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Rediscovering Angolan Biodiversity:
Patterns and regulation processes underlying large
mammal community structure across South Angola

Luís Filipe Pinho Rocha

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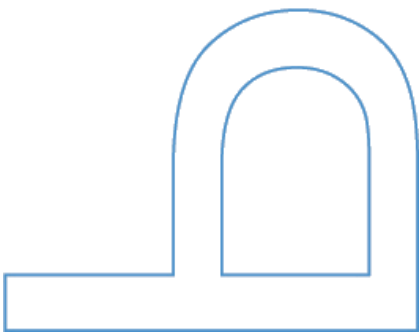
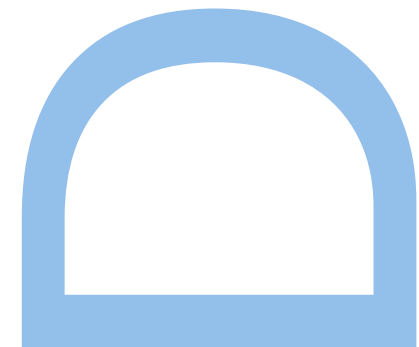
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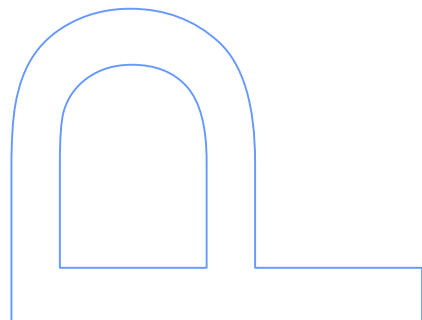
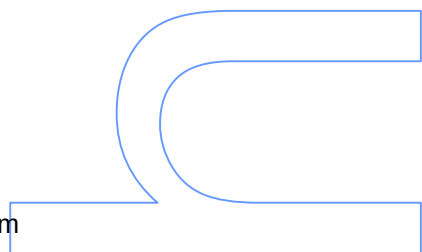
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Resumo

Várias teorias têm sido propostas na tentativa de elucidar os mecanismos que regem a regulação das estruturas das comunidades. Inicialmente, uma teoria dominante postulava que a composição das comunidades era principalmente determinada por efeitos “bottom-up”, em que a disponibilidade de recursos atuava como a principal restrição na estrutura da comunidade. No entanto, à medida que a compreensão da intrincada interação entre os níveis tróficos se aprofundou, emergiu uma perspectiva mais holística, que destacava o papel crucial dos efeitos “top-down” na definição da dinâmica e estrutura da comunidade. Atualmente, a hipótese mais consensual entre a comunidade científica é a Hipótese da Exploração do Ecossistema. Esta teoria afirma que a regulação da comunidade ocorre principalmente através de efeitos “top-down”, enquanto o número de níveis tróficos é determinado pela produtividade primária do sistema. Existem ainda inúmeras questões por responder e que requerem atenção da comunidade científica. Entre essas questões está a investigação acerca do funcionamento e da regulação da estrutura de comunidades perturbadas, bem como compreender as repercussões da extinção de predadores na estrutura, dinâmica e comportamento das espécies em níveis tróficos inferiores. Para abordar essas questões, é necessário examinar um sistema perturbado, como Angola, que enfrentou instabilidade política e conflitos armados, e que resultaram em impactos significativos nas populações de mamíferos de médio e grande porte. No entanto, apesar dessa compreensão, poucos estudos têm sido realizados com o objetivo de caracterizar a comunidade de mamíferos existente e determinar as consequências reais da guerra sobre as populações selvagens em Angola.

O objetivo desta tese é estudar o papel das forças reguladoras “top-down” e “bottom-up” em comunidades perturbadas, contribuindo também para o preenchimento do vazio de conhecimento existente em relação à composição da comunidade de mamíferos no sul de Angola. Os objetivos específicos desta tese são: (i) avaliar a influência das medidas de proteção da paisagem implementadas após a guerra, nas comunidades de mamíferos, (ii) investigar os efeitos da dependência de água e da disponibilidade de recursos tróficos na abundância local e utilização do espaço por herbívoros selvagens, num ambiente com recursos limitados, (iii) compreender a dinâmica espacial do uso da paisagem por herbívoros em resposta a incêndios florestais e (iv) avaliar como os processos de “top-down” e de “bottom-up” moldam os padrões

espaciotemporais das espécies de presas dentro de uma comunidade com baixa abundância de predadores.

Para responder a estas questões foram amostradas três áreas no Sul de Angola: os Parques Nacionais do Iona e do Bicular e também a Área de Conservação de Cuatir. A recolha de dados no Bicular e em Cuatir fez-se com recurso a armadilhagem fotográfica, enquanto no Iona se realizaram observações diretas regulares.

Os principais resultados desta tese destacam que: (i) a vida selvagem em Angola teve declínios significativos na riqueza específica nos últimos 50 anos, sendo que os mamíferos de maior porte foram os mais afetados. Apesar das perdas serem transversais e dos níveis de diversidade serem semelhantes entre as áreas, os resultados sugerem que as áreas protegidas (especificamente o Parque Nacional do Bicular) podem ser mais eficientes na preservação das populações de espécies maiores e ameaçadas, em comparação com áreas não protegidas (Área de Conservação de Cuatir). Além disso, esta pesquisa destaca a descoberta de várias espécies que não tinham sido previamente documentadas nas áreas de estudo. (ii) Os processos de “bottom-up” dominam nos sistemas estudados, independentemente da disponibilidade de recursos, desafiando a “Hipótese da Exploração do Ecossistema”. Os padrões observados podem ser consequência da baixa pressão de predação, que faz com que as espécies presa não precisem de restringir as suas atividades para evitar serem predadas. (iii) A invasão humana e do gado em áreas naturais influencia o uso do espaço pela vida selvagem, deslocando as espécies de seus habitats preferidos, o que é particularmente problemático em ambientes desérticos com reduzida disponibilidade de água e vegetação. (iv) Os incêndios florestais têm um impacto prejudicial nos padrões de ocupação de herbívoros. A alteração observada nos regimes de incêndios na região, para fogos mais intensos e frequentes, juntamente com a baixa abundância de herbívoros, podem contribuir para a homogeneização da comunidade vegetal, sendo dominada por espécies de crescimento rápido mas menos palatáveis, criando habitats indesejáveis. (v) A limitada abundância de predadores parece ser um fator determinante na ausência de respostas anti predatórias espaço-temporais, uma vez que dificulta a perceção do risco de predação, que é essencial para a definição de estratégias anti predatórias proativas.

Em geral, esta tese oferece avanços significativos para a compreensão do funcionamento e regulação da estrutura das comunidades de mamíferos em sistemas simplificados, em particular por fornecer evidências de que comunidades de animais reduzidas e a expansão humana têm implicações tanto para a comunidade de vida

selvagem como para o funcionamento do ecossistema. Essas implicações são demonstradas por mudanças nos padrões de uso do espaço das espécies, à medida que selecionam habitats sub-ótimos para evitar pressão humana, redução na percepção de risco levando à falta de estratégias anti predatórias proativas e os efeitos negativos dos incêndios para as espécies de herbívoros.

Palavras-chave

Angola, Armadilhagem fotográfica, Coexistência humanos-vida selvagem, Declínio da vida selvagem, Dependência de água superficial, Estrutura de comunidades, Fogo, Hipótese de controlo do risco, Interações predador-presa, Mamíferos Africanos, Modelação de comunidades, Modelos de ocupação dinâmicos, Modelos hierárquicos, Modelos N-Mixture, Paisagem do medo, Processos “Bottom-up”, Processos “Top-down”, Respostas antipredatórias proativas, Teoria de alimentação otimizada

Abstract

Several theories have been proposed in an attempt to elucidate the mechanisms governing the regulation of community structures. Initially, one prevailing theory posited that the composition of communities was primarily determined by bottom-up effects, whereby resource availability acted as the primary constraint on community structure. However, as the understanding of the intricate interplay between trophic levels deepened, a more holistic perspective emerged, underscoring the pivotal role of top-down effects in shaping community dynamics and structure. Currently, the prevailing hypothesis in ecological research is the Ecosystem Exploitation Hypothesis, which asserts that community regulation primarily occurs through top-down effects, while the number of trophic levels is determined by the primary productivity within a given system. However, there are still numerous unresolved inquiries that demand attention. These include investigating the functioning and structure of disrupted communities, as well as comprehending the repercussions of predator extirpation on community structure, dynamics, and behavior of species at lower trophic levels. To address these questions, it is necessary to examine a disrupted system, such as Angola, which has experienced political instability and armed conflicts, potentially resulting in significant impacts on its mammal populations. However, despite this understanding, only limited number of studies have been undertaken to characterize the extant mammal community and ascertain the actual consequences of the war on wild populations in Angola.

The objective of this thesis is to study the role of top-down and bottom-up regulation forces in disrupted communities, while contributing to filling the existing knowledge gap regarding the composition of the mammal community in southern Angola. This research aims to achieve the following specific goals: (i) evaluate the influence of landscape protection measures implemented after the war on mammal communities, (ii) investigate the effects of water dependency and forage availability on the local abundance and spatial utilization of wild herbivores in an environment with limited resources, (iii) comprehend the spatial dynamics of herbivore landscape use in response to bushfires, and (iv) assess how top-down and bottom-up processes shape the spatiotemporal patterns of prey species within a community characterized by low predator abundance.

To address these questions, three regions in Southern Angola were systematically surveyed: the Iona and Bicuar National Parks, along with the Cuatir Conservation Area.

Data collection in Bicuar and Cuatir involved the use of camera traps, while direct observations were conducted in the Iona National Park.

The main findings of this thesis stress that: (i) Angolan wildlife has experienced significant declines in species richness over the past 50 years, with larger mammals being more severely affected. Despite the losses, the results suggest that protected areas (specifically Bicuar National Park) may be more efficient at preserving populations of larger and endangered species, comparing to non-protected lands (Cuatir Conservation Area). Furthermore, this research highlights the discovery of several previously undocumented species within the study areas. (ii) Bottom-up processes dominate in the studied systems regardless of resource availability, challenging the "Ecosystem Exploitation Hypothesis" and suggesting that poorly enforced top-down constraints play a role in the mechanisms regulating the structure of communities. (iii) Human and livestock encroachment in natural areas influence wildlife space use, displacing species from their preferred habitats, which is particularly problematic in desert environments with reduced water and vegetation availability. (iv) Bush fires have a detrimental impact on the occupancy patterns of herbivores. The changes observed in fire regimes within the region, more intense and frequent fires, coupled with the low abundance of herbivores, may contribute to the homogenization of grassland compositions, being dominated by less palatable tall grass species, creating undesirable habitats. (v) The limited abundance of predators appears to be a crucial factor contributing to the absence of spatiotemporal anti-predator responses, as it hinders the perception of predation risk, which is essential for the development of proactive anti-predator strategies.

Overall, this thesis significantly advances our understanding of the structure and functioning of mammal communities, particularly providing evidence that the disruption of animal communities and human encroachment have implications for both wildlife community and ecosystem functioning. These implications are demonstrated through changes in species' space use patterns, as they select suboptimal habitats, reduced risk perception leading to a lack of preemptive anti-predator strategies, and the negative effects of altered fire regimes on herbivore species.

Keywords

African Mammals, Angola, Bottom-up processes, Camera trapping, Community modelling, Community structure, Control of risk hypothesis, Dynamic occupancy models, Fire, Hierarchical models, Human-wildlife coexistence, Landscape of Fear, N-Mixture models, Optimal forage theory, Predator-prey interactions, Proactive antipredator

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Abbreviations and Acronyms

AO – Activity overlap
BNP – Bicular National Park
BVP – Bayesian P-value
CCA – Cuatir Conservation Area
CPR – Cuatir Private Reserve, initial name of the Cuatir Conservation Area
°C – Celsius degrees
DH – distance to human settlements
DNW – distance to natural water sources
DOM - Dynamic Occupancy Models
DW – distance to all water sources (natural and artificial)
EEH – Ecosystem Exploitation Hypothesis
EVI - Enhanced Vegetation Index
FO – Frequency of Occurrence
FSI – Fire Severity Index
GWH – Green World Hypothesis
INP – Iona National Park
IUCN - International Union for Conservation of Nature
km – kilometres
LST - Land Surface Temperature
m - metres
m.a.s.l. – Meters above the sea level
MCMC – Markov Chain Monte Carlo
mm – Millimetres
MRCM - Multi-Region Community Models
NA - Not evaluated
OFT – Optimal Forage Theory
PA – Protected Area
SD – Standard Deviation
SSC - Species Survival Commission
TRI - topographic ruggedness index

Chapter 1

General Introduction

1.1. Community Ecology

Wildlife populations are constantly interacting with each other within ecosystems, forming biological communities. Consequently, a wildlife community is defined as an assemblage of interacting populations of species living within a particular area or habitat (Ricklefs, 2001). Community ecology is the branch of the ecology that focuses on understanding the organization and functioning of these wildlife communities (Mittelbach and McGill, 2019). All biological communities have a basic structure of interactions, a trophic pyramid (Neutel, Heesterbeek and de Ruiter, 2002). In a simplistic representation of a pyramid with three trophic levels (Fig. 1.1), the level at the bottom of the trophic pyramid is composed by primary producers - autotrophs (e.g., plants) -, that harness solar energy by photosynthesis or, more rarely, chemical energy by oxidation (Jannasch and Wirsen, 1979). Plants are consumed by herbivores, located in the intermediate level of the pyramid, which in turn are consumed by carnivores in the top level. These latest two levels are composed by heterotrophs (i.e., consumers) that directly or indirectly depend on producers to obtain energy. In essence, energy is passed from one level of the trophic pyramid to the next, along a trophic chain.

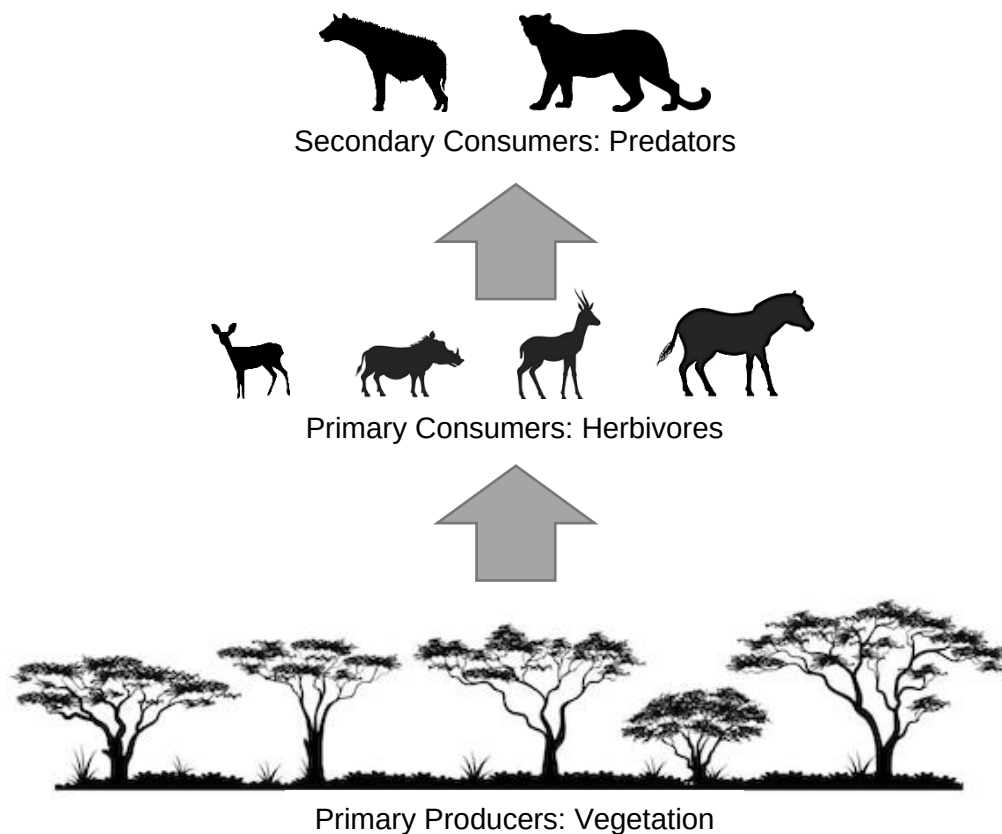


Figure 1.1 - Three-level trophic pyramid (silhouettes from PhyloPic©).

The interactions between species within and across trophic levels have captured the attention of the scientific community who strived to study the factors regulating the structure of the communities and the factors driving this regulation. Several ecological theories have been proposed to explain how populations regulate each other within a community and how trophic levels interact with each other to maintain the ecosystem in balance. The proposed theories are divergent, from theories that predict community structure solely governed by bottom-up processes (Elton, 1927, Lindeman, 1942) to others that support top-down constraints are the key drivers keeping ecosystems in balance (Hairston, Smith and Slobodkin, 1960). These contradicting theories were finally converged into an intermediate theory proposing the regulation force may change across ecosystems depending on the primary productivity (Oksanen *et al.*, 1981). In the following section, I provide an overview of each of these theories.

1.2. The evolution of community ecology theory

After the advent of evolutionary theories (Darwin, 1859, Wallace, 1871), naturalists (e.g. Phillips (1931), Shelford (1931), Allee and Park (1939)) started to understand that species from different trophic levels interact with each other and evolved in a way that fit in the community, and so the regulation of the trophic pyramid is directly dependent on the evolution of the species.

1.2.1. Bottom-up Hypotheses

One of early attempts to explain how wildlife community structure is regulated was the Eltonian pyramid (Fig. 1.2), proposed by Charles S. Elton (1927). The Elton's pyramid proposes that the regulation of community structure is resource-based, such that the availability of resources in an ecosystem governs the abundance of the species in the trophic levels above (e.g. primary consumers and secondary consumers). Elton's theory was supported by Weaver and Clements (1929) who defended that food rather than physical factors, controls the growth of animal populations, and, since plants are the

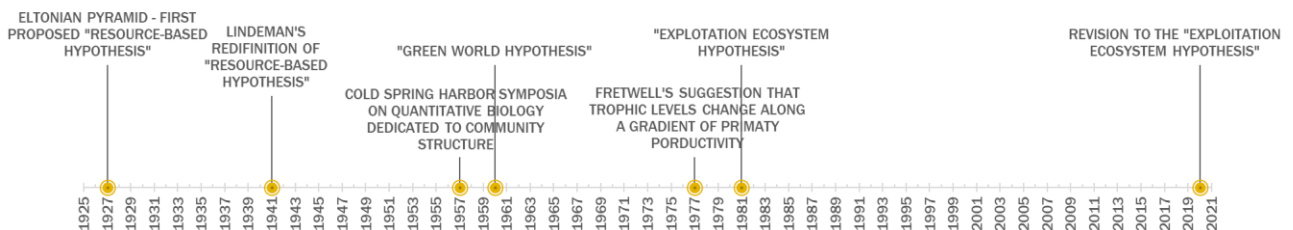


Figure 1.2 - Timeline depicting when multiple theories about the structuring of wildlife communities were proposed, and when most import events that lead to the development of said theories.

direct or indirect food of all animals, the biotic community has unity through food relations. The resource-based theory was redefined by Raymond L. Lindeman (1942) to incorporate the concept of the transmission of energy across trophic levels, but it remained strongly anchored in the idea that community structure is resource-based.

Three main limitations to the Elton's and Lindeman's theories were subsequently identified: (i) the theories are valid for systems with few trophic levels but not for more complex communities, (ii) fail to account for the possibility of any increase in predator's efficiency at a certain level that will increase the chances of the extermination of the level below. If that happens either the predator adapt itself to consume the second level bellow (shortening of a food chain) or itself goes extinct (Hutchinson, 1959); and (iii) not all vegetation is available as food for the subsequent levels, because is either toxic or is lacking in nutritional value that it is inedible to consumers (e.g. Murdoch, 1966, Birch and Ehrlich, 1967).

Despite its caveats, Elton's pyramid provided the foundation for the development of modern theories describing the regulation of community structure, including the resource-based hypothesis, which attempts to explain competition between sessile species (e.g. plants (Tilman, 1994; Hubell 2005) and algae (Titman, 1976)), the structure of wildlife communities and within trophic level competition in arthropods (Polis and Strong, 1996), or biological invasions (Davis and Pelsor, 2001, Shea and Chesson, 2002).

