	↑ proportion exploring pre-crossing
Are there benefits to fence crossing?	t-test, GLMM	EVI and distance to water	↑ EVI & ↓ distance post-crossing
Do roan ranges expand in the wet season?	GLMM	range area $\sim$ season | ID	roan ranges greater in wet season
Do roan *encounter* fences more than gemsbok do?	χ^2	encounters : fixes	more roan fence encounters than gemsbok
Do roan *cross* fences more than gemsbok do?	χ^2	crosses : encounters	more roan fence crosses than gemsbok
Do roan *encounter* fences more often in the wet season?	χ^2	wet season : dry season encounters	more roan encounters in wet than dry season
Do roan *cross* fences more often in the wet season?	χ^2	wet season : dry season crosses	more roan fence crosses in wet than dry season

be greater in the 24 hours before a crossing than average, and will be greater than the exploring proportions before other non-crossing fence encounters.

We compared the total proportion of GPS fixes in each activity state for 24 hours before and after a crossing. We used a χ^2 test to determine whether, in either the 24 hours before or after an encounter, any of the budgets for each encounter type was significantly different from the total group proportion. We then used pairwise χ^2 tests to compare the budgets of each pair of fence encounters with a Bonferroni adjusted significance threshold of 0.05/10 (10 pairwise tests) = 0.005, to account for multiple testing.

Table 4.4: Seasonal differences in total range area (k-Nearest Neighbor Convex Hull, k-NNCH). When compared with an ANOVA, roan range area increases from dry to wet season for k-NNCH were statistically significant ($p = 0.027$, indicated with boldface and asterisk), while no range shift was evident for gemsbok ($p = 0.68$).

	Gemsbok	Roan
average dry season range (ha)	8,067	5,641
average wet season range (ha)	8,808	8,560
dry-to-wet area increase	741	2,919
p-value	0.68	**0.027***

Benefits: Surface water and vegetation pre- and post-crossing

For each crossing into Botswana, we expected a statistically significant increase in EVI (better resources) and water density (more water access) on the post-crossing side from the pre-crossing side. For each GPS fix in the 24 hours pre- and post-crossing, we calculated the density of "water" pixels and median EVI (within a 300m buffer around the GPS fix point). We then used a paired t-test ($\alpha = 0.05$) to compare each individual crossing's mean EVI and water density from the Namibian side to the Botswanan side of the BCF. Finally, we incorporated EVI, season, and water density in a Generalized Linear Mixed-Effects Model to determine how all three contributed to the individual's choice of fence side. Fence side was modeled in the binary family, with EVI, water density, and season as fixed effects and antelope ID as a random effect.

4.5 Results

4.5.1 Responses: Roan expanded ranges seasonally, gemsbok did not

We found that roan exhibited wet-season range expansion, while gemsbok did not. Roan total range extent expanded on average by 5,421ha in the wet season compared to the dry season ($p = 0.007$), and actual area used increased on average by 2,919ha in the wet season ($p = 0.027$). In addition, there was no evidence of seasonal range expansion for gemsbok ($p = 0.23$) (Table 4.4)

Table 4.5: Number of fixes, fence encounters, and crosses for each individual that encountered the Border Cordon Fence. The rate of encounters per fix and cross per encounter are given in total and broken down by season. Roan encountered and crossed the BCF at rates significantly higher than those of gemsbok ($p = 0.005$ for encounter:fix and $p \ll 0.01$ for cross:encounter, marked with asterisk and bolded). There was no difference in seasonal encounter rate for gemsbok ($p = 0.88$), and no gemsbok crossed the fence. Roan encountered the fence significantly more often during the wet season than the dry ($p \ll 0.01$), but crosses occurred equally across seasons given the number of encounters ($p = 0.18$). All p-values were calculated using a χ^2 test of proportionality.