1.2.2. Top-down Hypotheses

Refuting the until then dominating paradigm that ecological communities are "bottom-up" regulated, Hairston *et al.* (1960) proposed the "Green World Hypothesis" (GWH), which postulates that predators are key to keeping the world green, because they prevent herbivore numbers from growing out of control, therefore creating conditions for plants to grow and flourish. These authors argued that herbivore populations are seldomly regulated by resources, and cases where it happens generally result from the disruption of predation. The lack of empirical support to this "top-down" theory attracted criticisms, particularly questioning how predators could regulate herbivore populations if they only catch the sick, the weak and the older individuals (Murdoch, 1966, Birch and Ehrlich, 1967). The first evidences of the influence of carnivores on plants were only demonstrated in the 1970s with empirical and theoretical research. Hurlbert, Zedler and Fairbanks (1972) found that predators control herbivores, promoting plants' expansion, in size and numbers. In other study, Rosenzweig (1973) demonstrated by a general

theoretical analysis of exploitation between species from three different trophic levels. Since then the ideas the GWH have been more accepted and there are many examples of natural and manipulative experiments identified beneficial indirect effect of predators on vegetation (Schoener and Spiller, 1999, Schmitz, 2006, Ripple and Beschta, 2007a, b, Terborgh and Estes, 2010). However, several other studies have shown weak or negligible indirect effects of predators on plant biomass or performance (Finke and Denno, 2004, Gruner, 2004, Van Bael and Brawn, 2005, Schmitz, 2006).

Despite the evidence of the influence of consumers on vegetal communities, the debate about the validity of GWH continued. The discussion was no longer whether there was top-down regulation, but which effect would exert higher influence on ecological communities. For instance, Polis (1999) argued that terrestrial vegetation is largely determined by climate, locally modified by the amount of nutrients in the soil, with consumer-control sometimes occurring but localized in space and time. Conversely, Bond (2005) debated that large areas of the world are 'consumer controlled', while recognizing that consumers can be biotic (e.g. large mammals) or abiotic (e.g. fire), since both consume vegetal biomass and recycle nutrients. Therefore, consumers should influence directly vegetal community, but also indirectly increasing the availability of nutrients, i.e. resources.

Even with the identified caveats to the GWH and the continuous discussions around the validity of its assumptions, this theory remained cornerstone to understanding community structure regulation. The ideas of the GWH were even extended to explain the regulation of detritivores, hence preventing the degradation of most organic material in soils (Allison, 2006). The importance of top-down effects is currently largely accepted among the scientific community, and provide feedstock for the development of ecological theories (Terborgh and Estes, 2010).

Although the idea of top-down forces shaping communities is widely accepted, the "Green World Hypothesis" only considered three trophic levels: plants, herbivores, and carnivores. This limitation is problematic because many systems have more than three links. However, Fretwell and Barach (1977) argued that the number of levels in a system depends on the rate of primary production and the average efficiency of consumers. If consumer efficiency remains constant, increasing primary productivity is enough to lengthen food chains.

The "Exploitation Ecosystems Hypothesis" (EEH; Oksanen *et al.*, 1981) was proposed as a natural development of the GWH, and accommodates the idea that trophic dynamics change along gradients of productivity (Fretwell and Barach 1977), and

Rosenzweig's three-dimensional exploitation models, i.e. a framework for describing the dynamics of predator-prey interactions and how they are influenced by environmental factors (Rosenzweig, 1973). The EEH acts as each trophic level consists of a single population, despite many different species being involved (Oksanen *et al.*, 1981, Oksanen and Oksanen, 2000), and postulates that productive terrestrial ecosystems support three (or more) trophic levels – e.g., plants, herbivores and predators. These ecosystems are carnivore-based, whereby predators suppress herbivore populations, therefore releasing plants from herbivore control and enabling them to increase in biomass — a community-level trophic cascade. Less productive ecosystems only support two trophic levels and are herbivore-based as herbivore populations are typically too small to support predators. Consequently, herbivores regulate plant biomass. Finally, extremely unproductive ecosystems, are plant-based as would only support producers (plants). The EEH relies on seven assumptions:

1. All plants are vulnerable to some herbivores, and each herbivore is vulnerable to at least one predator. This assumption can be regarded as the hard premise of EEH;
2. Herbivory-based food webs are dynamically independent from other food webs;
3. Trophic levels are discrete;
4. Trophic levels act as homogeneous blocks for organisms with similar energetic efficiency;
5. Dynamics of consumers are determined by consumer-resource encounter rates;
6. The maximum per biomass unit rate of plant biomass increase (r) and the maximum sustainable above ground plant biomass (plant carrying capacity, K), are directly proportional to potential primary productivity (G), defined as the maximum primary productivity allowed by the physical environment;
7. All influences of climate on food web dynamics are mediated via the annual average value of potential primary productivity (G).

Several studies have supported EEH predictions in that the strength of the top-down regulation enforced by predators on herbivores increases in importance in more productive areas, with a rich and diverse predator community (Hopcraft *et al.*, 2010). Conversely, bottom-up constraints increase in importance in deserts and arid ecosystems because of resource scarcity (Hopcraft, Olff and Sinclair, 2010, Veldhuis *et al.*, 2019). For example, a large-scale study across North America and Eurasia confirmed an

increasing deer biomass from the High Arctic southwards, along a gradient of primary productivity, a trend that is disrupted within wolf (*Canis lupus*; the key deer predator) range (Crête, 1999, Ripple and Beschta, 2012). Similarly, in African savannas, the prevalence of top-down or bottom-up forces varies seasonally with resource availability, i.e herbivore populations are governed by bottom-up forces during the resource-limited season while top-down forces prevail when resources are widely available (Owen - Smith and Traill, 2017, Davies *et al.*, 2021). Finally, upon Eurasian lynx's (*Lynx lynx*) recolonization and expansion in Finland, lynx biomass was found to follow a gradient of primary productivity (Elmhagen *et al.*, 2010).

Despite empirical validation, some limitations have been identified to the EEH, and redefinitions have been proposed during the last 30 years. The initial EEH model (Oksanen *et al.*, 1981) supposed constancy of the physical environments, ignoring the seasonality that is present in most of the world's ecosystems. Although the EEH model works for herbivores with low reproduction rates and juveniles that are not very affected by moderate shortages of resources, which controls the effect of seasonality as a destabilizing force. However, it does not work for rapidly reproducing herbivores with short generation times since seasonality becomes a strong destabilizing force, contradicting assumption 7. Generalist predators can control the destabilizing potential by switching between small and intermediate-sized prey, but this leads to continuous population fluctuations in environments where such switching is not possible (Oksanen, 1990). Given that seasonality is more pronounced in areas with low net primary productivity, the degradation/overgrazing of vegetation during the limiting season should be the proximate cause for herbivore decline (Mendoza and Araújo, 2019). Conversely, fluctuations should be cyclic in productive environments, and herbivore population declines should be driven by the combined action of social regulation and predation. These scenarios were empirically supported in a community of hare, fox and lynx in Finland, where hare biomass was lower in the more productive areas, whilst fox biomass appeared to be controlled by top-down constraints or competition in those areas, since it did not respond to primary productivity heterogeneity (Elmhagen *et al.*, 2010).

To overcome this limitation, a revision of EHH was proposed (Oksanen *et al.*, 2020). The revised EEH converges with the GWH in persistently warm environments, but with the additional prediction that strength of the three trophic level cascade is re-enforced by increased primary productivity. Supporting this prediction are observations of moderated declines in grass cover following predator exclusion from a hot desert

(Morris and Letnic, 2017, Letnic, Feit and Forsyth, 2018) or massive habitat destructions in absence of predators in a highly productive tropical forest of Venezuela (Rao, Terborgh and Nuñez, 2001).

Compared to the original theory (Oksanen *et al.*, 1981), the revised version of EEH (Oksanen *et al.*, 2020) predicts smaller geographic ranges for two- and one-trophic-level ecosystems, limited to areas with low primary productivity and cold seasonal climate compared to the original version. Moreover, the revised EEH predicts that Earth contains three widely spread ecosystem categories with distinct food web dynamics and unique organisms that have evolved to varying levels of resource competition and apparent competition.

Nowadays, the EEH is the most complete and accepted theory explaining the regulation of community structure and attempts to identify the relative importance of resource limitation (bottom-up) or consumption/predation pressure (top-down) as structuring forces in natural ecosystems, suggesting a stronger influence of top-down effects in communities with high levels of primary productivity. However, bottom-up and top-down constraints act simultaneously in almost every community (Sinclair, Mduma and Brashares, 2003). Consequently, most herbivores' populations face a trade-off between the need of acquiring fundamental resources (e.g. food and water), while avoiding predation. This trade-off has intrigued scientists and several theories have been proposed to explain how prey manage the risk of predation to secure the access to resources. Despite the broad acceptance of EEH, some questions remain unexplained, for instance how the community structure is regulated in incomplete communities or if the top-down constraints prevail in productive systems with low-predator abundance.

1.3. The food vs safety trade-off

The "Optimal Foraging Theory" suggests that animals aim to maximize their fitness by adopting a foraging strategy that allows them to obtain the most energy while minimizing effort (Pyke, Pulliam and Charnov, 1977). However, environmental factors such as predation risk can influence a prey's ability to access resources. Therefore, the optimal decision rule is the one that maximizes caloric intake while taking environmental constraints into account (Sinervo, 1997). Predators are a significant constraint on prey access to resources (Valeix *et al.*, 2009, Thaker *et al.*, 2011, Lone *et al.*, 2014), often forcing them to respond to perceived predation risk by adapting anti-predator strategies - "the Ecology of Fear" (Brown, Laundré and Gurung, 1999, Ripple and Beschta, 2004). These strategies can take various forms, including changes in habitat use (Thaker *et al.*,

2011), adjustments in diel activity patterns (Monterroso, Alves and Ferreras, 2013, Gaynor, McInturff and Brashares, 2021c, Rocha *et al.*, 2022b), alterations in the patterns of access to key resources (Valeix *et al.*, 2008), increased vigilance (Hunter and Skinner, 1998, Périquet *et al.*, 2010, Makin, Chamaillé-Jammes and Shrader, 2017b, Sirot, 2019), and group foraging (Thaker *et al.*, 2010, Makin *et al.*, 2017b, Palmer and Packer, 2021). Furthermore, humans are often perceived as predators (Crosmar *et al.*, 2012, Lone *et al.*, 2014, Darimont *et al.*, 2015, Smith *et al.*, 2017) and, if functionally present, impose a spatiotemporal anthropogenic-based landscape of fear, which builds on the wildlife-based one, and results in a perceived multi-risk landscape (Lone *et al.*, 2014, Gaynor *et al.*, 2021c, Moleón and Sánchez-Zapata, 2023, Palmer *et al.*, 2023). Under these assumptions, optimal foraging is only achieved if environmental constraints are not efficiently imposed, or if the resource in question is of vital importance such that animals have no choice but to expose themselves to high risk situations in order to access it (Lima and Bednekoff, 1999, Valeix *et al.*, 2008, Valeix *et al.*, 2009, Périquet *et al.*, 2010, Thaker *et al.*, 2011, Périquet *et al.*, 2012, Courbin *et al.*, 2017, Courbin *et al.*, 2019). Seasonal variation in resource availability can also impact the role of top-down and bottom-up constraints (Owen-Smith, 2015, Veldhuis *et al.*, 2019), with prey tolerating higher predation risk when resources are limited (Owen-Smith, 2015, Riginos, 2015, Davies *et al.*, 2021) and exhibiting stronger anti-predator responses when resources are widely available (Hopcraft *et al.*, 2010).

Different authors have described that the processes regulating prey populations also change with prey body size (Sinclair *et al.*, 2003, Hopcraft *et al.*, 2012). Smaller herbivores are more likely to be top-down constrained because they are generally more susceptible for predation than larger species and require less amounts of forage (Fig. 1.3). Conversely, larger herbivores and megafauna are less susceptible to predation, but require large amounts of food to fulfil their nutritional and energetic needs, becoming more likely to be constrained by bottom-up forces (Fig. 1.3; Owen-Smith and Mills, 2008, Hopcraft *et al.*, 2010, Hopcraft *et al.*, 2012, Périquet *et al.*, 2012, Burkepile *et al.*, 2013, Davies *et al.*, 2021). In fact, mega-herbivores may even counteract the effects of fear-triggered trophic cascades (le Roux, Kerley and Croomsigt, 2018), because they are not spatially constrained by predation risk. They forage and spread fecal nutrients throughout the landscape, promoting its homogenization (Pringle, 2018, Monk and Schmitz, 2022). This effect contrasts with that produced by fear-driven herbivores, which aggregate in safer areas consuming vegetation and depositing fecal material unevenly, promoting the heterogeneity of the landscape.

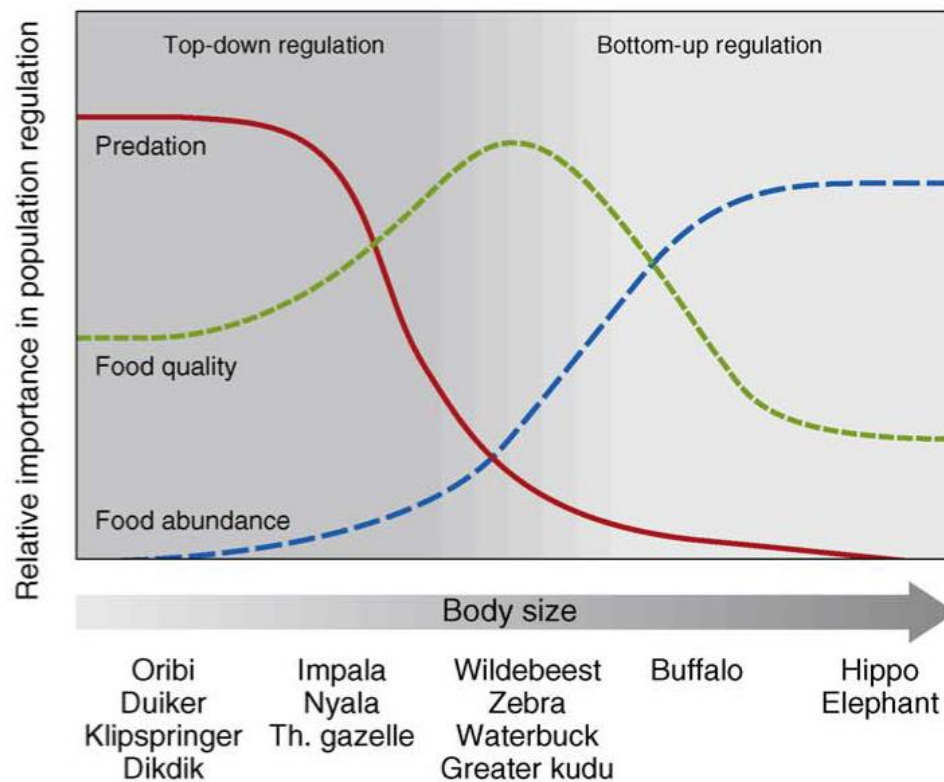


Figure 1.3 - Relative importance of predation, food quality and food abundance for different size guilds of African herbivores. Adapted from Hopcraft et al. (2010).

1.4. Adaptations of herbivores to resource limitation

Prey guilds differ in resource requirements, and some species have developed strategies and physiological mechanisms to overcome resource limitation, especially related to food and water availability (Cain III *et al.*, 2005, Cain III *et al.*, 2017, Abraham, Hempson and Staver, 2019). For instance, in arid ecosystems, species have developed specific adaptations to prevent water loss (Hempson, Archibald and Bond, 2015, Kihwele *et al.*, 2020), such as reducing standard metabolic rates and respiratory rates (Cain III *et al.*, 2005, 2006). Additionally, ungulates adapted to dry environments have developed compensatory mechanisms to prevent circulatory failure by taking water from the rumen and other body tissues (Cain III *et al.*, 2006). They also have the capacity to reabsorb higher quantities of water in their intestines and kidneys, allowing them to save up to 50% more water than temperate species when dehydrated (Cain III *et al.*, 2006, Boyers *et al.*, 2019, Kihwele *et al.*, 2020). Another key adaptation refers to the rumen, that works as a water reservoir. For example, it can store up to 20% of an individual's body weight in water for use during water-deprived periods. Moreover, some species like camels (*Camelus* sp.) can drink up to 40% of their body weight in a single visit to a waterhole

(Cain III *et al.*, 2006). Additionally some species, such as springbok (*Antidorcas marsupialis*), are able to retrieve dietary water (Nagy and Knight, 1994), if the consumed vegetation has enough moisture.

Moisture content is usually higher in woody vegetation than in grass (especially senescent grass) (Fynn, Augustine and Fuhlendorf, 2019), such that browsers are generally less dependent on surface water than grazers (Kihwele *et al.*, 2020), with important consequences for the food vs. safety trade-off since water-dependent grazers need to take higher risks to access surface water (Valeix *et al.*, 2009). Grazers face the additional challenge of limited soil moisture when grass becomes senescent. However, multiple grazer species have developed three different strategies to overcome this shortcoming: i) some species (especially larger herbivores) consume large quantities of low-nutritive vegetation to obtain enough nutrients (Hopcraft *et al.*, 2012); ii) other species prioritize the access to nutritious grass and make large movements in search for it (e.g. the gemsbok, *Gazella oryx*) (Keeping and Pelletier, 2014, Boyers *et al.*, 2019), or engage in seasonal migrations (e.g. the blue wildebeest, *Connochaetes taurinus*, or the plains zebra, *Equus quagga*, in the Serengeti National Park, Tanzania) (Wilmschurst *et al.*, 1999, Bukombe *et al.*, 2018); or iii) some grazer species (variable grazers) are able to seasonally shift their diet and are capable to digest woody vegetation (Weeber, Hempson and February, 2020).

1.5. Adaptations of prey to predation risk

An adequate management of the trade-off food vs. safety, described in section 1.3, requires prey species to perceive and understand the risk of predation. Predators may produce two types of effects on prey (Fig. 1.4): “consumptive” or “lethal” effects, that result from the removal of individuals from the populations, therefore directly influencing prey populations’ demography (Preisser, Bolnick and Benard, 2005); or “non-consumptive” or “risk” effects, that result in changes in behavioral and physiological traits of prey in response to the risk of predation (Lima and Dill, 1990, Say-Sallaz *et al.*, 2019, Wirsing *et al.*, 2021). These changes entail in costs for prey (Creel and Christianson, 2008) that can affect growth, survival and reproduction, hence ultimately impacting prey population demography (Sheriff *et al.*, 2020). Non-consumptive effects are reflected in prey’s antipredator response and can be classified as: i) reactive, when predation risk is unpredictable or uncontrollable; or ii) proactive, when prey are able to anticipate predation risk. On the latter, one of the most accepted theories to explain prey survival

mechanisms is the “Landscape of Fear” (Laundré, Hernández and Altendorf, 2001, Gaynor *et al.*, 2019), which presumes that prey are able to perceive the spatial variation of the predation risk in a landscape, building a mental map of the more and less risky areas. This strategy allows individuals to use the landscape in a way that minimizes the risk of an encounter with a predator.

The “Landscape of Fear” concept has been supported by several empiric research from different ecosystems, with important contributions and updates for the understanding of how prey manage the risk of predation in different scenarios. However, some caveats to this theory have also been identified. For example, while prey are able to recognize the most dangerous areas and balance the benefits from accessing them with the risk of being predated in heterogeneous landscapes (Donadio and Buskirk, 2016), the same becomes more challenging in homogeneous landscapes. Consequently, in areas where high risk predation pressure is chronic, prey have no choice but to face the inevitable risk when accessing resources (Schmidt and Kuijper, 2015). In such cases, landscape use by herbivores might be mostly driven by spatial heterogeneity in forage quality (Gaynor *et al.*, 2019), or temporally constrained whereby prey use the small windows of low predation risk, for instance predators downtimes, to access particularly high risk areas (Smith *et al.*, 2019). Coherently, there has been an increasing debate regarding the suitability of predator-prey spatial overlap metrics as a surrogate for predation risk (Suraci *et al.*, 2022), with the justification that predator and prey can use the same area but never meet. For example, predator and prey might exhibit different activity patterns, or the latter might shift its spatial distribution during the predators’ hunting period (Smith *et al.*, 2019, Veldhuis *et al.*, 2020). Suraci *et al.* (2022) argue that a predation event requires predator and prey to meet in space and time and engagement by the predator (i.e. it must have to desire to hunt). Moreover, the spatial patterns of perceived predation risk are typically represented as temporally static, however prey can also perceive temporal changes in predation risk and respond accordingly. These ideas have contributed to an upgrade of the theory to include the temporal dimension, describing the so called “Dynamic Landscape of Fear” (Palmer *et al.*, 2022).

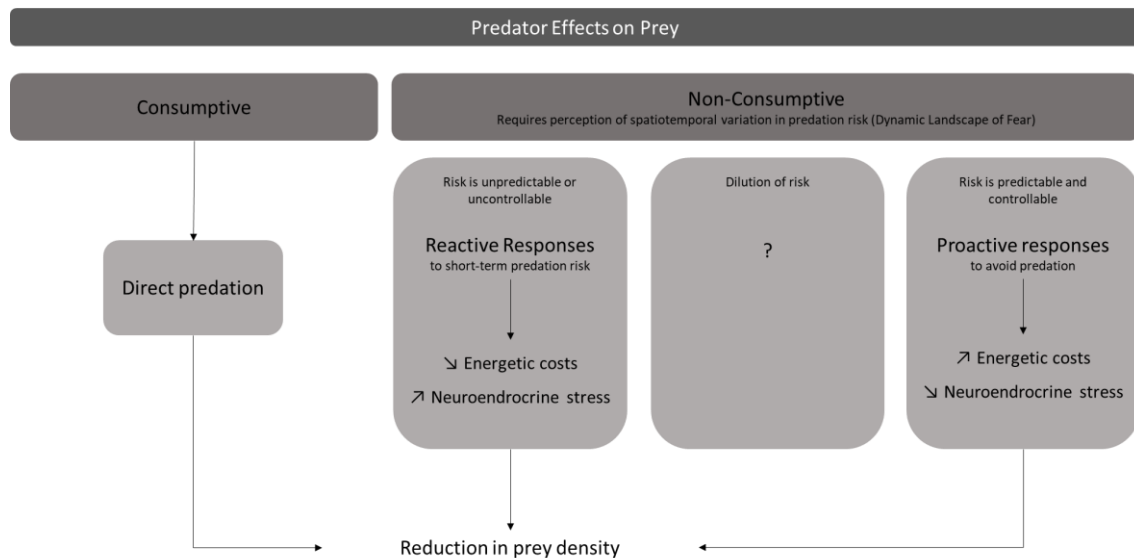


Figure 1.4 - Cascading effects a predator can inflict to the prey and the alternative responses with the associated costs.

Risk perception depends on several features of the landscape and of the concerned species, such as direct cues (carcasses, markings, calls, predator activity), indirect cues (vegetation cover or refugia), prey cognition and sensory perception, prey learning (memory or previous experience), and evolutionary history (Gaynor *et al.*, 2019). After perceiving and quantifying the risk, prey should be able to decide whether an antipredator response is worth employing or not (Wirsing *et al.*, 2021), considering that any proactive response carry costs. In an attempt to describe this decision process, Creel (2018) proposed the “Control of Risk Hypothesis”, which predicts that the cost of antipredator responses should be food (Sinclair and Arcese, 1995) or stress mediated (Boonstra *et al.*, 1998, Clinchy, Sheriff and Zanette, 2013), and be based on the degree to which prey can proactively predict and control their exposure to risk (Fig. 1.4). In short, the type of antipredator response should depend on prey’s ability to perceive the risk of predation: (i) when predation risk is predictable or controllable, prey can proactively control the risk of facing a predation event by constraining their space use (Valeix *et al.*, 2009, Thaker *et al.*, 2011, Makin, Chamaillé-Jammes and Shrader, 2017a) and/or activity patterns (Tambling *et al.*, 2015) to avoid predators, but it carries obvious energetic costs derived from lower food intake (Barnier *et al.*, 2014, Donadio and Buskirk, 2016) or suboptimal thermoregulation (Gaynor *et al.*, 2021c, Rocha *et al.*, 2022b), potentially compromising survival and reproduction of individuals (Preisser *et al.*, 2005, Gaynor *et al.*, 2021a). Conversely, (ii) when prey are not able to anticipate predation risk (e.g. when the landscape is homogeneous, lacks predator cues or in multi-predator systems) it is

more benefic for prey to reactively respond to an eminent attack. i.e. to short-term risk. As reactive responses are expected to be less frequent, the energetic costs should also be lower than in proactive responses. However, in these cases, prey live in constant alert with increased endocrine stress (Creel, Winnie and Christianson, 2009). Long exposure to high stress levels will ultimately lead to decreased progesterone levels and decreased fecundity, with consequences for prey demography (Creel *et al.*, 2007, Sheriff *et al.*, 2020). A less explored scenario describes that the (iii) dilution of risk may weaken the antipredator response (Creel, 2018). Although this scenario was introduced by Creel (2018) as a part of antipredator responses, to the best of my knowledge there is no empirical studies investigating this response type, or at least using the same terminology. It can comprise systems where the risk is diluted due to low predator abundance, or where the risk is diluted across several individuals of a group – “Risk Dilution Models” (Foster and Treherne, 1981, Turner and Pitcher, 1986, Wrona and Dixon, 1991, Lehtonen and Jaatinen, 2016). The former is seldomly studied, but seminal examples agree that in such situations the risk is not predictable. However, they diverge in the consequence: Palmer *et al.* (2022) argue that in such systems consumptive effect should dominate over non-consumptive effects, while Middleton *et al.* (2013) described the employment of reactive responses of elk (*Cervus elaphus*) over gray wolf (*Canis lupus*) at low density. The latter refers to grouping behavior in gregarious species or even mixed-species groups. These species benefit of the numbers to decrease the chance of being predated (Lehtonen and Jaatinen, 2016, Meise, Franks and Bro-Jørgensen, 2020). Nevertheless, further studies are required to understand how herbivores respond when the predation risk is diluted and better define the category, eventually discuss if it is a third scenario of risk perception or if it should be included in the ‘risk is unpredictable or uncontrollable’ category.

Despite all the research that has been devoted to this thematic, several topics are still hardly addressed, for instance how prey manage the predation risk in low predator abundance systems. Predators have experienced population declines and range contractions throughout the world (Ripple *et al.*, 2014), and this may have implications in the perceptiveness of predation risk by prey. Moreover, the population declines are not restricted to predators, and herbivores also have experienced collapse of their populations (Craigie *et al.*, 2010, Ripple *et al.*, 2015), which may have implication in predator-prey dynamics. The likelihood of encounters between predator and prey may decrease, which may bring changes in the types of preys’ antipredator responses, since it may be worthless to employ preemptive behaviors against low predation risk.

1.6. Angola: from a former wildlife hotspot to an opportunity to investigate ecological processes in incomplete communities

Angola possesses remarkable climatic, physiographic, and biome diversity, along with a well-developed water network, which creates favorable conditions for supporting a high level of biodiversity (Huntley *et al.*, 2019b). Although Angola covers only 4% of the African continent's land surface, it boasts the greatest variety of biomes (seven in total) and the second-highest number of ecoregions ($n = 15$; Fig. 1.5; Burgess *et al.*, 2004). This biogeographic richness has motivated several expeditions to explore and describe Angolan ecosystems and biodiversity during the XIX century and the first half the XX century. However, due to political instability during the latter half of the XX century, these explorations were discontinued. As a result, a significant portion of Angola's biodiversity remains unexplored, and there is little information available about it in the scientific literature (Simões-Paias, 1971, Crawford-Cabral and Simões, 1988b, a, Crawford-Cabral and Veríssimo, 2005), museum collections (Hill and Carter, 1941, Rodrigues, Figueira and Beja, 2018) and biodiversity databases (GBIF.org, 17 September 2021) regard the historical biodiversity. Field surveys attempting to characterize Angolan wildlife (namely large mammals) populations, performed before the independence of the country, reported 99 terrestrial large mammal species as occurring in the country (Table 1.1).

1.6.1. Wildlife research and conservation before the independence

Until the independence, in 1975, the knowledge about the Angolan biodiversity resulted from the remarkable achievements of few explorers, such as Friedrich Welwitsch, José Anchieta or John Gossweiler (Huntley *et al.*, 2019b). The known literature state that, until the beginning of the XX century, the country hosted important communities of large herbivores (Statham, 1924, Beja *et al.*, 2019, Huntley *et al.*, 2019a). The rich and diverse large mammal community made sport hunting frequent in the country, with reports of extensive hunting sessions (Andrade, 1985, Stassen, 2010).

Rediscovering Angolan Biodiversity: Patterns and regulation processes underlying large mammal community structure across South Angola

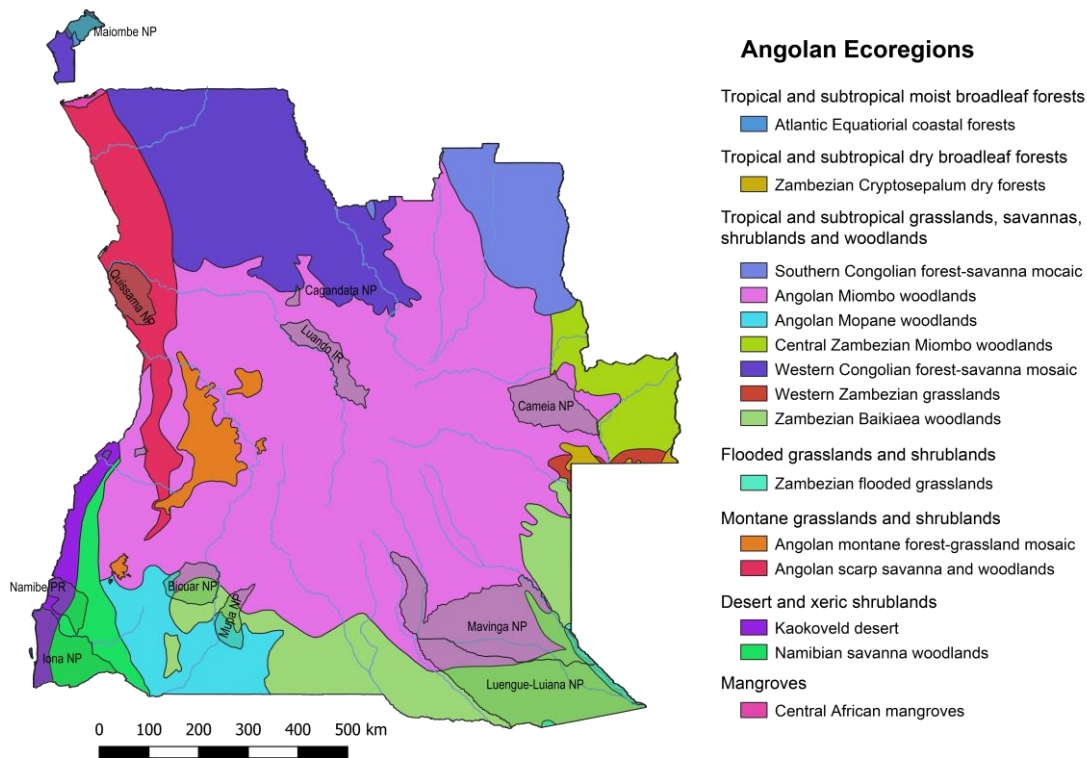


Figure 1.5 - Distribution of the Angolan ecoregions and the indication to which biome each ecoregion is included.

By the beginning of the XX century, overhunting led to the depletion of many wild game populations (Huntley, 2017). To control and manage hunting activities, the Angolan colonial government followed the lead of neighboring countries and created game reserves (i.e. a protected area of land where wild animals can live safely or be hunted in a controlled way), in the 1930's. The game reserves managed wildlife populations until the early 1950's. However, the expansion of the cattle ranching industry in southwestern Angola raised concerns about the transmission of diseases from wild populations to livestock. In response to these concerns, there was an increase in the persecution, intensified hunting, and significant reduction of wild herbivore populations in the region (Huntley *et al.*, 2019a). To prevent the persecution over wildlife populations, the Angolan colonial government upgraded the category of Angolans protected areas to 'National Parks', 'Partial Reserves' and 'Strict Reserves' in late 1950's and early 1960's (Huntley, 1974, 2017).

Table 1.1 – Checklist of species with known occurrence in Angola before the independence (before 1975) and after the period of political unrest (after 2002). “Historical references” indicate the references describing the occurrence of the species before the independence of Angola, while the “Present References” indicate the occurrence of the species after the civil war, assigned with a ✓ in the “Extant” column.

Species	Common Name	Historical References	Extant	Present References
ORDER ARTIODACTYLA		FAMILY BOVIDAE		
<i>Aepyceros melampus</i>	Impala	1-8	✓	24
<i>Alcelaphus buselaphus</i>	Red Hartebeest	4-6		
<i>Antidorcas marsupialis</i>	Springbok	1-6	✓	21-23
<i>Cephalophus dorsalis</i>	Bay Duiker	4-6		
<i>Cephalophus nigrifrons</i>	Black-fronted Duiker	4-6		
<i>Cephalophus silvicultor</i>	Yellow-backed Duiker	1, 4-6	✓	14, 16, 25
<i>Connochaetes taurinus</i>	Blue Wildebeest	1-8		
<i>Damaliscus lunatus</i>	Common Tsessebe	1-7		
<i>Hippotragus equinus</i>	Roan Antelope	1-8	✓	12-17, 19
<i>Hippotragus niger</i>	Sable Antelope	2, 3	✓	16, 17, 26, 28
<i>Kobus ellipsiprymnus</i>	Waterbuck	1, 2, 4-8		
<i>Kobus leche</i>	Lechwe	1-7	✓	14
<i>Kobus vardonii</i>	Puku	4-6		
<i>Madoqua kirkii</i>	Kirk's Dik-dik	1, 2, 4-6	✓	22, 23
<i>Oreotragus oreotragus</i>	Klipspringer	1, 2, 4-6	✓	21-23
<i>Oryx gazella</i>	Gemsbok	1, 2, 4-6	✓	21-23
<i>Ourebia ourebi</i>	Oribi	1, 2, 4-7	✓	14,16
<i>Philantomba monticola</i>	Blue Duiker	1, 4-6	✓	14, 18, 19, 25
<i>Raphicerus campestris</i>	Steenbok	1, 2, 4-7	✓	12-15, 21, 22, 23
<i>Redunca arundinum</i>	Southern Reedbuck	1, 2, 4-8	✓	16, 19
<i>Sylvicapra grimmia</i>	Common Duiker	1, 2, 4-8	✓	12-16, 18, 19, 25
<i>Syncerus caffer</i>	African Buffalo	1-8	✓	16, 17, 19
<i>Taurotragus oryx</i>	Common Eland	1-8	✓	13, 15, 17, 19, 24

<i>Tragelaphus scriptus</i>	Bushbuck	1-6	✓	16, 18, 19, 25
<i>Tragelaphus spekii</i>	Sitatunga	1-6	✓	14, 16
<i>Tragelaphus strepsiceros</i>	Greater Kudu	1-7	✓	12, 13, 15, 17, 22-24

ORDER ARTIODACTYLA

FAMILY GIRAFFIDAE

<i>Giraffa giraffa angolensis</i>	Angolan Giraffe	2-6	✓	17, 24
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ORDER ARTIODACTYLA

FAMILY HIPPOPOTAMIDAE

<i>Hippopotamus amphibius</i>	Common Hippopotamus	1-8	✓	19
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ORDER ARTIODACTYLA

FAMILY SUIDAE

<i>Phacochoerus africanus</i>	Common Warthog	1, 2, 4-6, 8	✓	12-16, 19
<i>Potamochoerus larvatus</i>	Bushpig	4 – 6	✓	12, 13, 15, 16, 19
<i>Potamochoerus porcus</i>	Red River Hog	1 – 6	✓	14

ORDER ARTIODACTYLA

FAMILY TRAGULIDAE

<i>Hyemoschus aquaticus</i>	Water Chevrotain	2, 3	✓	
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ORDER CARNIVORA

FAMILY CANIDAE

<i>Canis adustus</i>	Side-Striped Jackal	1, 2, 5, 6, 9	✓	13, 14, 16, 19
<i>Canis mesomelas</i>	Black-Backed Jackal	1, 2, 5, 6, 8, 9	✓	13, 21-23
<i>Lycaon pictus</i>	African Wild Dog	1-3, 5, 6, 10	✓	12-15, 17, 19
<i>Otocyon megalotis</i>	Bat-Eared Fox	1-3, 5, 6, 8, 9	✓	13, 15
<i>Vulpes chama</i>	Cape Fox	1-3, 5, 6, 9	✓	13, 21-23

ORDER CARNIVORA

**FAMILY
FELIDAE**

<i>Acinonyx jubatus</i>	Cheetah	1-3, 5, 6, 10	✓	14, 17, 21-24
<i>Caracal caracal</i>	Caracal	2, 5, 6, 9	✓	12-15, 21-24
<i>Felis silvestris</i>	African wildcat	1, 2, 5, 6, 8, 9	✓	12-15, 19, 21-23
<i>Leptailurus serval</i>	Serval	1, 2, 5, 6, 8, 9	✓	12-16, 19, 20, 24
<i>Panthera leo</i>	Lion	1, 2, 5, 6, 8, 10	✓	14, 17, 19, 20

<i>Panthera pardus</i>	Leopard	1-3, 5, 6, 8, 10	✓	12-17, 19, 20, 22-24
ORDER CARNIVORA		FAMILY HERPESTIDAE		
<i>Atilax paludinosus</i>	Marsh Mongoose	1, 5, 6, 9	✓	14, 16
<i>Bdeogale nigripes</i>	Black-footed Mongoose	1, 5, 6, 9		
<i>Crossarchus ansorgei</i>	Angolan Kusimanse	1, 5, 6, 9		
<i>Cynictis penicillata</i>	Yellow Mongoose	1, 5, 6, 9		
<i>Galerella sanguinea</i>	Slender Mongoose	1,	✓	15, 21, 23
<i>Helogale parvula</i>	Common Dwarf Mongoose	1, 5, 6, 9	✓	15
<i>Herpestes ichneumon</i>	Egyptian Mongoose	1, 5, 6, 9		
<i>Ichneumia albicauda</i>	White-Tailed Mongoose	1, 5, 6, 9	✓	14-16
<i>Mungos mungo</i>	Banded Mongoose	1, 5, 6, 9	✓	13, 14, 16, 25
<i>Paracynictis selousi</i>	Selous' Mongoose	1, 5, 6, 9	✓	13, 15
<i>Suricata suricatta</i>	Meerkat	5, 6, 9	✓	22
ORDER CARNIVORA		FAMILY HYAENIDAE		
<i>Crocuta crocuta</i>	Spotted Hyaena	1, 2, 5, 6, 8, 10	✓	12-15, 17, 19, 24
<i>Hyaena brunnea</i>	Brown Hyaena	1-3, 5, 6, 10	✓	21-23
<i>Proteles cristata</i>	Aardwolf	1, 2, 5, 6, 8, 9	✓	13, 14, 21-23
ORDER CARNIVORA		FAMILY MUSTELIDAE		
<i>Aonyx capensis</i>	African Clowless Otter	1, 5, 6, 9		
<i>Hydrictis maculicollis</i>	Spotted-necked Otter	1, 5, 6, 9		
<i>Ictonyx striatus</i>	Zorilla	1, 5, 6, 9	✓	14, 15, 22, 23
<i>Mellivora capensis</i>	Honey Badger	1, 5, 6, 9	✓	12-15, 19, 22, 23
<i>Poecilogale albinucha</i>	African Striped Weasel	1, 5, 6, 8, 9		
ORDER CARNIVORA		FAMILY NANDINIIDAE		
<i>Nandinia binotata</i>	African Palm Civet	5, 6, 9		
ORDER CARNIVORA		FAMILY VIVERRIDAE		

<i>Civettictis civetta</i>	African civet	1, 5, 6, 9	✓	13-16, 18, 19
<i>Genetta angolensis</i>	Miombo Genet	1, 5, 6, 8, 9	✓	13, 15
<i>Genetta genetta</i>	Common Genet	1, 5, 6, 9	✓	15
<i>Genetta maculata</i>	Large-Spotted Genet	5, 6, 9	✓	14, 19
ORDER HYRACOIDEA		FAMILY PROCAVIIDAE		
<i>Dendrohyrax arboreus</i>	Southern Tree Hyrax	4 – 6		
<i>Heterohyrax brucei</i>	Yellow-spotted Rock Hyrax	1, 4 – 6		
<i>Procavia capensis</i>	Rock Hyrax	1, 4 – 6	✓	18, 21-23
ORDER PERISSODACTYLA		FAMILY EQUIDAE		
<i>Equus quagga</i>	Plains Zebra	1-8	✓	17, 24
<i>Equus zebra</i>	Hartmann's mountain zebra	1 – 6	✓	21-23
ORDER PERISSODACTYLA		FAMILY RHINOCEROTIDAE		
<i>Diceros bicornis</i>	Black Rhinoceros	1 – 7		
ORDER PHOLIDOTA		FAMILY MANIDAE		
<i>Manis gigantea</i>	Giant Ground Pangolin	2, 3		
<i>Manis temmincki</i>	Ground Pangolin	1, 2	✓	15, 22
<i>Manis tricuspis</i>	Tree Pangolin	1, 2	✓	18
ORDER PRIMATA		FAMILY CERCOPITHECIDAE		
<i>Cercopithecus ascanius</i>	Red-tailed Monkey	1-3	✓	25
<i>Cercopithecus cephus</i>	Mustached Monkey	2, 3		
<i>Cercopithecus mitis</i>	Blue Monkey	1, 2	✓	18, 19
<i>Cercopithecus neglectus</i>	De Brazza's Monkey	2, 3		
<i>Cercopithecus nictitans</i>	Putty-nosed Monkey	2, 3		
<i>Chlorocebus cynosuroides</i>	Malbrouck Monkey	1, 2, 8	✓	12-16, 18, 19, 22, 23
<i>Colobus angolensis</i>	Angolan Colobus	1-3	✓	25
<i>Lophocebus aterrimus</i>	Black Mangabey	1, 2		