		Totals			encounters per fix			crosses per encounter		
ID	Species	fix	enc.	cross	total	dry	wet	total	dry	wet
1510	Roan	3219	64	27	0.02	0.02	0.02	0.4	0.4	0.4
1511	Roan	1293	12	3	0.009	0.003	0.01	0.25	0	0.27
1729	Roan	11029	54	6	0.005	0.003	0.007	0.11	0.07	0.13
1731	Roan	11560	62	7	0.005	0	0.01	0.1	0	0.1
975	Roan	3368	34	3	0.01	0.001	0.01	0.09	0	0.09
977	Roan	3699	31	3	0.008	0.0007	0.01	0.1	0	0.1
					$p = 0.005$*			**$p \ll 0.01$***		
1516	Gemsbok	3151	1	0	0.001	0.001	0	0	0	0
1517	Gemsbok	2151	17	0	0.008	0.009	0.007	0	0	0
1518	Gemsbok	3219	39	0	0.01	0.02	0.01	0	0	0
1521	Gemsbok	3385	9	0	0.003	0	0.004	0	0	0
1724	Gemsbok	3837	9	0	0.002	0.005	0	0	0	0
					$p = 0.88$			NA		

4.5.2 Responses: Roan encountered the fence more often in the wet season

To determine if range expansion needs motivated roan fence crossings, we predicted that roan fence encounters would occur more often in the wet season than the dry. We found that roan encountered the BCF significantly more often in the wet season than the dry season ($p \ll 0.01$). While the distribution of encounter types did not differ across seasons for either roan ($p = 0.66$) or gemsbok ($p = 0.37$), 85% of roan fence encounters occurred in the wet season. The number of gemsbok encounters did not differ by season ($p = 0.88$), nor did the ratio of roan crossings to encounters ($p = 0.18$) (Table 4.5).

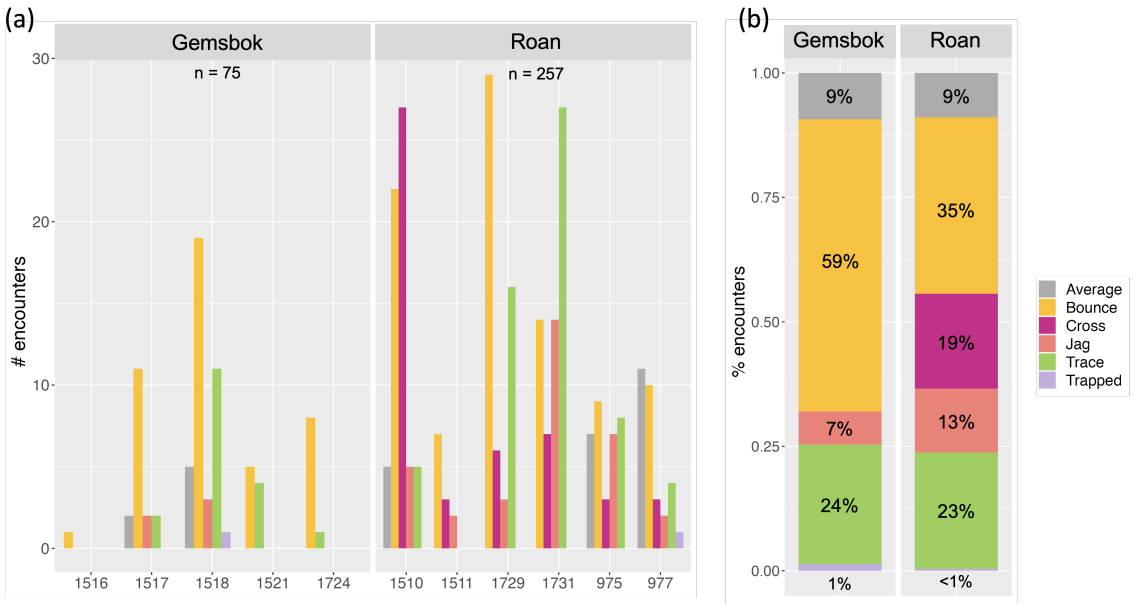

FIGURE 4.6**:** Encounter type frequencies tabulated by individual (a) and by species as a percentage of total encounters (b). Encounter types were determined using modified Barrier Behavior Analysis code from Xu et al. 2021 (See Fig. 4.5). Encounter types vary by individual, but gemsbok never cross at a fence encounter, while roan cross and remain over the fence line in 19% of encounters.