<i>Miopithecus talapoin</i>	Angolan Talapoin	1-3	✓	18, 19, 25
<i>Papio kindae</i>	Kinda Baboon	1-3		
<i>Papio ursinus</i>	Chacma Baboon	1, 2	✓	21, 22, 23
ORDER PRIMATA		FAMILY GALAGIDAE		
<i>Euoticus elegantulus</i>	Southern Needle-clawed Galago	2		
<i>Galago senegalensis</i>	Northern Lesser Galago	2		
<i>Galagoides demidoff</i>	Demidoff's Dwarf Galago	2		
<i>Otolemur crassicaudatus</i>	Thick-tailed Greater Galago	2	✓	14, 16, 19
<i>Sciurocheirus alleni</i>	Allen's Galago	2		
ORDER PRIMATA		FAMILY HOMINIDAE		
<i>Gorilla gorilla</i>	Western Gorilla	2, 3		
<i>Pan troglodytes</i>	Common Chimpanzee	2, 3		
ORDER PRIMATA		FAMILY LORISIDAE		
<i>Actocebus calabarensis</i>	Calabar Angwantibo	2		
<i>Perodicticus potto</i>	West African Potto	2		
ORDER PROBOSCIDEA		FAMILY ELEPHANTIDAE		
<i>Loxodonta africana</i>	African Savannah Elephant	1-8	✓	11-15, 17, 19, 27
<i>Loxodonta cyclotes</i>	African Forest Elephant	2-6	✓	25, 27
ORDER TUBULIDENTATA		FAMILY ORYCTEROPODIDAE		
<i>Orycteropus afer</i>	Aardvark	1, 4-6, 8	✓	12-15, 19, 22, 23

References: 1 - Hill and Carter (1941); 2 - Huntley (1973); 3 - Huntley (1974); 4 - Crawford-Cabral and Veríssimo (2005); 5 - Rodrigues *et al.* (2018); 6 - GBIF.org (17 September 2021); 7 - Statham (1924); 8 - Simões-Paias (1971); 9 - Crawford-Cabral and Simões (1988a); 10 - Crawford-Cabral and Simões (1988b); 11 - Chase and Griffin (2011); 12 - Fabiano *et al.* (2017); 13 - Overton *et al.* (2017); 14 - Taylor *et al.* (2018); 15 - Chicomo (2018); 16 - Elizalde *et al.* (2019); 17 - Petracca *et al.* (2019); 18 - Gonçalves *et al.* (2019); 19 - Braga-Pereira *et al.* (2020b); 20 - Braga-Pereira *et al.* (2021b); 21 - Chicomo (2021); 22 - Freixial (2021); 23 - Nunes (2021); 24 - Ribeiro (2021); 25 - Teutloff *et al.* (2021); 26 - Vaz Pinto (2019); 27 - Schlossberg *et al.* (2018); 28 - Vaz Pinto *et al.* (2016).

1.6.2. War-driven neglect in wildlife research and conservation

The history of Angola, and of the Angolan livelihoods is deeply marked by 41 years of political instability and war, the War of Independence (1961 - 1974) and Civil War (1975 - 2002). The Angolan Civil War had profound impacts in people's livelihood, and many people were displaced or moved to safer areas (Wilson, 2004, Huntley, 2017). The consequences were also evident in Angolan protected areas, since the parks were abandoned and neglected, allowing the increase of poaching that led to the decimation of wildlife populations (Chase and Griffin, 2011, Braga-Pereira *et al.*, 2020b, Braga-Pereira *et al.*, 2021b). One of the few expeditions allowed in Angola during that period was led by International Union for the Conservation of Nature (IUCN) in 1992. This study concluded that "Since 1975, most, if not all populations of large mammals have been severely reduced, if not eliminated" (Huntley, 2017, Huntley *et al.*, 2019a). The devastating consequences of the war for wildlife populations are further supported by reports of extensive hunting in Angolan protected areas during the occupation by armies, as documented in coronel memories (Breytenbach, 2001, 2015) and commission inquiries into the illegal trade of ivory and rhino horn into South Africa (Kumleben, 1996).

Despite the described direct impact of the war in wildlife populations, the main impacts are thought to have been indirect and arise from socio-economic changes (Braga-Pereira *et al.*, 2020b, Braga-Pereira *et al.*, 2021a). Many human populations turned to refugees and occupied new areas, sometimes closer to protected areas. These human movements also brought new hunting methods, species-specific hunting tactics and rifles that increased poaching pressure (Braga-Pereira, Bogoni and Alves, 2020a, Braga-Pereira *et al.*, 2020b). Supporting the importance of the indirect effects of the war is the continued decline of the populations after the end of the war, because human impacts remained, i.e. people continued to actively poach, occupy the land and compete with wildlife for the same resources (Petracca *et al.*, 2019). No comprehensive study has been published in scientific literature documenting the effects of the Angolan civil war on wildlife populations, but social surveys in Quiçama National Park by Braga-Pereira *et al.* (2020b) suggest a depletion of 77% of the species across the mammal community. Only 16% of the small and intermediate body-sized species experienced post-war population increases, while the rest maintained (46%) or decreased (38%) their abundance. The same study reports the extirpation of most large-bodied herbivores (Braga-Pereira *et al.*, 2020b) and carnivores (Braga-Pereira *et al.*, 2021b) in that same National Park.

1.6.3. Contemporary research of Angolan mammal communities

With the end of the war, Angola slowly reinvested in its protected areas, attempting to rehabilitate the infrastructures and headquarters, nominated administrators, and recruited and deployed wildlife rangers in an attempt to limit poaching. However, many national parks still lack the basic management capacity and effectiveness (Huntley *et al.*, 2019a). Alongside, during the early 2000s, there was a notable scarcity of scientific surveys focusing on the flora and fauna of Angola. However, there were more frequent surveys conducted on flora, while surveys specifically targeting fauna were relatively limited. In this context, several national naturalists, including Domingos Francisco, Francisco Maiato-Gonçalves, José Daniel, or Liz Matos, played a pivotal role in collecting specimens for Angolan Herbarium collections (Goyder and Gonçalves, 2019). In what regards to the fauna, the examples are expeditions organized by Mike Mills to survey birds (Dean, Melo and Mills, 2019), Vaz Pinto (2019) expeditions to assess the population status of the Angola's national icon, the giant sable (*Hippotragus niger variati*), Chase and Griffin (2011) expedition in the southeast of the country to assess savannah-elephants (*Loxodonta africana*) decline and recolonization in Cuando-Cubango province; or in the final of the decade, an expedition organized by Brian J. Huntley to survey several taxa: plants, invertebrates, mammals, birds, reptiles and amphibians (Baptista *et al.*, 2019).

The second decade of 2000 brought a new dawn for the scientific research of Angolan's biodiversity. Several national and international organizations have conducted and financed scientific expeditions targeting the documentation of the extant biodiversity, and efforts have started to restore some of the old communities. One example is the "Fundação Kissama", a non-governmental organization from Luanda, which has been involved in several expeditions, surveys and conservation action in Angola, for instance the translocation of animals to Quiçama National Park.

At least 16 scientific papers, books, BSc. and MSc. thesis and reports were published in the last 5 years (Fig. 1.6 and Table 1.1), focusing on the community of intermediate and large mammals. To the moment, and excluding the species detected in this work, 65 mammal species are known to still occur in the country (Table 1.1). Despite these recent efforts, most of the studies focus essentially on some of the Angolan's protected areas, while the situation in non-protected land remains largely overlooked (Fig. 1.6). The studies outside protected areas are almost restricted to surveys in bushmeat markets (Gonçalves *et al.*, 2019, Teutloff *et al.*, 2021), the surveys in the upper Okavango catchment in the scope of the National Geographic's project 'Into

the Okavango' (Taylor *et al.*, 2018) and CIBIO's surveys in Cuatir Conservation Area (Monterroso *et al.*, 2020b, Ribeiro, 2021).

Moreover, little is known about the demographic and distributional status of the extant populations. Although many works mention depleted populations (Schlossberg *et al.*, 2018, Elizalde *et al.*, 2019, Petracca *et al.*, 2019, Overton *et al.*, 2020), robust estimates of population abundance remain absent. The exceptions are: i) the giant sable with an estimated population of around 70 individuals in Cangandala National Park in 2018, and of 150 individuals in the Integral and Natural Reserve of Luando (Vaz Pinto, 2019); and ii) the Hartman's mountain zebra (*Equus zebra hartemannae*) with a population estimate of 478 individuals in Iona National Park in 2019 (Chicomo, 2021).

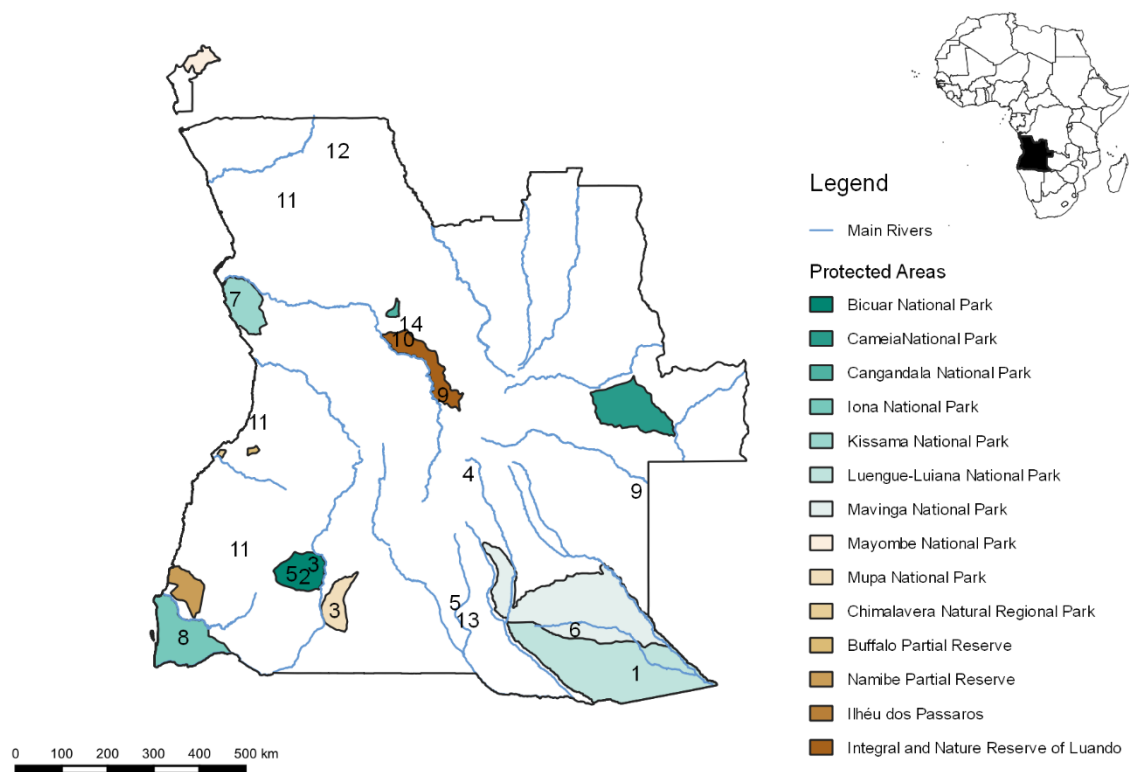


Figure 1.6 - Angolan protected areas and location of the post-war wild mammal population assessments in the country: 1 - Chase and Griffin (2011), Schlossberg *et al.* (2018); 2 - Fabiano *et al.* (2017); 3 - Overton *et al.* (2017); 4 - Taylor *et al.* (2018); 5 - Monterroso *et al.* (2020b); 6 - Petracca *et al.* (2019); 7 - Braga-Pereira *et al.* (2020b) 8 - Chicomo (2021), Freixial (2021), Nunes (2021), Rocha *et al.* (2022a); 9 - Valério *et al.* (2021); 10 - Elizalde *et al.* (2019), 11 - Gonçalves *et al.* (2019); 12 - Teutloff *et al.* (2021); 13 - Ribeiro (2021); 14 - Vaz Pinto (2019).

Despite the recent efforts to document the Angolan large mammal communities, there is still a substantial knowledge gap that needs to be filled. For instance, (i) a

continuous survey is needed to accurately describe the large mammal community compositions and allowing the robust estimation of abundance and occupancy patterns and trends in the extant wildlife populations. Additionally, the identification of potential wildlife hotspots and identify potential ecological corridors that allow the connectivity between populations is crucial for the conservation and rehabilitation of the communities and ecosystems. For this end, it is necessary to survey remote non-protected lands.

1.7. Study Areas

Southern Angola used to be particularly rich in biodiversity and abundance of wild mammal species (Huntley, 1974, Beja *et al.*, 2019), which increases the interest of the area to study the mammal community. Moreover, the varying topography and precipitation patterns across southern Angola explain its environmental gradients, ranging from desertic Atlantic coast in the Southwest, to savannas, woodlands and wetlands in the Southeast, and miombo and mopane woodlands in between (Fig. 1.7). The southwestern part of Angola, include the hot and arid environment of the northern limit of the Namib desert (Fig. 1.7). The northern tip of the desert converges with the southern edged of the Angolan escarpment, where the altitude raises to almost 2000 m.a.s.l. (Fig. 1.7 A). The sudden increase in altitude originates a contrasting climatic environment (Fig. 1.7 B and C) that provides conditions for the development of forests and woodlands (Fig. 1.7 D). Towards the Southeast of the country, the temperature raises, and the precipitation decreases. Consequently, the landscape gradually transitions to lower vegetation density, characterized by open forests and savannahs (Fig. 1.7).

Three different areas were sampled for this work: the Iona National Park, the Bicular National Park and Cuatir Conservation Area (Fig. 1.7).

1.7.1. Iona National Park

The Iona National Park (INP) expands over 15 000 km² and is located in the northern fringe of the Namibe desert, along the southwestern border with Namibia (from N: – 15° 43' 31"; E: 11° 44' 06" to N: – 17° 17' 17"; E: 13° 20' 29"), and together with the Skeleton Coast National Park (Namibia), constitutes the Iona-Skeleton Coast Transfrontier Conservation Area, one of the largest transboundary conservation areas of southern Africa.

INP is part of the Namib desert, which is classified as a hot arid desert (BWh; Belda *et al.*, 2014, Beck *et al.*, 2018). Despite being one of the hottest and driest deserts in the world, Namib is one of the most biodiverse, hosting multiple endemic species (Gurera and Bhushan, 2020). Similarly to the rest of the Namib, the INP presents a gradient of temperature, pluviosity and altitude from the Atlantic coast (0 m.a.s.l.) in the west to the mountains in the east (2041 m.a.s.l.; Fig. 1.7 A, B and C). The mean annual temperature is 24.7° C [16.5° C; 27.0° C] and the mean annual precipitation is 130 mm [15 mm; 447 mm] (Brun *et al.*, 2022a, Brun *et al.*, 2022b). Despite occurring at low levels, rainfall plays a fundamental role for vegetation growth (Li *et al.*, 2016). However, water is also available in the form night fog and dew, originated from evaporation from the nearby Atlantic Ocean (Kaseke *et al.*, 2018, Mendelsohn and Mendelsohn, 2018, Wang *et al.*, 2019). Morning dew moisturizes the soil, and Namib plants have evolved to use this water in their benefit (Wang *et al.*, 2019, Gurera and Bhushan, 2020).

INP is located in the 'Deserts and Xeric Shrublands' biome and belongs to two different ecoregions: 'Kaokoveld desert' on the west and 'Namibian savanna woodlands' to the East (Fig. 1.6). The area is divided in three main habitats: i) mobile sand dunes (Fig. 1.9 C), broadly at the Northwest of the park; ii) plains of rock and gravel (Fig. 1.9 B, E and F), which occupies the central plains; and iii) mountainous bushland and dry mopane forests, occurring mostly in the East and at higher elevations (Fig. 1.9 A and D). Several species of intermediate and large herbivores occur, of which the most iconic and common are the springbok (Fig. 1.9 H), gemsbok (Fig. 1.9 G) and Hartmann's mountain zebra. Regardless, several other species such as the meerkat (*Suricata suricatta*), steenbok (*Raphicerus campestris*), dik-dik (*Madoqua kirkii*), black-faced impala (*Aepyceros melampus petersi*) and greater kudu (*Tragelaphus strepsiceros*) also occur, but with more limited distributions (Chicomo, 2021, Freixial, 2021, Nunes, 2021). Large mammalian carnivores occurring at INP include the cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*) and brown hyaena (*Hyaena brunnea*) (Monterroso *et al.*, 2020b, Chicomo, 2021).

Despite being a National Park, several villages are enclosed within INP boundaries and surrounding the park edges at the North, Northeast to Southeast, where ca. 6000 people inhabit. Most villagers belong to the OvaCuroca, OvaCuvalé and OvaHimba ethnic groups, the latter of which lead a semi-nomadic life highly dependent on livestock herding. Although they use settlements, herders make seasonal movements with the livestock in search of the grazing areas and water (Mendelsohn and Mendelsohn, 2018). There are 15,000 cattle and 31,800 goats inside INP borders (De Cauwer and Lages,

2018), which often cluster in areas where resources of limited availability occur, such as surface water or grass, leading to the spatial convergence of livestock and wildlife with potential consequences in the form of competition for these resources (Chapter 4; Rocha *et al.*, 2022a), disease transmission or hybridization between domestic and wild species (Chicomo, 2021).

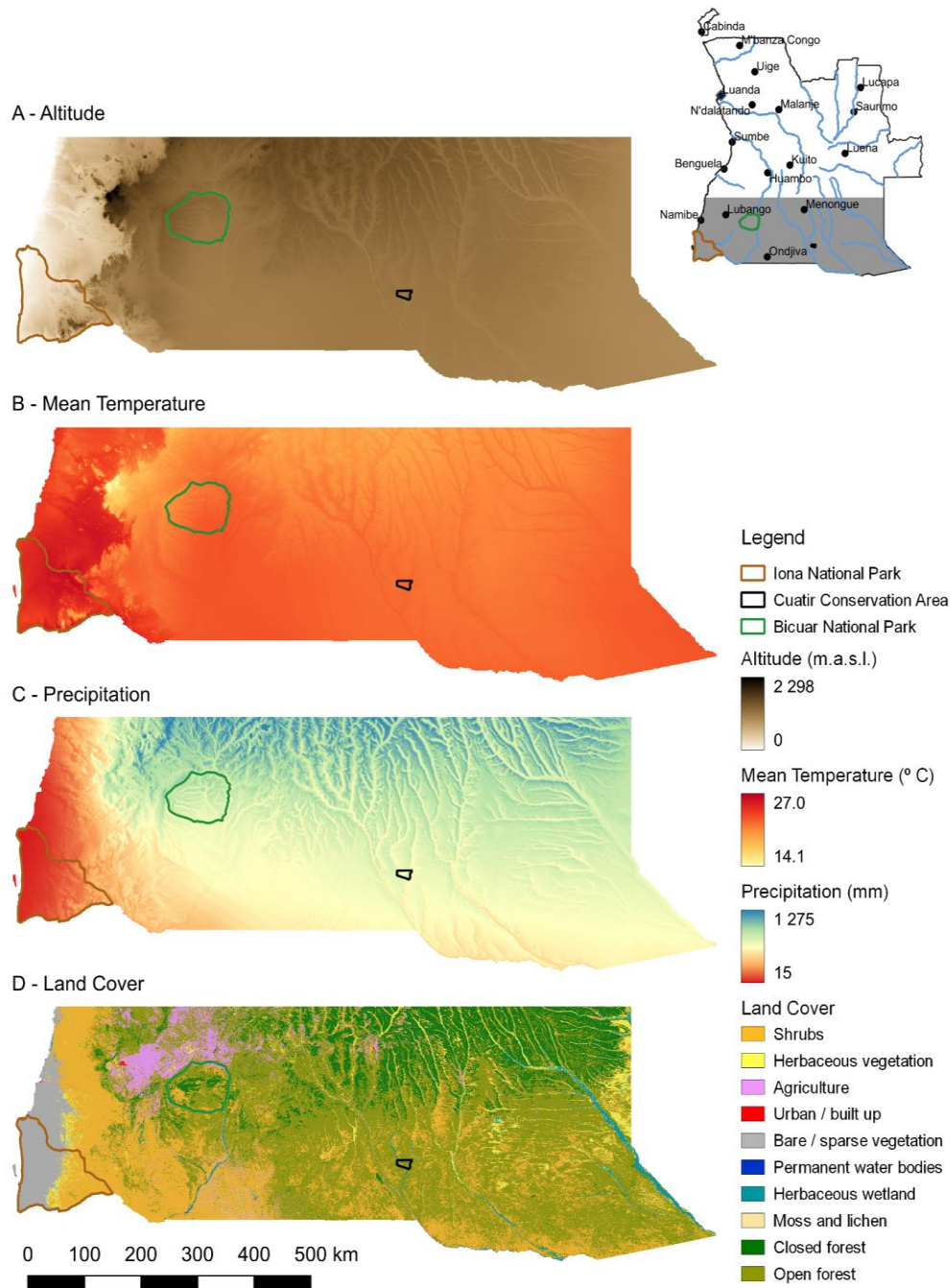


Figure 1.7 - Location of the study areas in southern Angola and the gradient of (A) altitude (Farr *et al.*, 2007), (B) mean annual temperature, (C) Annual precipitation (Brun *et al.*, 2022a, Brun *et al.*, 2022b) and (D) land cover (Buchhorn *et al.*, 2021) from the desertic southwestern Atlantic coast to the savannas in the Southeast

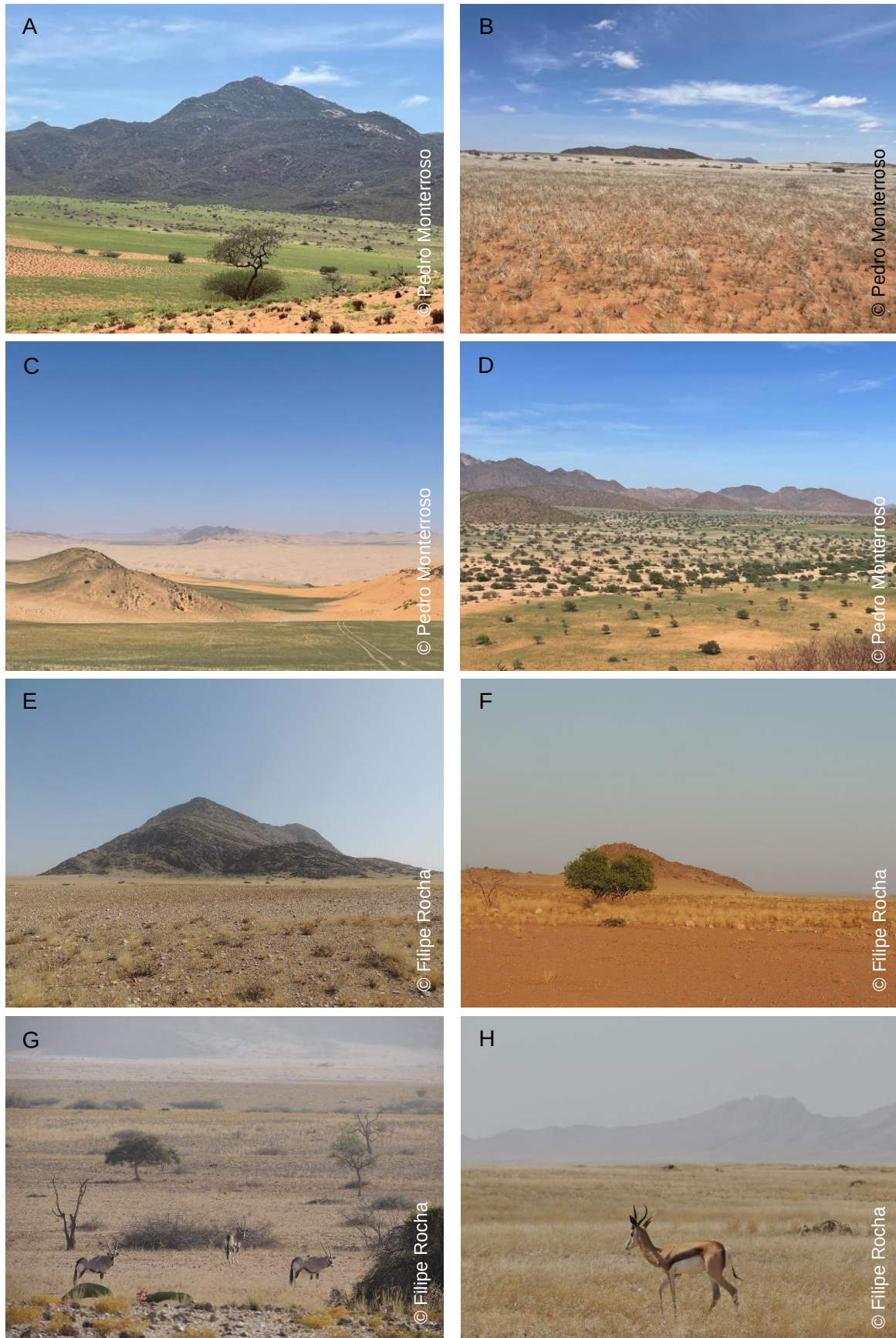


Figure 1.8 - Landscape of Iona National Park during wet (A-D) and dry season (E-H). A - show the flourishing plains by the mountains, B, E and F - dry savanna during wet and dry seasons, respectively, C - sand dunes, D - the woodlands, G - gemsbok and H - springbok in the dry savanna.

1.7.2. Bicular National Park

The Bicular National Park (BNP) is located in the Huíla province (from N: -15° 41' 28"; E: 14° 13' 17" to N: -14° 52' 36"; E: 15° 18' 11"), and spreads over 6900 km² in the Angolan plateau, 1276 m.a.s.l. with reduced ruggedness (altitude range: 1154 – 1493 m.a.s.l.; Fig. 1.7). BNP is in the transition between 3 ecoregions of the 'Tropical and subtropical grasslands, savannas, shrublands and woodlands' biome: 'Angolan Miombo Woodland', 'Zambezian *Baikiaea* Woodland' and 'Angola Mopane Woodland'. While the Park boundaries feature a fragmented landscape of natural habitat encroached by agriculture and livestock husbandry practices (Fig. 1.9 F), the largely intact core area of BNP is comprised of a mosaic of miombo woodland (Fig. 1.9 B and D), *Baikiaea-Burkea* woodland (Fig. 1.9 B and C), shrub/thicket vegetation and seasonally flooded grasslands Fig. 1.9 A) (Godlee *et al.*, 2020). The climate is warm temperate, with dry winter and hot summer (Cwa; Belda *et al.*, 2014). The mean annual temperature is 21.8° C (ranging from 20.2° C in the coldest places and 22.8° C in the hottest parts of the park; Brun *et al.*, 2022a, Brun *et al.*, 2022b). The mean annual precipitation is 819 mm [661 mm – 1006 mm] (Brun *et al.*, 2022a, Brun *et al.*, 2022b), mostly concentrated between November and April, providing good availability of food and water for herbivores. Precipitation is near absent from May through October, gradually reducing the availability of water, and the quantity and quality of vegetation.

BNP was established as a 'hunting reserve' in 1938 and upgraded to National Park in 1965. However, as many other Angolan protected areas, the protection of BNP was neglected during the civil war because it was used as army headquarters and park rangers were expelled (Huntley, 2017). The protection was re-established in 2007 in an attempt to control poaching activities and human encroachment in the area (José Maria Kandungu, personal communication). Despite the efforts, when the protected area was re-activated, human populations had already occupied its edges, especially along the Cunene riverbed, which marks the eastern boundary of the park. Despite human encroachment and activities along the park borders, there are no villages in the central part of BNP and human activities are very limited.

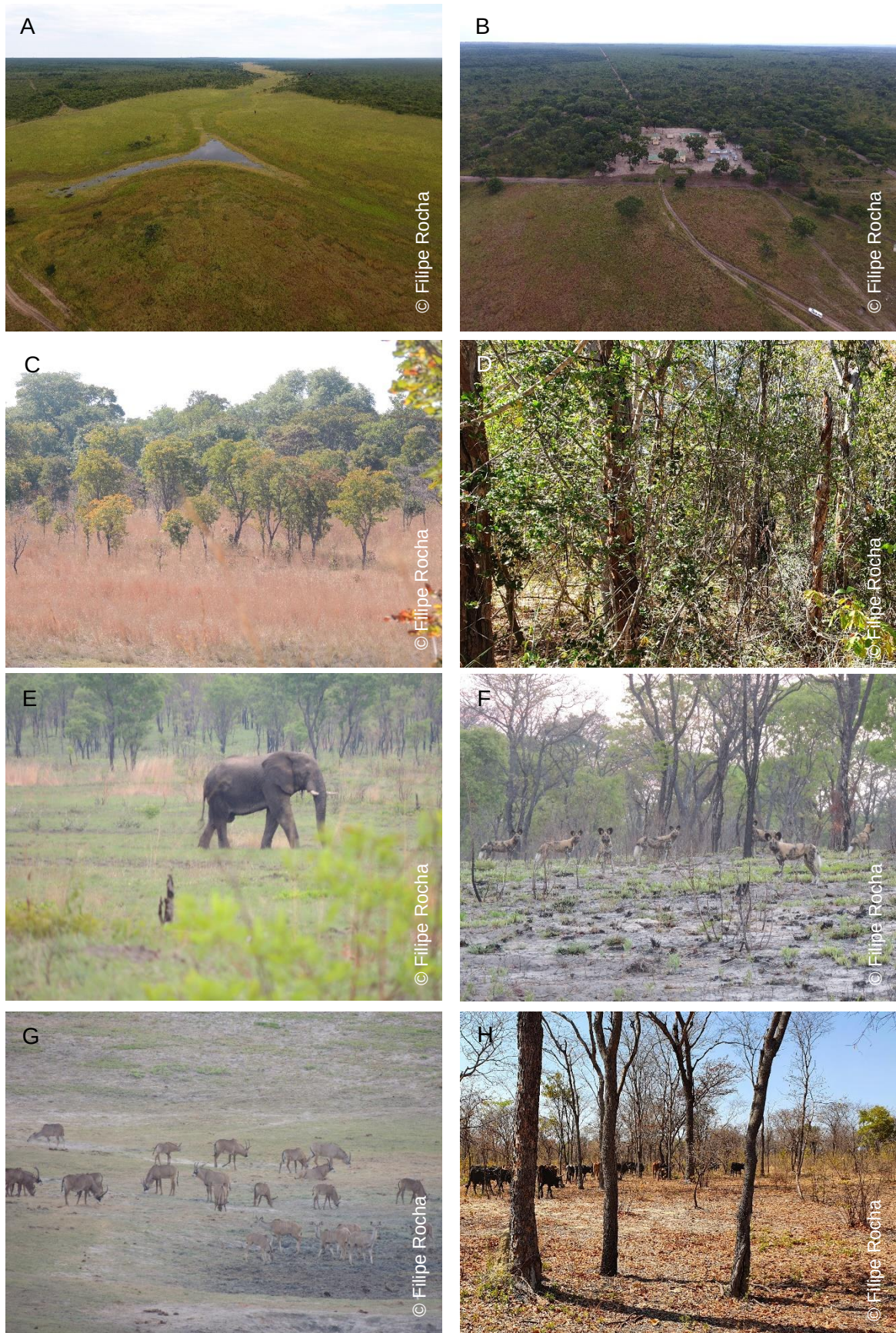


Figure 1.9 - Landscape, some charismatic wildlife and human encroachment in Bicular National Park. A - Aerial picture of a lagoon surrounded by a seasonally flooded grasslands in the wet season, B - the park's main camp and the extensive woodlands behind, C – *Baikiaea-Burkea* woodland, D – thick miombo woodland, E – male elephant, F – pack of wild dogs, G – herds of greater kudu and roan antelope grazing by a dry lagoon in the end of the dry season, H – cattle herd inside the park.

The inaccessibility of the core area of the park may have played a crucial role in the conservation and survival of much of the remaining wildlife during the period of war and years of abandonment (Chapter 2). Coherently, BNP still hosts important wildlife diversity. The most iconic extant species are the savannah elephant (Fig. 1.9 E), common eland (*Taurotragus oryx*), roan antelope (*Hippotragus equinus*), greater kudu (Fig. 1.9 G), bushpig (*Potamochoerus larvatus*), warthog (*Phacochoerus africanus*), common duiker (*Sylvicapra grimmia*), steenbok, leopard, spotted-hyaena (*Crocuta crocuta*), African wild dog (*Lycaon pictus*; Fig. 1.9 F), serval (*Leptailurus serval*) and caracal (*Caracal caracal*) (Beja *et al.*, 2019, Monterroso *et al.*, 2020b).

1.7.3. Cuatir Conservation Area

The Cuatir Conservation Area (CCA) is located in the western section of the Cuando-Cubango province (from N: -16° 35' 16"; E: 18° 5' 26" to N: -16° 26' 35"; E: 18° 20' 46"). CCA belongs to the 'Zambezian *Baikiaea* Woodland' ecoregion, from the 'Tropical and subtropical grasslands, savannas, shrublands and woodlands' biome (Fig. 1.6). The habitat of CCA is dominated by *Baikiaea-Burkea* woodlands (Fig. 1.10 B and C), with a ca. 1 km wide grasslands and floodplains along the Cuatir (a tributary of the Okavango River) and Luatuta Rivers (Fig. 1.10 A, D and E). Although there are some human settlements and small villages around the CCA, the landscape is almost pristine with little habitat destruction, as opposed to the surroundings of BNP.

CCA is also in the Angolan plateau with altitude ranging from 1131 to 1213 m.a.s.l. The climate is hot arid steppe (BSh; Belda *et al.*, 2014), with the mean annual temperature of 21.9° C [21.7° C – 22.1° C] and 701 mm of annual precipitation (603 mm – 819 mm; Fig. 1.7), concentrated between November and April.

CCA has never benefited from any legal protection by the Angolan Government nor has any game rangers patrolling the area. However, the area is currently managed for ecotourism and conservation (Uncharted Safaris), and several conservation measures have been implemented to restore the area and its wildlife. The measures include the erection of a semipermeable fence to protect local wildlife, which divided CCA into two distinct regions: i) an outer area, and ii) a core conservation area, delimited by the artificial fence towards the surrounding woodlands, but open to the Cuatir floodplains, along which the two regions are connected. The core conservation area encompasses 8 km², which extends to the peripheral woodlands and floodplains. The fence is 3m high, and is not buried in the ground, making it permeable to multiple wildlife species (e.g., carnivores and smaller herbivores), but limits the movements of large herbivores.

Rediscovering Angolan Biodiversity: Patterns and regulation processes underlying large mammal community structure across South Angola

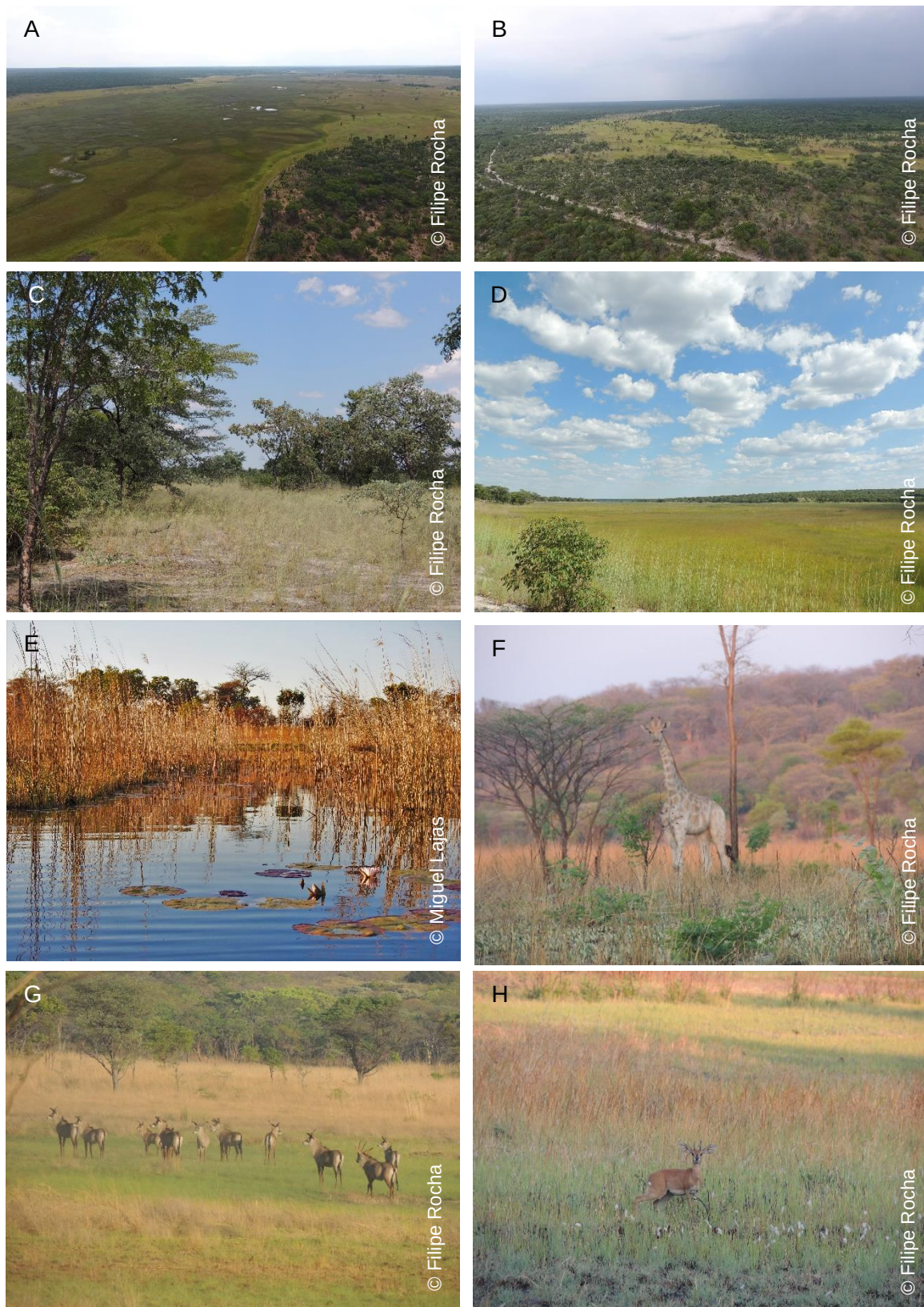


Figure 1.10 - Landscape and examples of wild mammals from Cuatir Conservation Area. A – Aerial view toward the Cuatir river floodplains, B – Aerial picture of woodlands and savanna, C – Woodlands, D – grasslands in the floodplain, E – Cuatir river channel, F – Giraffe introduced in 2020, G – herd of roan antelope and H – steenbok, one of the most common antelope in the area.

Despite the absence of landscape protection, CCA retains stable populations of steenbok (Fig. 1.10 H), duiker, reedbuck (*Redunca arundinum*), bushpig, warthog, greater kudu, and roan (Fig. 1.10 G), while sitatunga (*Tragelaphus spekii*) is only occasionally detected. In 2020, the manager reintroduced species that had gone locally extinct (e.g. impala, plains zebra, common eland and Angolan giraffe (*Giraffa giraffa angolensis*; Fig. 1.10 F)) and re-stocked the depleted greater kudu population (Stefan van Wyk, personal communication). CCA's large predators' community is not abundant (Monterroso, unpublished data), but there are resident populations of cheetah, leopard, serval and caracal; while transient populations of African wild dog and spotted-hyaena are seasonally detected in the area (Monterroso *et al.*, 2020b).

1.8. Objectives

In the preceding sections, I provided a concise overview of community dynamics, emphasizing ecological theories that elucidate how species balance the need to acquire resources while avoiding predation. I also discussed the recent history of mammal populations in Angola and stressed the importance of evaluating the conservation and demographic status of remaining wildlife populations. Although protected areas were created in regions with historically important wildlife diversity and population numbers (Huntley *et al.*, 2019a), non-protected areas, especially in between protected areas, are crucial for the conservation of species and ecosystems at a wider scale. These areas may work as ecological corridors between core conservation areas and maintain the connectivity between populations and allow the movement of animals, allowing the exchange of individuals which maintain the genetic flow and diversity and reduces the inbreeding in the metapopulation structure (von Staden *et al.*, 2022). Increasing the knowledge about the structure and functioning of mammal communities and regulation mechanisms governing this structure is though crucial for the establishment and the implementation effective conservation measures. Angolan mammal community offers a good research opportunity to study bottom-up and top-down regulation forces in disturbed communities. Therefore, the dissertation aims to contribute to filling this knowledge gap by:

- 1 – Understanding the role of post-war landscape protection in mammal diversity and occupancy rates in southern Angola. More specifically by: (i) characterizing mammal communities, (ii) assessing current species richness, and comparing it with historical

records, and (iii) evaluating the effectiveness of landscape protection on biodiversity patterns.