4.5.3 Responses: Roan encountered and crossed the fence more often than gemsbok

Finally, again to determine if range expansion needs motivated roan fence crossings, we predicted that roan would encounter and cross the BCF more often than gemsbok. We found that roan were significantly more likely to encounter a fence than gemsbok ($p = 0.005$). Roan encountered the BCF 257 times in 34,168 total GPS fixes for the six individuals with ranges close to the fence, while gemsbok only encountered the BCF 97 times in 15,743 fixes for five individuals (Fig. 4.6a,b; Table 4.5).

Roan were also significantly more likely to cross the fence than gemsbok ($p \ll 0.01$, Table 4.5). Of all fence encounters, the proportion of average, trace, and trapped encounters (those in which crossings did not occur) was similar for the two species (9%, 23-24%, and ~1%, respectively). The proportions of *cross, bounce, jag* were 0%, 59%, and 7% for gemsbok and 19%, 35%, and 13% for roan, respectively (Fig. 4.6c).

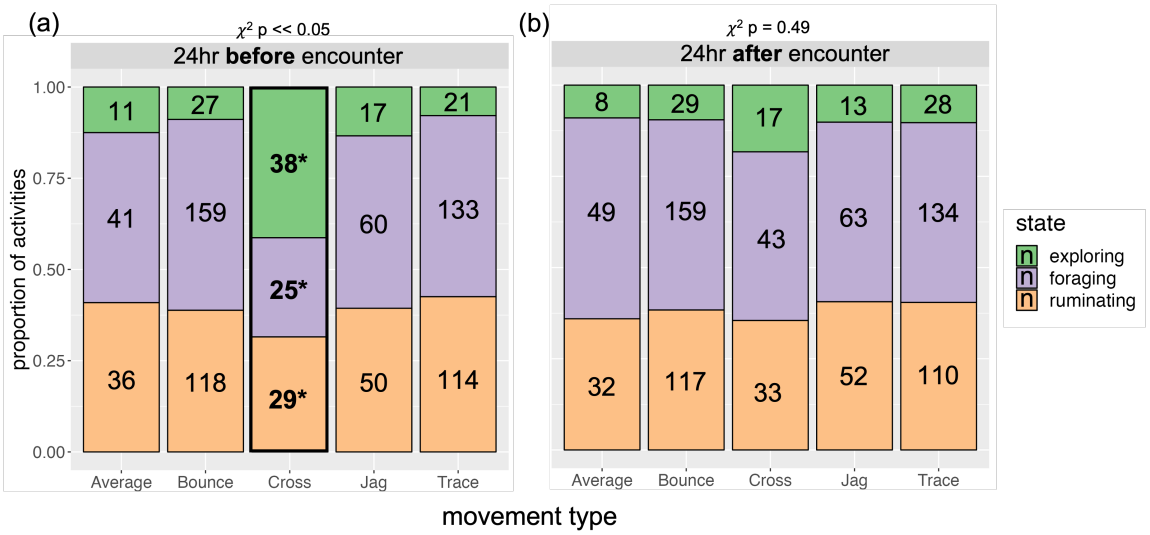

FIGURE 4.7**:** Activity budgets for roan 24 hours before (a) and after (b) a fence encounter. Each activity budget is sorted by encounter type and labeled with the number of fixes which fall into each of three activities: exploring (green), foraging (purple), and ruminating (orange). A series of group-wide comparisons (testing all proportions within "before" and "after") and pairwise comparisons (testing each encounter type's activity budget proportion to each other proportion within "before" and "after") χ^2 tests confirmed that the only significantly different proportioning of activities is in the 24 hours before a border crossing ($p \ll 0.005$).

Because only roan crossed the BCF (Fig. 4.3), results for costs and benefits of crossing are only analyzed for roan antelope.

4.5.4 Costs: Fence crossing required high-energy exploration

In our first hypothesis we predicted that, if fence crossings imposed an energetic cost, then there would be a significant loss of foraging and ruminating time prior to fence crossing. We found a statistically significant trade-off before a fence crossing: more exploration for less foraging.