2 – To investigate how surface water dependency and forage availability shapes the local abundance and space use by wild and domestic herbivores in a resource-depleted environment, and how the availability this understanding could inform conservation strategies.

3 - To investigate the spatial dynamics of landscape use by herbivores in response to bush fires. Particularly I aim to understand if (i) herbivores stop using burned areas after a fire event; (ii) browsers are the first herbivore functional group to recolonize burned areas, especially in low-severity fires, and if (iii) recolonization of burned areas by grazers is dependent on rainfall, which allow grass to sprout.

4 – To understand how the effects of top-down and bottom-up processes shape the spatiotemporal patterns of prey species, in a community with low predator abundance. Particularly, I aim to understand if (i) the predominant regulation force changes seasonally with the availability of resources, (ii) prey species more susceptible to predation show higher proactive antipredator behaviors, and (iii) the prey antipredator response varies with the predator hunting mode.

1.9. Thesis outline

The thesis is organized in seven chapters. The first chapter corresponds to the general introduction, setting the context and objectives of the thesis. The next five chapters correspond to papers published (two), submitted (two) or in the final stages of preparation (one) for submission in peer-reviewed scientific journals, detailing the findings of the research carried out during the thesis. In Chapters 2 and 3 we augmented the existing knowledge regarding the present state of mammal assemblages in the southern region of Angola, thereby presenting a comprehensive assessment of the extant communities. Chapters 4, 5 and 6 use Southern Angola's mammal community as a case study to investigate interactions between two trophic levels - primary and secondary consumers -, namely the role of top-down and bottom-up forces in the regulation of prey species. We test how different ecological theories such is the "Optimal Foraging Theory" (Sinervo, 1997), the "Landscape of Fear" (Brown *et al.*, 1999) and the "Control of Risk Hypothesis" (Creel, 2018) apply in systems with reduced populations. Finally, the last chapter provides a general discussion and main conclusions of the thesis, along with future research directions. Below I present a short summary of each chapter:

Chapter 1 – General Introduction

The general introduction provides an overview of the current state of knowledge about community ecology, and described an historical perspective on the evolution of theories proposed to explain the regulation between trophic levels. Subsequently, I elucidate the mechanisms employed by species to navigate the delicate balance between acquiring essential resources and evading predation, as well as the utilization of perceived predation risk by prey species to enact diverse antipredator strategies.

Finally, I give a brief context of the history of the wild mammal populations in Angola over the last century, and how the political instability affected the protected areas network, the politics for conservation and the consequences for the native mammal biodiversity.

Chapter 2 - Official protection secures threatened species, but not higher diversity in postwar Angola.

In this chapter we compare the wild mammal community of two areas with different levels of landscape protection, one national park and one privately managed area. Our results support that biodiversity levels are similar in both areas, but the occupancy probability of larger and threatened species is higher in the national park. Conversely, the mammal community in the non-protected landscape is dominated by smaller and 'least concern' species.

Chapter 3 - Updated ranges of the Vulnerable cheetah and Endangered African wild dog in Angola.

Article published in 'Oryx' (Monterroso *et al.*, 2020b), and I am co-author.

This chapter presents a comprehensive update on the current understanding of the distribution of cheetah and African wild dog, integrating newly acquired data from three distinct areas within southern Angola.

Chapter 4 - Understanding top-down and bottom-up processes in an ungulate community to define conservation priorities in a desert environment.

Article published in 'Biodiversity and Conservation' (Rocha *et al.*, 2022a).

In this chapter we analyzed how three herbivore species with different food and water requirements use the landscape in response to the availability of resources and to livestock and human-induced pressures. We found that Hartmann's mountain zebra and gemsbok are constrained by human-induced top-down pressure and are relegated to suboptimal habitats. Conversely, we found that springbok tolerate some levels of human-induced pressure to secure the access nutritious vegetation.

This information was integrated to identify the areas more susceptible for co-occurrence between wildlife and livestock and the most important areas for wildlife conservation in the Iona National Park.

Chapter 5 - Unveiling the impacts of fire severity in herbivore occupancy patterns in disrupted communities

In this chapter, we conducted an assessment of herbivore responses to bush fires of different severities over a period of six months following the occurrence of a fire. Our findings indicate that, although we observed a temporary rise in the occupancy patterns of grazing species and elephants in the immediate aftermath of a severe fire, as well as in the vicinity of the burned areas within the first approximately 60 days, our results suggest a consistent overall decline in occupancy probability beyond that initial period. The decline in the occupancy patterns is evident across all target species, with the exception of bushpig, which increase the occupancy in areas affected by mild fires.

Chapter 6 - Landscape use by prey: Bottom-up regulation prevails under reduced perception of risk.

We investigate the role of bottom-up and top-down constraints on herbivores in a mammal community with low predator abundance. We found community-wide predator-prey association patterns, which indicate that predation pressure is insufficient to displace prey from their preferred habitats or to adjust their endogenous clock, and support predominantly bottom-up regulated prey behaviors. We suggest that, in landscapes where predator density is low, limited perception of risk may prevent the employment of preemptive antipredator behavior, likely relegating prey to rely on reactive responses to short-term predation risk.

Chapter 7 – General Discussion

In this chapter I discuss the main findings of the chapters and present the main conclusions of this thesis. I also discuss the implication of our findings for the understanding of how wildlife community structure is regulated, especially in systems with disturbed communities. I finish this chapter suggesting future directions for research in community ecology and predator-prey relationships. I also advise some conservation priorities to rehabilitate Angolan biodiversity and restore the ecological processes.

Chapter 2

Official protection secures threatened species, but
not higher diversity in postwar Angola

2.1 Abstract

Protected areas (PAs) are recognized as strongholds for biodiversity. However, armed conflicts limit their effectiveness, as many end up being occupied by military or paramilitary forces. Although the impact of warfare in PAs has been target of research, its effect on non-protected land remains largely underexplored. We aim to assess the effects of almost 40 years of political instability and armed conflict in intermediate- and large-sized mammal communities in southern Angola: a National Park with little protection on the ground - Bicuar National Park (BNP) -, and an ecotourism reserve, privately managed and without legal or on the ground protection, except for a semipermeable fence in its core area - Cuatir Conservation Area (CCA). We applied multi-region community models to camera trapping data from both study areas to contrast the diversity and occupancy of intermediate- to large-sized mammals between the two areas. Specifically, we tested for between-area differences in species richness and relative to historical records, species occupancy, and evenness-weighted diversity.

Our results reveal the likely loss of ca. 40% and 50% of mammal species in the PA and non-PA, respectively. Furthermore, we found that contemporary biodiversity levels are similar in both study areas, but with different composition and structure. Although the non-PA still retains a relatively intact small- and intermediate-sized mammal community, the PA exhibits a more well-conserved larger species community. Furthermore, the occupancy levels of species with unfavorable conservation status are higher in the PA than in the non-PA. We argue that the contemporary community structure is a consequence of different species' survival during the troubled period in both areas, since no reintroductions took place prior the surveyed period and the natural recolonizations are unlikely due to habitat degradation and human encroachment in the surrounding landscape. We stress that non-PAs may play a pivotal role in the conservation of species and ecological processes at a broader scale. As such, they should be the focus of policies that encourage their restoration and facilitate functional connections with protected areas.

Keywords: Angola, armed-conflict, biodiversity levels, multi-region community models, non-protected area, protected area, mammal community structure, wildlife decline.

2.2 Introduction

African savannas are one of the most iconic terrestrial ecosystems on Earth, hosting a wide diversity of large mammals (Anderson *et al.*, 2016). Over the last 50 years, these ecosystems have experienced severe declines in species' abundance and diversity (Craigie *et al.*, 2010, Scholte, 2011, Geldmann *et al.*, 2013, Ripple *et al.*, 2014, Brugière, Chardonnet and Scholte, 2015, Ripple *et al.*, 2015, Daskin, Stalmans and Pringle, 2016), mainly as a consequence of increasing human population (Caro, 2015, Darimont *et al.*, 2015), climate change (Hetem *et al.*, 2014) and armed conflicts (Chase and Griffin, 2011, Daskin *et al.*, 2016, Gaynor *et al.*, 2016). These threats have led to increasing levels of poaching and defaunation (Teutloff *et al.*, 2021), and constitute key drivers for a widespread 'empty forest' phenomenon (Redford, 1992), whereby apparently well-conserved ecosystems are deprived of large parts of their native fauna. Negative impacts on wildlife arise from the use of ordnance and chemicals (Orians and Pfeiffer, 1970), bushmeat hunting (de Merode *et al.*, 2007, Gaynor *et al.*, 2016, Daskin and Pringle, 2018), and trade on wildlife products to finance military activity or to fulfill disrupted livelihoods (Dudley *et al.*, 2002, Gaynor *et al.*, 2016). The overexploitation of wildlife leads to profound disturbances that reverberate through entire ecosystems by direct and indirect pathways (Ripple *et al.*, 2016a, Wolf and Ripple, 2016, Ripple *et al.*, 2019), and range from local extinctions to altered disease dynamics or to changes in water quality and carbon storage (Ripple *et al.*, 2014).

Protected areas (PAs) have been created to protect biodiversity and habitat integrity (Geldmann *et al.*, 2013), and are currently recognized as strongholds for iconic, threatened, and endemic species (Pringle, 2017, Riggio *et al.*, 2019). Therefore, effectively managed PAs are important from ecological, economic and social perspectives, namely through the provision of ecosystem services (Dudley, MacKinnon and Stolton, 2014, Castro *et al.*, 2015, Ripple *et al.*, 2015). Despite the invaluable role of PAs for protecting wildlife populations and habitats (Joppa, Loarie and Pimm, 2008), inefficient management may hamper their success (Craigie *et al.*, 2010, Scholte, 2011, Watson *et al.*, 2014, Lindsey *et al.*, 2017). Human incursions and illegal activities in and around PAs remain as major threats (Lindsey *et al.*, 2017), often responsible for declines in wildlife populations (Craigie *et al.*, 2010, Scholte, 2011). Poaching for bushmeat and illegal trading of wildlife products is a leading threat for wildlife (Ayling, 2013) and is estimated to generate US\$5-\$23 billion yearly (Kar and Spanjers, 2017). PAs without

proper management and protection are known as ‘paper parks’, i.e., those that in reality provide little or no protection (Joppa *et al.*, 2008).

South Angola used to harbor a wide diversity of wildlife (Huntley, 1973, 1974), but extensive and unsustainable hunting activities until the 1930s led to depletion of wildlife populations (Huntley, 2017). Therefore, the first hunting reserves were created with the goal of regulating hunting activities, some of which were upgraded to National Park status in the early 1960s (Huntley, 1974, Huntley *et al.*, 2019b). However, after these initial conservation efforts, Angola suffered from two almost consecutive armed conflicts that severely affected both society and ecosystems: the independence war (1961-1974) and a civil war (1975-2002). The detrimental effects on Angolan wildlife during its period of political unrest are suspected to have been particularly intense. Park staff gradually left their posts as the PAs were progressively occupied by rebel forces (Huntley, 2017), and abandoned to their new occupants’ and poachers (Braga-Pereira *et al.*, 2020a, Braga-Pereira *et al.*, 2021a). Furthermore, the war also led to a significant displacement of people, resulting in the augmentation of rural inhabitants and human expansion into natural habitats. This escalation in human presence inside and outside protected areas further intensified the strain on wildlife populations (Petracca *et al.*, 2019, Braga-Pereira *et al.*, 2020a). Consequently, the already depleted wildlife populations before the civil unrest (Huntley, 1973, 1974) were subjected of massive hunting pressures and likely extirpation of many species (Chase and Griffin, 2011, Huntley, 2017, Braga-Pereira *et al.*, 2020b).

Unlike many southern African countries where estimates of assessments of wildlife population dynamics have been recorded over decades, a profound knowledge gap remains regarding wildlife distribution, population numbers, and trends in Angola (Huntley *et al.*, 2019b). After the war, several initiatives have strived to characterize remnant mammal biodiversity (e.g. Chase and Griffin, 2011, Fabiano *et al.*, 2017, Overton *et al.*, 2017, Schlossberg *et al.*, 2018, Taylor *et al.*, 2018, Beja *et al.*, 2019, Petracca *et al.*, 2019, Braga-Pereira *et al.*, 2020b, Monterroso *et al.*, 2020b, Overton *et al.*, 2020, Valério *et al.*, 2021; mapped in the Fig. 2.1). Despite these studies, some aspects remain overlooked: (i) the consequences of the war in mammal communities, and (ii) an explicit comparison of biodiversity and wildlife community composition and structure inside and outside PAs to inform the debate around conservation land-tenure, i.e. the value of private wildlife land vs. formally protected areas, to identify potential wildlife hotspots and possible ecological corridors that facilitate the connection between communities.

In this study we aim to understand the role of post-war landscape protection in mammal diversity and occupancy rates in southern Angola. More specifically, we aim to (i) characterize the composition and structure mammal communities in southern Angola, (ii) assess and compare current species richness with historical records, and (iii) compare mammal biodiversity patterns and community structure in two areas with different levels of landscape protection.

Given the neglect of Angolan PAs during the recent period of armed conflict, we expect a loss of biodiversity, particularly marked by the loss of larger and iconic species. We expect that (H1) current levels of species richness are lower than pre-war historical records; (H2) biodiversity levels in the PA are higher than in the non-protected landscape, (H3) biodiversity and occupancy levels of larger species are higher in the PA, and (H4) species with unfavorable conservation status have higher occupancy probability in the PA than in the non-protected landscape.

2.3 Methods

2.3.1 Study area

This study was carried out in two areas in southern Angola with different levels of landscape protection: Bicuar National Park (BNP) and Cuatir Conservation Area (CCA). Bicuar National Park (S 15.1°, E 14.8°; Huíla Province; Fig. 2.1) was established as a hunting reserve in 1938 and upgraded to National Park status in 1964 (Huntley *et al.*, 2019b). It was abandoned and occupied by rebels between 1975 and 2002, during the Angola's civil war (Huntley, 2017), and landscape protection was re-established in 2007. BNP is classified as a level II IUCN Protected Area (Dudley, 2008), however the protection on the ground remains inadequate since it only accounts with 56 game rangers distributed through 11 ranger posts, with very limited resources and budget. No ecosystem rehabilitation measure was taken since re-establishment of the protection. The altitude ranges between 1200 and 1400 m.a.s.l., the mean maximum temperature is approximately 33°C and the mean minimum temperature is ca. 4°C. The annual rainfall reaches 857 mm, mostly between November and May (i.e., wet season; <http://www.sasscalweathernet.org/>). The BNP spans over 6,900 km² in the transition between the Angolan Miombo Woodland, the Zambezian *Baikiaea* Woodland and the Angola Mopane Woodland ecoregions (Huntley *et al.*, 2019b). While park boundaries exhibit a fragmented landscape of natural habitats encroached by agriculture and livestock husbandry practices, the core area remains a largely intact and constitutes a

mosaic of miombo, *Baikiaea-Burkea* woodlands, shrub/thicket vegetation and seasonally flooded grasslands (Godlee *et al.*, 2020).

The Cuatir Conservation Area (S 16.5°, E 18.2°; Cuando-Cubango Province; Fig. 2.1) is a ca. 100 km² section of a near-pristine environment along the Cuatir riverbed. It is located in the Zambebian *Baikiaea* Woodland ecoregion (Huntley *et al.*, 2019b), and is dominated by *Baikiaea-Burkea* woodlands, with a ca. 1 km wide grasslands and floodplains along the Cuatir (a tributary of the Okavango river) and Luatuta rivers (Fig. 2.1). CCA is ca. 1140 m.a.s.l., and accounts for a mean maximum temperature of ca. 30°C and a mean minimum temperature of ca. 9° to 12°C. Rainfall can reach 800 mm during the wet season (Werger and Coetzee, 1978). The area was concessioned ecotourism in 2013 and has never benefited from any legal landscape protection nor has any game rangers patrolling the area. In 2018, a semipermeable fence was erected to protect local wildlife, which divided CCA into two distinct regions (Fig. 2.1): i) an outer

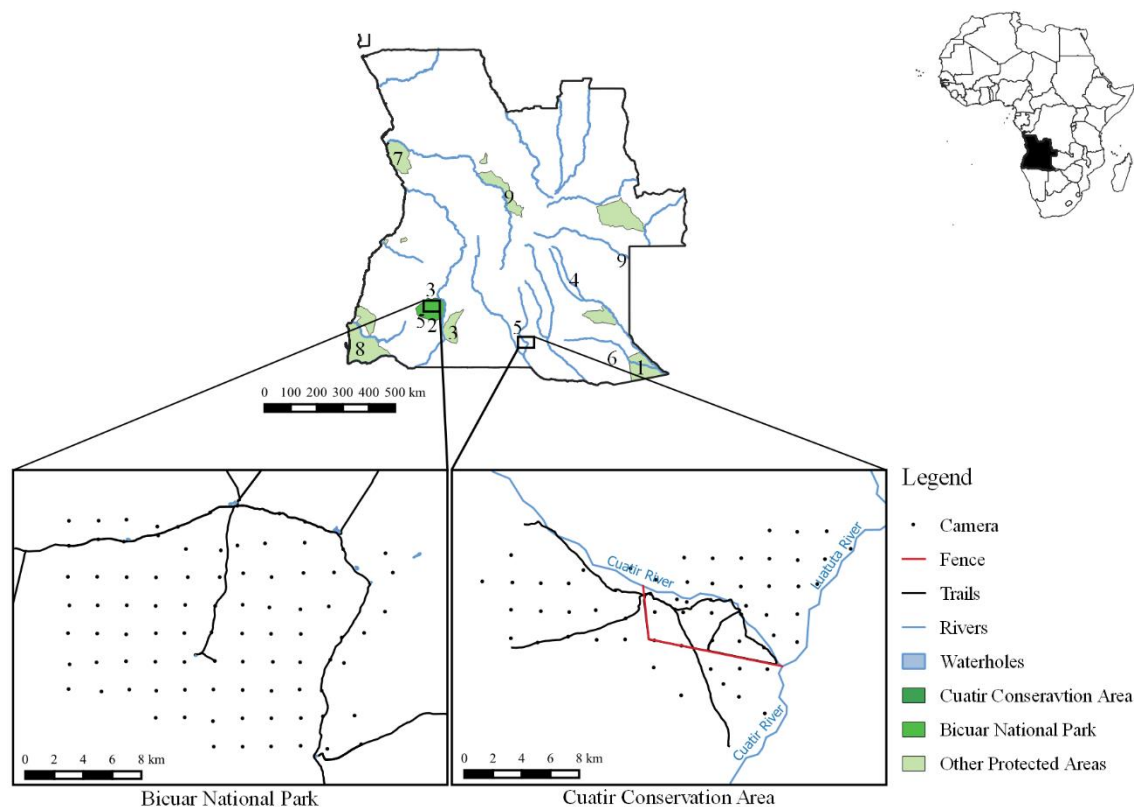


Figure 2.1 - Location of the study areas in Angola, along with the location of the other post-war wild mammal population assessments in the country: 1 - Chase and Griffin (2011), Schlossberg, Chase and Griffin (2018); 2 - Fabiano *et al.* (2017); 3 - Overton *et al.* (2017); 4 - Taylor *et al.* (2018); 5 - Monterroso *et al.* (2020b); 6 - Petracca *et al.* (2019); 7 - Braga-Pereira *et al.* (2020b) 8 - Chicomo (2021), Freixial (2021), Nunes (2021), Rocha, Bennett and Monterroso (2022a); 9 - Valério, Elizalde and Elizalde (2021). The small insets depict the camera trapping sampling scheme used in Bicular National Park and in Cuatir Conservation Area, their main features in the respective sampling areas such as trails, water sources, and the semi-permeable fence in CCA.

area, and ii) a core conservation area, delimited by the artificial fence towards the surrounding woodlands (i.e. outer area), but open to the Cuatir floodplains, along which the two regions are connected. The core conservation area encompasses 8 km², which extends to the peripheral woodlands and floodplains. The fence is 3m high, and is not buried in the ground, making it permeable to multiple wildlife species (e.g., carnivores and smaller herbivores), but limits the movements of large herbivores. Large-bodied herbivores might overcome this artificial barrier along the floodplains, especially when water levels are low. Besides the fence, no other rehabilitation measure had been implemented when this research was performed.

Despite the differences in habitat and ecoregions between the study areas, both are included within the same biogeographical region for mammals (Rodrigues *et al.*, 2015), i.e. homogeneous regions in terms of species assemblages.

2.3.2 Historical mammal richness

The historical mammal diversity of BNP and CCA was assessed from 10 different sources (Table 2.1), comprising museum collection reports, mostly published in the Global Biodiversity Information Facility (GBIF.org), scientific papers, unpublished reports, books, and expedition and hunting reports published or collected before the independence of Angola in 1975. Species records prior to the establishment of Angolan PAs were regarded as historically occurring if described within a 25 km buffer of each respective study area. All historical records were cross-validated with known historical distributions from IUCN (2021) to exclude possible misidentification of species whose occurrence in the study areas was extremely unlikely. We also excluded species with historical occurrence in the study areas, but whose preferred habitat was not sampled during our camera trapping survey, such as the common-hippopotamus (*Hippopotamus amphibius*), the common reedbuck (*Redunca arundinum*) and yellow-spotted rock-hyrax (*Heterohyrax brucei*) in BNP.

2.3.3 Field data collection

We conducted systematic camera trap surveys to assess the structure of the mammal communities of BNP and CCA. An equivalent sampling design was set up in both study areas, allowing for direct comparability: camera stations (one camera per station) were uniformly deployed, following a grid-sampling scheme at a ca. 2 km inter-camera distance, ensuring spatial independence (Monterroso *et al.*, 2013, Meek *et al.*, 2014, Fig. 2.1). The surveys in BNP and CCA occurred simultaneously, between May 1st

and October 31st 2019, encompassing the entire dry season. We deployed 86 Reconyx Hyperfire 2 (Reconyx, Holmen, Wisconsin, USA) camera traps in BNP, while a total of 60 camera traps in CCA consisted of three different models: Cuddeback C1 Strobe Flash (n=6; Cuddeback, Green Bay, Wisconsin, USA), Reconyx Hyperfire HC600 (n=24) and Reconyx Hyperfire 2 (n=30; Reconyx, Holmen, Wisconsin, USA). Cameras were deployed on trees approximately 0.6 m off the ground without any lures or artificial attractants, however, some cameras were set on trails. The cameras were set to shoot a burst of 5 (Cuddeback) or 10 (Reconyx) photos when triggered and without any time delay (0 s), to maximize the number of photos taken per activation. Camera stations were serviced at the middle of the survey period for maintenance, troubleshooting, and for battery and memory card replacement, as needed.

Initial processing of camera trapping data was performed using the “camtrapR” v.2.0.2 R package (Niedballa *et al.*, 2016). We considered detection records as independent whenever timing between consecutive detections of the same species was >30 min, unless animals could be clearly individually distinguished (Monterroso *et al.*, 2013).

2.3.4 Data analysis

We fitted Bayesian multi-region community models (MRCM; Tenan *et al.*, 2017) to estimate the probability of occupancy for all species potentially occurring at BNP and CCA. Tenan *et al.* (2017) described a model for stratified communities, where each species is assigned to a group (g), defined based on some ecological stratification of the community (e.g., guild). This approach allows estimating the number of species per region's community stratum ($N_{g,r}$). We considered species that share behavioral and body mass traits as belonging to the same guild. This clustering approach facilitates numerical convergence and increases the precision of the estimates of detection probability parameters (Kéry and Royle, 2015). Species were assigned to one of six guilds: (1) small-intermediate mammals, (2) intermediate-large mammals, (3) large ungulates, (4) megafauna, (5) small and meso-carnivores, and (6) large carnivores (Table 2.1). The conservation status of each species was retrieved from the ‘IUCN Red List of Threatened Species’ (IUCN, 2021). Considering that a species can only be assigned to one guild, the total number of species in each community r is thus given by:

$$N_r^T = \sum_g N_{g,r}.$$

The number of species within guilds and communities ($\lambda_{g,r}$) was modelled as:

$$N_{g,r} \sim \text{Poisson}(\lambda_{g,r})$$

By conditioning the Poisson model on the total number of species in the community r , the vector N_r of guild- and region-specific community sizes ($N_{g,r}$) has a multinomial distribution:

$$N_r \sim \text{MN}(N_r^T, \pi_r)$$

Where π_r represents a vector of probabilities that a species, member of the community of the region r , belongs to the guild g , i.e. $\pi_{g,r} = \lambda_{g,r} / \sum_g \lambda_{g,r}$.

Data augmentation (Dorazio and Royle, 2005, Royle, Dorazio and Link, 2007) was used to estimate the number of unobserved species in a community r , such that N_r^T is marginalized over a $\text{Binomial}(M, \Omega_r)$ prior distribution, where M represents the potential species richness, such that $M \gg \max(N_r^T)$. Here we defined M as the total confirmed extant species (N) plus all non-detected species historically occurring in the areas (H), such that $M = N + H$. Ω_r denotes the probability that a species present in the community r was never detected and is specified as $\Omega_r = (\sum_g \lambda_{g,r}) / M$. The latent binary variable ($\omega_{i,r}$) is described by a Bernoulli distribution with the probability Ω_r :

$$\omega_{i,r} \sim \text{Bern}(\Omega_r)$$

And denotes whether the species i is present in the community r ($\omega_{i,r} = 1$) or not ($\omega_{i,r} = 0$).

Single day detection histories were summarized in a 3-dimensional array Y with elements $y_{i,j,r}$ for species i in site j of the community r , under the assumption that the community remained closed for the duration of the survey. We modeled the true occupancy state of each species i at the site j of the community r ($z_{i,j,r}$) as a Bernoulli random variable with species-specific occupancy probability for each site in each community $\Psi_{i,j,r}$, conditional to the species presence ($\omega_{i,r}$), such that:

$$z_{i,j,r} \sim \text{Bernoulli}(\Psi_{i,j,r} \omega_{i,r})$$

Species-specific occupancy ($\Psi_{i,j,r}$) was modelled as logit-transformed hyperparameters of the occupancy of species i ($\gamma_{0,i,r}$), such that:

$$\text{logit}(\Psi_{i,j,r}) = \gamma_{0,i,r}$$

$\gamma_{0,i,r}$ was considered to be described by a normal distribution of the mean interspecific variability in occupancy (μ_{γ_0}) with variance of the interspecific variability in the occupancy ($\sigma_{\gamma_0}^2$) as the standard deviation, i.e. $\gamma_{0,i,r} \sim \text{Normal}(\mu_{\gamma_0}, \sigma_{\gamma_0}^2)$. The

community-specific hyperparameter for mean interspecific occupancy was calculated by the difference between log-transformed mean probabilities of occupancy and non-occurrence of species i species i in the community r

$$\mu_{\gamma_0} = \log(\bar{\Psi}_{i,r}) - \log(1 - \bar{\Psi}_{i,r})$$

The standard binomial observation model relates the true underlying occupancy state ($Z_{i,j,r}$) to the observed detection frequency data, such that

$$y_{i,j,r} \sim \text{Binomial}(K_{j,r}, p_{i,j,r}^{Z_{i,j,r}}),$$

where $K_{j,r}$ represents the effort at the site j of the community r and $p_{i,j,r}$ represents detection probability for species i at the site j of the community r , given presence. $p_{i,j,r}$ is considered to be influenced by whether a camera was deployed in a trail or not. Trail was therefore incorporated as a dummy variable taking the value ‘1’ if a camera was set on a trail and ‘0’ otherwise.

$$\text{logit}(p_{i,j,r}) = \delta_{0i,r} + \delta_{1i} \times \text{trail}_{j,r},$$

Where $\delta_{0i,r}$ denotes the baseline species-specific detection probability in the community r and is described by a normal distribution of the hyperparameters for the detectability of the species i in the community r , i.e. $\delta_{0i,r} \sim \text{Normal}(\mu_{\delta_0}, \sigma_{\delta_0}^2)$, where μ_{δ_0} and $\sigma_{\delta_0}^2$ refer to the mean and variance interspecific variability in the detectability, respectively. δ_{1i} indicate the influence of trails in the detection of the species i .

Models were fit in JAGS (version 4.3.0), executed from R (version 4.1.2; R Core Team, 2021) using “jagsUI” (Kellner and Meredith, 2019). We ran three Markov Chain Monte Carlo (MCMC) chains with 50,000 iterations after a 20,000 iteration burn-in and thinned by 30. We used non-informative priors, i.e. uniform(0,1) for μ_{γ_0} and μ_{δ_0} and uniform(0,10) for σ_{γ_0} and σ_{δ_0} . Model convergence was assessed from a visual inspection of chain trace plots and from the Gelman-Rubin statistic (i.e. R-hat), where values < 1.1 suggested reliable convergence (Gelman and Rubin, 1992). All results are presented as the posterior mean [95% posterior credibility intervals], unless explicitly stated otherwise.

Shannon’s diversity index (Shannon, 1948) was calculated using the package R “vegan” (version 2.5-7; Oksanen *et al.*, 2019), for the entire community and for each guild in BNP and CCA, per each MCMC iteration chain to compare biodiversity levels estimated in both areas, such that:

$$H' = - \sum_{i=1}^N p_i \ln p_i$$

where p_i denotes the mean occupancy of the species i in each community, and N the number of detected species in each study area. H' was not computed for megafauna because a single species was detected for this guild. H' distributions compared using a distribution-free overlapping index ($\hat{\eta}$) (Pastore and Calcagnì, 2019).

We compared two study areas (BNP and CCA) from different ecoregions, and differences in their habitat structures could potentially lead to variations in community composition. To validate our comparison, we assess whether the habitat structures of both study areas are similar. The habitat structure in each study area was calculated as the mean proportion of grassland, shrubland and tree cover, as extracted from the Copernicus Global Land Cover raster with a 100m resolution (Buchhorn *et al.*, 2021). A χ^2 test (Pearson, 1900) was used to assess whether habitat structure in BNP and CCA is statistically different.

2.4 Results

We collected a total of 3864 independent records from 32 mammal species over a sampling effort of 13412 trap-days in BNP. The sampling effort in CCA comprised 8834 trap-days and resulted in 3503 independent records from 29 mammal species (Table 2.1, Appendix 2: Table S.2.1).

Although BNP and CCA have statistically different proportions of habitat cover ($\chi^2 = 16.53, df = 2, p - value < 0.01$; Appendix 2: Table S.2.2), we found that 69% (25 out of 36) of mammal species with confirmed occurrence are shared between the two study areas. Coherently, Shannon's diversity index indicates similar levels of biodiversity between the communities ($H'_{BNP} = 3.55[3.45; 3.64]$ vs. $H'_{CCA} = 3.58[3.48; 3.67]$; $\hat{\eta} = 0.86$; Fig. 2.2).

The similarities between community-wide diversity indices are consistent across most guilds (Fig. 2.2; Appendix 2: Table S.2.3), being highly pronounced for small and meso-carnivores ($H'_{CCA} = 2.59[2.42; 2.73]$ vs. $H'_{BNP} = 2.56[2.33; 2.75]$, $\hat{\eta} = 0.80$) and large ungulates ($H'_{CCA} = 1.89[1.63; 2.09]$ vs. $H'_{BNP} = 1.94[1.71; 2.11]$, $\hat{\eta} = 0.85$), but also significant for intermediate-large mammals ($H'_{CCA} = 2.21[2.04; 2.35]$ vs. $H'_{BNP} = 2.12[1.93; 2.28]$, $\hat{\eta} = 0.63$) and large carnivores ($H'_{BNP} = 1.46[1.24; 1.59]$ vs. $H'_{CCA} = 1.30[0.97; 1.52]$, $\hat{\eta} = 0.53$). Significant differences were only found for small-intermediate

mammals, which are more diverse in CCA than in BNP ($H'_{CCA} = 1.45[1.22; 1.59]$ vs. $H'_{BNP} = 1.24[1.01; 1.40]$, $\hat{\eta} = 0.26$).

Table 2.1- Historical mammal community of BNP and CCA, the respective guild and detection/non-detection in the present study.

Guild	Common Name	BNP		CCA		References
		Historical	Current	Historical	Current	
Small-intermediate mammals	Scrub Hare		✓		✓	
	Southern Galago		✓			
	Malbrouck Monkey	✓	✓		✓	[1, 2, 8]
	Spring Hare		✓		✓	
Intermediate-large mammals	Kirk's Dik-dik	✓				[2, 4-6]
	Steenbok	✓	✓	✓	✓	[2, 4-7]
	Klipspringer	✓				[4-6]
	Common Duiker	✓	✓	✓	✓	[1, 2, 4-8]
	Oribi	✓		✓		[1, 2, 4-7]
	Blacked-Faced Impala	✓				[1, 2, 4-8]
	Impala			✓		[1-3, 7]
	Southern Reedbuck			✓	✓	[1, 2, 4-8]
	Sitatunga			✓	✓	[3]
	Lechwe			✓		[1-3, 7]
	Bushpig	✓	✓		✓	[4-6]
	Common Warthog	✓	✓	✓	✓	[2, 4-6, 8]
	Ground Pangolin	✓	✓			[2]
	Cape porcupine		✓		✓	
Large ungulates	Aardvark	✓	✓	✓	✓	
	Common Tsessebe			✓		[1-3, 7]
	Hartebeest	✓				[4-6]
	Blue Wildebeest	✓		✓		[1-8]

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	Waterbuck			✓		[4-6]
	Greater Kudu	✓	✓		✓	[2, 4-7]
	Roan Antelope	✓	✓	✓	✓	[1, 8]
	Plains Zebra	✓				[2-8]
	Common Eland	✓	✓	✓		[1-6, 8]
	Cape Buffalo	✓		✓		[2, 3, 4-8]
	Common Hippopotamus			✓		[3-8]
Megafauna	Angolan Giraffe			✓		[3]
	Black Rhinoceros	✓		✓		[3-7]
	African Savannah Elephant	✓	✓	✓		[1-8]
Small and meso-carnivores	Bat-Eared Fox	✓	✓		✓	[2, 5, 6, 8, 9]
	Black-Backed Jackal	✓	✓			[1, 5, 6, 8, 9]
	Side-Striped Jackal	✓	✓	✓	✓	[2]
	Wild Cat	✓	✓		✓	[8]
	Caracal	✓	✓		✓	[2]
	Serval	✓	✓	✓	✓	[1, 2, 8]
	Common Dwarf Mongoose	✓	✓			[1, 5, 6, 9]
	Slender Mongoose		✓	✓	✓	
	Selous' Mongoose	✓	✓		✓	[5, 6, 9]
	Marsh Mongoose			✓	✓	
	White-Tailed Mongoose		✓	✓	✓	
	Aardwolf	✓				[1, 2, 5, 6, 8, 9]
	African Striped Weasel	✓				[1, 5, 6, 8, 9]
	Zorilla	✓	✓	✓	✓	[1]
	Honey Badger	✓	✓	✓	✓	[1]
	Common Genet	✓	✓		✓	[1, 5, 6, 9]
	Miombo Genet	✓	✓		✓	[1, 5, 6, 8, 9]

	Large-Spotted Genet	✓				[5, 6, 9]
	Cape Genet	✓				[1]
	African Wild Dog	✓	✓	✓	✓	[1, 3, 5, 6, 10]
	Cheetah	✓			✓	[2]
Large carnivores	Leopard	✓	✓		✓	[2, 5, 6, 8, 10]
	African Lion	✓		✓		[1, 2, 5, 6, 8-10]
	Spotted Hyaena	✓	✓			[2, 5, 6, 8, 10]

References: 1 - Hill and Carter (1941); 2 - Huntley (1973); 3 - Huntley (1974); 4 - Crawford-Cabral and Veríssimo (2005); 5 - Rodrigues *et al.* (2018); 6 - GBIF.org (17 September 2021); 7 - (Statham, 1924); 8 - Simões-Paías (1971); 9 - Crawford-Cabral and Simões (1988a); 10 - Crawford-Cabral and Simões (1988b).

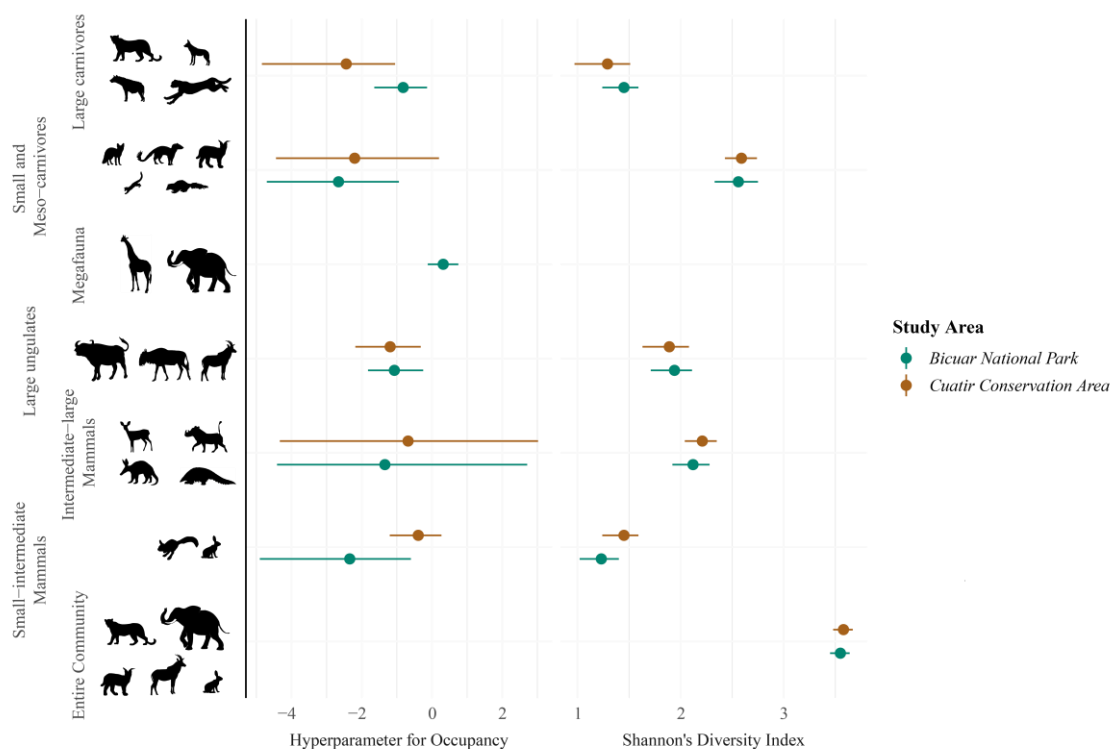


Figure 2.2 – Estimates for the occupancy hyperparameter by guild and study area, and Shannon's diversity index calculated considering the mean occupancy of each species. Diversity index was calculated for the entire community and for each guild independently, for the BNP's and CCA's mammal community.

We found mammal species richness decreased significantly in BNP and CCA compared to historical records. In BNP, we only detected 61% (25 out of 41) and in CCA, 54% (15 out of 28) of mammal species with known historical distribution (Table 2.1). The African savannah elephant (*Loxodonta africana*; hereafter elephant) was the only megafauna species detected, solely in BNP. Large ungulate species were present in

43% (3 out of 7) historically occurring in BNP and 33% (2 out of 6) in CCA. Cape buffalo (*Syncerus caffer*), plains zebra (*Equus quagga*), blue wildebeest (*Connochaetes taurinus*), and hartebeest (*Alcelaphus buselaphus*) were not detected. We found 60% (3 out of 5) of historically occurring large carnivore species in BNP, while CCA only had one, the African wild dog (Appendix 2: Table S.2.1). The presence of cheetah and leopard (*Panthera pardus*) in CCA is not described in historical records.

Among intermediate-large mammals, 60% (6 out of 10) were recorded in BNP and 66% (6 out of 9) in CCA. Four species in BNP and three in CCA were not detected. Bushpig (*Potamochoerus larvatus*) was detected in CCA, which was not previously documented historically. In both study areas, 75% (12 out of 16) of small and meso-carnivores were detected, and all seven species with known historical occurrence in CCA were found. Several species in this guild were present in both study areas, including bat-eared fox (*Otocyon megalotis*) and miombo genet (*Genetta angolensis*), which were not historically described to occur in CCA. Only one species of small-intermediate mammals was historically documented, and we confirmed its presence, reporting three additional species whose distribution had not been previously documented.