In the 24 hours before a fence encounter, a χ^2 ($\alpha = 0.05$) test found an inequality in activity budgets across encounter types ($p \ll 0.01$). We then conducted pairwise χ^2 tests of budgets among *average, bounce, cross, jag,* and *trace* behaviors ($\alpha = 0.005$). The average budget in the 24 hours before non-crosses (*jag, trace, average,* and *bounce*) was

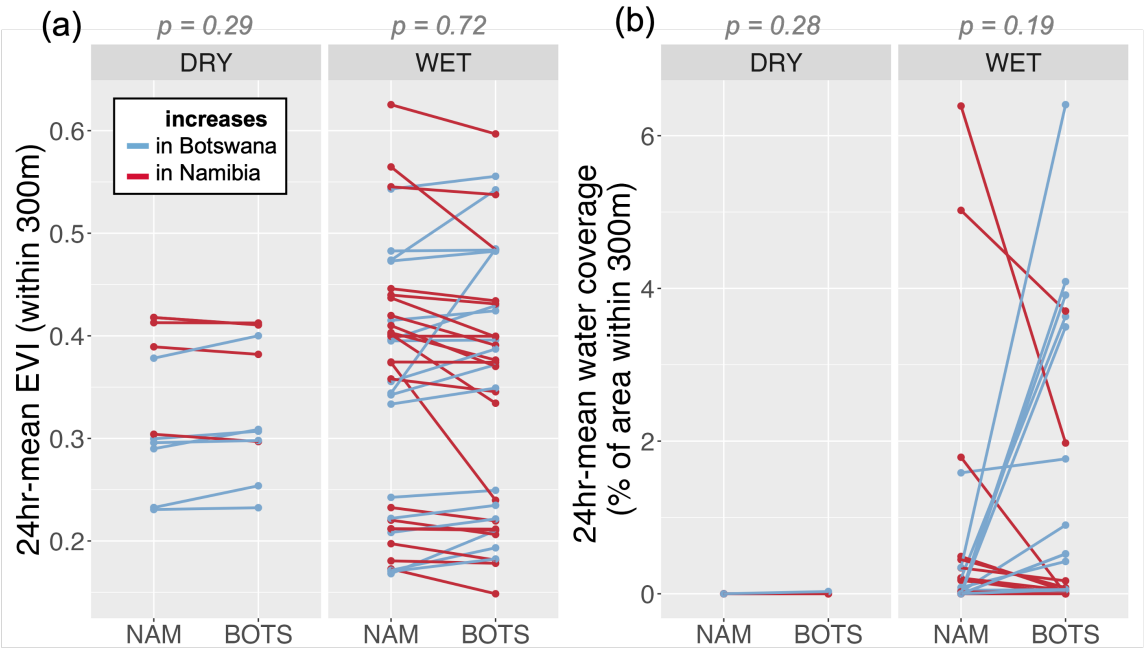

FIGURE 4.8**:** 24 hour means within a 300m-radius circle pre- and post- BCF crossing for (a) EVI and (b) density of natural water sources (% of landscape covered in water). Blue lines indicate higher EVI or distance on the Botswana side; red, higher in Namibia. A paired t-test found no significant difference in EVI (dry season: $p = 0.29$, wet season: $p = 0.72$) or water density (dry: $p = 0.28$; wet: $p = 0.19$) on either side of the BCF in either season.

about 10% exploring, 50% foraging, and 40% ruminating; none of these encounters was significantly different from any other. In the 24 house before a *cross*, however, budgets were significantly different ($p \ll 0.005$) from all other encounter types (Fig. 4.7). Exploration reached 41%, with an accompanying drop in foraging (27%) and rumination (32%). In addition, roan wet-season activity budgets far from fences were 13% exploration, 45% foraging, and 42% rumination, similar to that of non-crosses.

Finally, there was no evidence that roan changed their activity budgets in the 24 hours after any type of fence encounter ($p = 0.49$; Fig. 4.7b), or that gemsbok experienced any shift in activity budget ($p = 0.64$ 24 hours before, $p = 0.96$ 24 hours after).

4.5.5 Benefits: Roan did not cross to access more forage or water

In our second hypothesis we predicted that, if individuals cross the fence to access better or more abundant resources, then they would choose post-crossing locations with higher EVI and closer to water. Our results did not support this prediction.

When comparing the 24 hours of location data pre- and post-BCF crossing (Fig 4.8), a paired t-test showed no difference in EVI (dry season: $p = 0.29$, wet season: $p = 0.72$) or water density (dry: $p = 0.28$; wet: $p = 0.19$) on either side of the fence, in either season. Our GLMM for fence side choice did not find any evidence that EVI ($p = 0.72$), water density ($p = 0.24$), or season ($p = 0.78$) affected fence side choice.

4.6 Discussion

Understanding the relationship between seasonal movement behaviors and veterinary fencing structures is important for the long-term management of wild ungulates in southern African savannas. In this study, we aimed to investigate three aspects of the animal-fence interface in Khaudum National Park, Namibia: (1) Does the wet-season range expansion of water-dependent ungulates motivate them to cross the Border Cordon Fence (BCF) more than a sympatric, water-independent species? (2) Does fence-crossing in this system impose energetic costs on individuals as seen in another nearby system (Hering et al. 2022a)? (3) Are fence-crossing individuals doing so to access locations with higher vegetative productivity or water access? Our study found that roan encountered the BCF more often than gemsbok and that roan, but not gemsbok, appeared to cross the fence as part of a wet-season range expansion. This expansion was not linked to quantitative differences in water or food abundance on the Botswana side of the BCF. Finally, we found that roan fence crossings were associated with an increase in long-distance, directed travel in the 24 hours beforehand, a shift that minimized the amount of energy gained (through less foraging and ruminating) in favor of an energy-

intensive state of movement.

This study adds a seasonal movement and water dependence result to several recent studies comparing species' fence crossing rates. One study in Etosha NP, Namibia, found that female eland, kudu, and springbok (all water-independent species) frequently crossed the Etosha veterinary fence through elephant-created gaps, and that even resident (non-migratory) kudu still crossed the fence 345 times during their two-year study period (Hering et al. 2022b). Another study in Khaudum NP and Bwabwata NP, Namibia, found that male elephant (a water-dependent species) crossed the BCF frequently, but females in herds did not (Naidoo et al. 2022). From these two studies, we would expect to see both roan and gemsbok cross the fence, and that females in herds may face higher costs to fence crossings. The Etosha NP study found that individuals across a migratory gradient all crossed the veterinary fence. At 35% of encounters, their resident kudu (the most comparable movement-wise to gemsbok) crossed the fence at the same rate as we found range-expanding roan to cross. On the other hand, Naidoo and colleagues' elephant study (2022) suggested that females traveling in breeding herds would not cross due to the vulnerability to young and juveniles. Our findings did not support this reasoning for roan or gemsbok (Fig. 4.6); instead, we found that both male and female roan crossed the fence, while both male and female gemsbok did not. The answer here must be investigated in future studies, but one likely explanation is that differences in habitat quality on either side of the Etosha fence were larger than the differences we found on both sides of the BCF, therefore motivating even resident kudu to cross. Another possibility is that there is some unexplored similarity between female elephant herds and female gemsbok herds beyond the presence of juveniles, that is not present for female roan herds or bull elephant. Gemsbok and elephant have different dietary and water requirements, movement rates, herd and body sizes, and social structures; however, the elephant population in Khaudum NP has been functionally non-migratory since the installation of artificial waterpoints (Naidoo et al. 2022), in

perhaps the same way that gemsbok change their range little throughout the seasons. If seasonal range fidelity is stronger for female elephants in large herds than for solitary bulls (as suggested by Shannon 2005), then this could explain the similarities we see in the lack of female gemsbok and elephant crossings. Future research could test this theory by comparing the seasonal range shifts between elephant females and males in Khaudum, much as we have done here.

We find here that the BCF poses an energetic cost to roan who cross the fence, in the loss of foraging and rumination time in exchange for exploration (Fig. 4.7b). This confirms the findings of the previously cited Etosha NP study (Hering et al. 2022a), which showed through accelerometer data that fence-crossing is energetically costly to ungulates. Both roan and gemsbok can cross through holes created by elephant damage (Jori et al. 2011), and there is no evidence that roan differ in their ability to cross through fence gaps (van Rooyen 2002). There is also at least one instance in Mpumalanga, South Africa in which gemsbok do not cross a fence despite the presence of holes through which other similar-sized or larger species (kudu and eland) cross (Pirie et al. 2017). The lack of gemsbok crossings could therefore represent an unwillingness to expend energy to cross, rather than an inability to do so. The natural next question is, if it is costly to do so, then why cross?

Roan antelopes' need for a larger range during the wet season must then outweigh the energy expended before physically crossing the fence. Although our results did not support a vegetative quality or water access (Fig. 4.8, rejecting our Benefits hypothesis), this does not preclude other motivations for crossing. Roan are known to inhabit ranges where there are fewer competitors (Estes 1991). Given the hard barrier to gemsbok provided by the BCF, and the presence of more CBPP fences on the Botswanan side of the BCF (Fig. 1), there could be fewer competitors for similar resources on the Botswanan side. And, although we did not find that roan that crossed the fence adjusted their locations for more productive vegetation or better water access, our analysis was at the

coarse landscape level and therefore homogenized small-scale differences in hydrology or vegetation structure or composition (Muhar 2001). Future research with more fine-scale methods (both on the physical scale of analysis and on the scope of data analyzed) will uncover whether this finding at coarse scale is representative of local scale decision-making. For example, the recent interest in Convolutional Neural Networks (e.g., Brodrick et al. 2019), hyperspectral data (e.g. Pascucci et al. 2020, and others from the same special issue), and the increasing accessibility of LiDAR data (e.g. Dwiputra et al. 2023, Khoramak and Mahmoudi 2023) in landscape ecology could greatly improve an analysis of local-scale effects of vegetation and water access on roan behavior.

The evidence that roan expand their ranges in the wet season by over 2,000ha on average may also indicate that roan fence-crossing is an artefact of wet-season range expansion in all directions, and that the fence simply does not pose enough of a cost to be avoided entirely. This behavioral pattern of roan and other range-expanding mammals lies between migration (distinct seasonal ranges that are far from each other) and residency (fidelity to the same range year-round) (Avgar et al. 2014), however many of the cost-benefit considerations of migration may apply here as well. Migration can increase energy intake, nutritional diversity, and increase the chances of finding a mate; however, it also costs a great deal of energy, and animals in unfamiliar territory and on the move may be at higher risk of predation (Avgar et al. 2014). The genetic component of migration, too, could be at play. This genetic origin is well known in birds, insects, and fish (Berthold et al. 1990, Chernetsov et al. 2004, Liedvogel et al. 2011), but is understudied in mammals, likely due to the complexity of migratory behavior and the size of migratory mammals (Avgar et al. 2014, Liedvogel et al. 2011). However, one 2010 study of a re-established zebra migration in Botswana suggested that there may be a genetic component in ungulate migrations as well, given the multi-generational time period between the focal zebra herd's migration cessation and reestablishment (Bartlam-Brooks et al. 2011). If the expansion-contraction behavior of roan and other water-

dependent ungulates has a genetic basis, then perhaps roan expansions are partly environmental and partly genetic, and the combination of these two drives roan to cross the fence despite the energetic costs.

As long as humans and wildlife inhabit natural areas together, the intersection between fence and movement ecology will always be a key field of study for human and natural well-being. Nowhere is this relationship more complex and historic than in Africa, where humans have coexisted with megafauna since the Pleistocene. Fencing is the most prominent linear structure across southern Africa, and this study adds to the growing body of literature on fencing's ecological effects on the ecosystem engineers of African savannas. Our research here has demonstrated a surprising difference in fence encounter and crossing rates for two species that seem similarly equipped to cross fences. The introduction of range expansion and contraction to a story that has, until now, focused on distinct migratory or sedentary populations, is an important addition to the literature. Our findings here should serve as a launching point for future scientific studies on the subject (especially investigations on local-scale landscape drivers of fence crossings), as well as a guideline for those charged with installing and maintaining fences in semi-arid savannas where range expansion is common.

5

Conclusions

5.1 Major findings

Chapter 2 combined thirty years of aerial ungulate census data from Kruger NP for the first time, describing long-term population trends in fourteen species and applying a Bayesian probabilistic joint species distribution model. The GJAM analysis found that, while individual species traits had little impact on their population responses to drought, rare antelope responded similarly to environmental parameters and their enhancement by drought incidence. Particularly, rare antelope populations increased far from waterholes during droughts, and were less sensitive to river locations than other ungulates. This finding challenges black-and-white opinions from the 1960s that artificial waterholes were universally good for rare populations, and from the 1990s that artificial waterholes were solely responsible for species declines. Instead, rare antelope seem to depend on waterholes during drought; perhaps waterhole provision in moderation is a balanced approach to rare antelope management. In addition, rare antelope can be further subdivided by their sensitivities to environmental change: roan and eland are generally more sensitive than eland and sable to changes in surface water and

soil substrate.

Chapters 3 and 4 investigated how climate change and human infrastructure intersect with antelope thermoregulatory strategies to alter movement behaviors. **Chapter 3** found that antelope thermoregulatory strategies (reliance on surface water, cooler microclimates, and changing activity budgets) was stronger at higher temperatures and in the dry season. This shows that, while ungulate behavior is driven by many other factors (e.g., dietary needs and predation risk) that may change with a warming climate, thermoregulation is still important in determining their movement patterns. **Chapter 4** found that roan, which greatly expand their ranges in the wet season, frequently encounter and cross the eastern boundary fence, while gemsbok, which maintain small, steady ranges year-round, do not cross the fence. These findings were unique among recent fence-crossing and encounter literature, breaking the neatly drawn lines between migration status, sex, and group size with fence crossing incidences.

5.2 Future research directions

In Chapter 2, I used a Generalized Joint Attribute Model (GJAM, Clark et al. 2017) to jointly analyze species responses to drought and water access. However, this model does not incorporate temporal dependence, and therefore cannot truly report interactions between species. In future work, I will incorporate a time-series version of GJAM, "GJAMTime" (Clark et al. 2020), to explore species interactions and contributions to variation from immigration/emigration between regions, density-dependent growth, and density-independent growth. In addition, the harmonized dataset used in this chapter is the first of its kind for the Kruger census data, and many other researchers have expressed interest in using these data in their own models. I hope to publish a data paper exploring this dataset and the harmonization methods in more detail, to provide a resource to other researchers in Kruger.

In Chapters 3 and 4, I investigated the effects of water dependence on thermoregulatory strategy and responses to veterinary fencing in Khaudum National Park, Namibia. Chapter 4 is of particular interest to my future work, as my upcoming postdoctoral project will focus on mechanistic modeling of elephant movements in response to fencing. The findings from Naidoo and colleagues (2022) on sexual distinction between fence crossing rates will be instrumental in my modeling of elephant movements, and the insights from Chapter 4 will help temper previous expectations that sex, the presence of young, or herd size are the primary feature in females' lack of fence crossing. I will work closely with Dr. Naidoo to understand the implications of Chapters 3 and 4 for elephant individual behaviors in my mechanistic models of elephant movement.

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Biography

Maggie Swift (she/her) graduated from the College of William & Mary in 2017 with a degree in Computational and Applied Mathematics and Statistics, a concentration in mathematical biology, and a minor in Russian and Post-Soviet Studies. She worked as a developer and computer programmer at IBM in Washington, D.C. until starting graduate school at Duke University in August 2019. She is a recipient of the James B. Duke Fellowship (2019), the National Science Foundation Graduate Research Fellowship (2021), and the Cornell Atkinson Postdoctoral Fellowship (2023). She has shared her research at the Ecological Society of America annual meeting (2020) and the Savanna Science Network Meeting (2023), and has co-organized several seminars, including the Duke Ecology seminar series (2020-2022), the *People and Nature* seminar (2022), the *Decolonizing Ecology* workshop (2022), and the *Skukuza Soil & Herbivory* workshop (2023).

Maggie will continue her studies of southern African savanna herbivores at Cornell University, joining Dr. Steven Osofsky (Cornell, Animal & Human Health for the Environment And Development) and Dr. Robin Naidoo (World Wildlife Fund). Her project will use advanced computer modeling to investigate how elephants currently move about southern Africa's Kavango Zambezi Transfrontier Conservation Area, and how elephant movement patterns might change if alternative approaches to livestock disease management were adopted.