Despite sharing many species, occupancy rates varied within and between guilds among BNP and CCA. Our results revealed a slightly higher value for the occupancy hyperparameter of larger species guilds in BNP and of smaller species in CCA (Fig. 2.2 and 3; Appendix 2: Table S.2.4). Accordingly, species-specific occupancy results show that larger species are relatively common in BNP and rare or even not detected in CCA (e.g. leopard ($\hat{\Psi}_{BNP} = 0.33[0.23; 0.43]$ vs. $\hat{\Psi}_{CCA} = 0.19[0.10; 0.29]$) and wild dog ($\hat{\Psi}_{wild\ dog} = 0.22[0.14; 0.31]$ vs. $\hat{\Psi}_{CCA} = 0.03[0.01; 0.08]$; (Fig. 2.3; Appendix 2: Table S.2.5 and Fig. S.2.1)). Contrarywise, smaller species tended to exhibit lower occupancy rates in BNP than in CCA, for instance, steenbok ($\hat{\Psi}_{BNP} = 0.03[0.01; 0.07]$ vs. $\hat{\Psi}_{CCA} = 0.77[0.67; 0.86]$), or side-striped jackal ($\hat{\Psi}_{BNP} = 0.03[0.01; 0.08]$ vs. $\hat{\Psi}_{CCA} = 0.52[0.40; 0.64]$; Fig. 2.3; Appendix 2: Table S.2.5 and Fig. S.2.1). Duiker is the most common species in both study areas ($\hat{\Psi}_{BNP} = 0.91[0.85; 0.96]$ vs. $\hat{\Psi}_{CCA} = 0.93[0.85; 0.98]$).

We found a general pattern of higher occupancy of species with unfavorable conservation status in BNP than in CCA (Fig. 2.3). This is illustrated by the endangered African wild dogs and elephant, or by the vulnerable leopard, pangolin, and cheetah (Fig. 2.3; Appendix 2: Table S.2.5 and Fig. S.2.1).

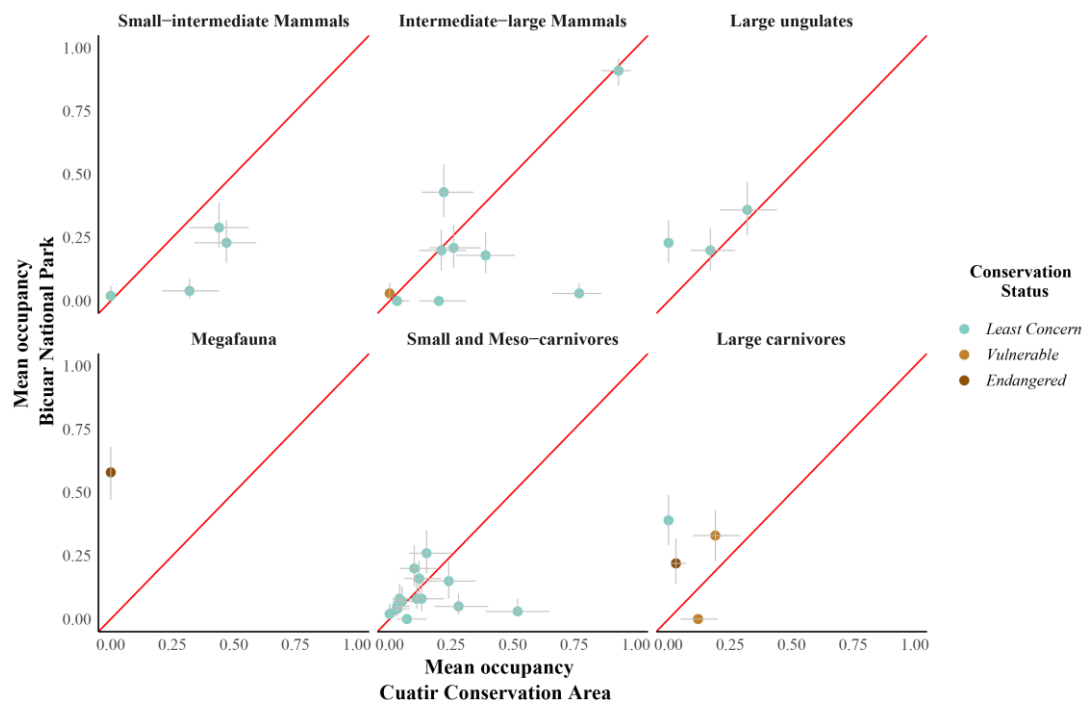


Figure 2.3 - Comparison of the median occupancy probability and the respective 95% Posterior Credible Intervals in BNP and CCA. Points above the red line indicate higher occupancy in BNP, while points below the red line represent higher occupancy in CCA. Species are distributed by guild: (1) small mammal, non-carnivore mammals with <10 kg body mass; (2) intermediate mammals, solitary or small-group living non-carnivore mammals with >10 and <100 kg body mass; (3) large mammals, gregarious herbivores with >100 and <1000 kg body mass; (4) Mega fauna, herbivores with >1000 kg body mass; (5) small carnivores, mammals from the order carnivora with <20 kg body mass; and (6) large carnivores, mammals from the order carnivora with >20 kg body mass; and by the conservation status from IUCN (IUCN, 2021).

2.5 Discussion

The effectiveness of PAs is keystone for the conservation of species and habitats (Watson *et al.*, 2014, Lindsey *et al.*, 2017, von Staden *et al.*, 2022). However, the effects of poaching (Vinks *et al.*, 2020), habitat loss (Wegmann *et al.*, 2014), armed conflicts, and/or abandonment (Gaynor *et al.*, 2016) have played a relevant role towards the negative trend of wildlife populations numbers observed across multiple PAs (Craigie *et al.*, 2010, Scholte, 2011). Wildlife declines have been particularly pronounced in countries and/or areas that experienced armed conflicts, as consequences for wildlife communities linger over decades (Gaynor *et al.*, 2016, Daskin and Pringle, 2018, Hanson, 2018). Here, we document the reduction in species richness in Southern Angola since before the civil unrest (Huntley, 1973, 1974). While some of the likely lost species, such as the African lion, have unfavorable conservation status (IUCN (2021), we also report the likely loss of non-threatened species, such as impala or oribi. The

ecological consequences resulting from changes in the diversity, demography, and behavior of species in post-conflict zones have been sporadically documented in PAs (Daskin *et al.*, 2016, Ripple *et al.*, 2016b) but remain largely unknown in non-protected land. Our results suggest similar biodiversity levels in the protected and non-protected area, but different community structures. Regarding community composition, both areas exhibit a relatively intact small and intermediate-sized mammal guilds, but BNP retains a more complex community of larger species. Yet, contemporary larger species guilds are very incomplete compared to historical records, and, although there is no prior knowledge or any kind of ecological benchmark to contextualize occupancy rates, the occupancy estimates are rather low.

Our results agree with our expectation of an important loss of wildlife (H1), as we report the loss of nearly a third of the mammal community from BNP and about half in CCA. Contemporary levels of biodiversity in Angola have been claimed to be a consequence of war and wildlife exploitation to finance warfare (Chase and Griffin, 2011, Huntley, 2017, Braga-Pereira *et al.*, 2020a). Furthermore, renewed access to previously unsafe and remote areas facilitated human intrusion, further contributing to dampen biodiversity levels (Petracca *et al.*, 2019, Braga-Pereira *et al.*, 2020b). War-driven decreases in species richness have been reported in other systems (e.g. Gaynor *et al.*, 2021b). For example, Gorongosa National Park lost 36% (6 in 17) of the species known to occur before the war (Tinley, 1977, Dunham, 2004).

Species loss was more pronounced for larger than for smaller species, since intermediate and smaller species accounted for ca. 80% of both contemporary communities (78% in BNP and 83% in CCA). The representativeness of smaller-species guilds for the broader community composition has increased relative to the historical composition because of local extinctions in larger-species guilds. Larger species are usually the prime target for hunting (Lindsey *et al.*, 2013) and human-wildlife conflict (Sharma, Chettri and Wangchuk, 2021). Moreover, their longer life cycles which hinders population recovery. Our results are consistent with studies elsewhere in Angola (Taylor *et al.*, 2018, Braga-Pereira *et al.*, 2020b) and other countries recently recovering from civil unrest (Lindsell, Klop and Siaka, 2011, Gaynor *et al.*, 2021b), which report a disproportionally high contribution of smaller-sized species in wildlife communities.

Although the reactivation of PAs aimed at reclaiming wildlife, we found similar biodiversity levels in CCA and BNP, which contradicts our hypothesis of higher biodiversity levels inside PAs (H2) (e.g. Gray *et al.*, 2016). Our results suggest that the efficacy of PAs may be hampered by inadequate or limited management, a pattern also

found in other landscapes where inefficient management has been identified as the main driver for reduced levels of biodiversity protection (Western, Russell and Cuthill, 2009).

Consistently with our hypothesis H3, we found higher biodiversity and occupancy rates for small and intermediate-sized species in CCA, while the opposite pattern was found for larger species. Similar patterns have been described in other landscapes across Africa such as in Gorongosa National Park (Mozambique) (Easter, Bouley and Carter, 2019, Gaynor *et al.*, 2021b) and in the Ngamiland District of northern Botswana (Rich *et al.*, 2016). These patterns highlight the importance of PAs as strongholds for larger species (Pacifici, Di Marco and Watson, 2020), while smaller species may find safe haven outside PAs, where competition with dominant competitors and predation pressure are lower (Anderwald *et al.*, 2015).

BNP tended to retain higher occupancy rates of “Vulnerable” and “Endangered”, while CCA revealed slightly higher occupancy of “Least Concern” species. Although consistent with our hypothesis H4, the lack of support for hunting activities by generals of the militias that occupied the BNP area (Huntley, 2017), might have contributed to the survival of several of the more susceptible species. Despite the presumably higher hunting pressure at CCA, we still confirmed the presence of three large sized threatened species. The low number and seasonality of wild dog detections suggest it is likely transient in the area, while leopard and cheetah appear to be resident (Monterroso *et al.*, 2020b). The fact that large carnivores are not targets of bushmeat poaching (e.g. Carter *et al.*, 2017) and also the low density and illusive nature of these species (Becker *et al.*, 2017, Yang *et al.*, 2021) in non-PAs (Lindsey *et al.*, 2013) reduce the probability of encounters between these species and poachers, which may aid their survival.

We recorded 6 and 11 new species for BNP and CCA, respectively, most of which are smaller and nocturnal species. Historical records are typically biased towards larger and diurnal species, because they relied mostly on the collection of specimens for museum collections (Hill and Carter, 1941), direct observation (Huntley, 1974) or hunting reports (Statham, 1924). Despite their absence in historical records, the presence of some species, for instance springhare, porcupine, caracal, or greater kudu, was expected based on habitat characteristics and on their respective IUCN (2021) assessments. Conversely, the presence of bushpig, bat-eared fox and miombo genet in CCA, as well as scrub hare (*Lepus saxatilis*) in both study areas was not expected, since the IUCN (2021) assessments for these species do not include any of our study areas. These documentations confirm the existence of these mammal species in areas that

have been barely explored, contributing to a more complete understanding of their distribution.

This study supports that PAs with limited management and law enforcement capacity have little effectiveness in protecting wildlife. However, they may still play an important role in the conservation of larger mammals and threatened species, since the proportion of the community composed by these species is larger than in the tested non-PA. Nevertheless, the recovery of ecosystems in areas with limited financial investment requires natural recolonization of animals. In the specific case of BNP, connectivity with other populations is severely restricted (Overton *et al.*, 2020, Tensen *et al.*, 2022) due to the surrounding habitat being extensively degraded by human and livestock encroachment (Huntley, 2017, Godlee *et al.*, 2020). Consequently, rehabilitation without human intervention is unlikely.

We also highlight that relatively pristine non-protected landscapes may retain high wildlife biodiversity levels and be cornerstone for conservation at the broader scale. Consequently, policies should be taken to preserve these systems, preventing habitat destruction (von Staden *et al.*, 2022), prevent further depletion of biodiversity outside protected areas (Western *et al.*, 2009, Gray *et al.*, 2016) and ensuring connectivity and the recovery of wildlife in these areas (Thapa *et al.*, 2021). Well preserved non-PAs that retain sustainable mammals populations may be cornerstone for the rehabilitation of the ecosystems and ecological processes from disrupted protected areas in contexts of little investment. These areas may be a source of animals and allow the connectivity with other populations, facilitating natural recolonizations. Future research should focus on the potential for restoration of natural areas that suffered severe declines in wildlife communities, namely in identifying extant wildlife hotspots and ecological corridors that can enhance the connectivity between wildlife populations and promote the recovery of ecosystem processes and services.

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Chapter 3

Updated ranges of the Vulnerable cheetah and Endangered African wild dog in Angola

Pedro Monterroso, **Filipe Rocha**, Stefan van Wyk, Telmo António, Milcíades Chicomo, Selma Kosmas, Fernanda Lages, Ezequiel Fabiano, & Raquel Godinho (2020). *Oryx* 54, 851–853. doi: 10.1017/S0030605319000966

3.1 Abstract

The civil unrest that ravaged Angola for nearly 30 years took a heavy toll on the country's wildlife, and led to a lengthy absence of reliable information for many threatened species, including the cheetah (*Acinonyx jubatus*) and African wild dog (*Lycaon pictus*). Using camera trapping we assessed the status of these two species in two areas of southern Angola, and complemented our findings by reviewing recent survey reports and observations to provide an update on the species' status. We found unequivocal evidence that African wild dogs are resident and reproducing in Bicuár National Park, where cheetahs appear to be absent. Conversely, cheetahs may be resident in western Cuando-Cubango province, where African wild dogs may only be transient. Based on these and other recent records in Angola, we recommend a revision of these species' distribution ranges and note the need for monitoring of these remnant populations and for appropriate attention to any threats.

Keywords: *Acinonyx jubatus*, *Lycaon pictus*, Distribution, Angola, Conservation status, southern Africa

Despite Angola's high biodiversity, the political unrest during 1975–2002 took a heavy toll on its wildlife, which suffered from widespread poaching and bushmeat hunting (Huntley, 2017). Although little is currently known about the status and trend of most Angolan wildlife populations, iconic and threatened species such as the cheetah (*Acinonyx jubatus*) and African wild dog (*Lycaon pictus*) are presumed to have suffered drastic declines and range contractions (Woodroffe and Sillero-Zubiri, 2012, Durant *et al.*, 2015). However, the Angolan government has recently shown signs of political will to improve knowledge of the country's biodiversity, including for the large carnivore species.

Globally, the African wild dog and cheetah are categorized as Endangered and Vulnerable, respectively, on the IUCN Red List because of population declines, range loss and the fragmentation of populations (Woodroffe and Sillero-Zubiri, 2012, Durant *et al.*, 2015). Although historical records indicate that both species formerly occurred widely in Angola (Beja *et al.*, 2019) the majority of the country is currently classified as unknown range for both species Fig. 3.1; IUCN/SSC, 2015). Updated knowledge about the

distribution, abundance and population dynamics of both species, and any threats, is required for conservation planning.

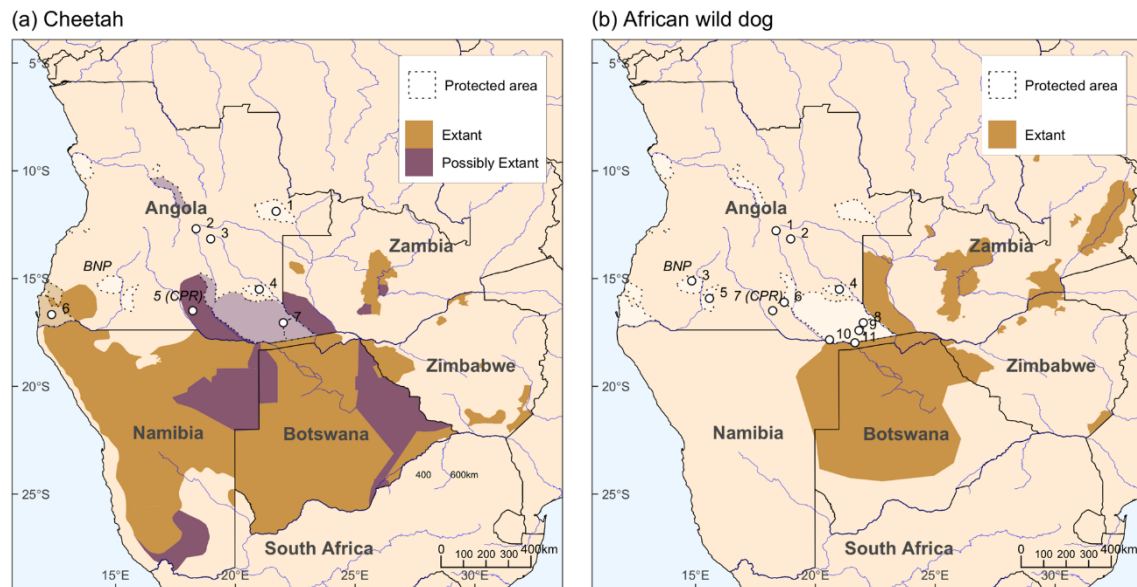


Figure 3.1 - Distribution status (IUCN/SSC, 2015) of (a) the cheetah *Acinonyx jubatus* in Angola, Namibia, Zambia, Zimbabwe and Botswana (Durant *et al.*, 2015), and of recent (2008–2018) records in Angola (1, Purchase *et al.* (2007); 2,3, Taylor *et al.* (2018); 4,7, Funston *et al.* (2017); 5, this study; 6, Marker, Fabiano and Nghikembua (2010); Bruce Bennett, pers. obs., 2017), and (b) the African wild dog *Lycaon pictus* in Angola, Namibia, Zambia, Zimbabwe and Botswana (Woodroffe and Sillero-Zubiri, 2012), and recent (2008–2018) records in Angola (1, BP Geological survey team, pers. obs., 2009; 2, Taylor *et al.* (2018); 3, this study, Overton *et al.* (2017), Fabiano *et al.* (2017); 4,8, Funston *et al.* (2017); 5, Overton *et al.* (2017); 6, John Mendelsson, pers. obs., 2012; 7, this study; 9–11, Verissimo (2008). Study sites: BNP, Bicular National Park and CPR, Cuatir.

Under the scope of ongoing institutional research and advanced training programmes, we surveyed c. 360 km² in Bicular National Park, which lies in the transition between the Angolan Miombo Woodlands and Zambezian *Baikiaea* woodlands ecoregions (Olson *et al.*, 2001) in the province of Huíla, and c. 300 km² in Cuatir Private Reserve in western Cuando-Cubango province, along the Cuatir river, one of the main tributaries of the Cubango (Okavango) river on its Angolan side, also in the Zambezian *Baikiaea* woodlands ecoregion (Olson *et al.*, 2001).

We deployed camera-trapping stations uniformly spaced at c. 2 km in the core of each study area using three camera-trap models: Hyperfire HC600 and HF2X Hyperfire 2 (Reconyx, Holmen, USA), and Cuddeback Model 1231 (Cuddeback, De Pere, USA). Fifty-one camera traps were deployed in Bicular National Park during July 2017–June 2018 (Appendix 3: Fig. S.3.1), and 43 traps in Cuatir Private Reserve during June–December 2018 (Appendix 3: Fig. S.3.2). Cameras were inspected every 2 months.

Additional records were obtained in Cuatir Private Reserve from unstructured surveys with six camera traps (Moultrie MP8, EBSCO Industries Inc., Birmingham, USA) during August 2013–December 2018. Additional recent records of the cheetah and African wild dog in Angola were obtained by reviewing surveys reports and the Global Biodiversity Information Facility database (GBIF, 2019, Purchase *et al.*, 2007, Veríssimo, 2008, Marker *et al.*, 2010, Fabiano *et al.*, 2017, Funston *et al.*, 2017, Overton *et al.*, 2017, Taylor *et al.*, 2018). We considered as independent any camera-trapping detections within 30 minutes, unless animals were unambiguously identified (Rich *et al.*, 2017a).

In Bicular National Park we recorded 16 independent detections of two African wild dog groups over a total of 14,232 trapping-days. We were able to assign 15 individuals to one group and three to the other. African wild dogs were detected consistently throughout the sampling period at a mean detected group size of $3.6 \pm \text{SD } 2.6$. No cheetahs were detected.

In Cuatir Private Reserve we obtained 13 independent detections of at least two cheetah individuals and no detections of African wild dogs over a total of 5,173 trapping-days of systematic surveying. Unstructured camera trapping provided records of an individual cheetah in July 2014, and a coalition of two male cheetahs in October 2017. We were not able to match any of these cheetahs with those of the 2018 survey. A group with ≥ 4 African wild dog individuals was detected in July, August and October 2014, and another of ≥ 5 individuals in October 2016.

Our findings build on recent surveys that indicate the occurrence of cheetahs and African wild dogs in Luengue-Luiana and Mavinga National Parks (Funston *et al.*, 2017), and in the Cuanavale and Cuito river catchments (Taylor *et al.*, 2018; Fig. 3.1). African wild dogs have also been observed in Bicular National Park by Overton *et al.* (2017) and Fabiano *et al.* (2017), Mupa NP (Overton *et al.*, 2017) and Mucusso reserve (Veríssimo, 2008), and cheetahs in and around Iona and Cameia National Parks (Purchase *et al.*, 2007). We found no records of cheetahs or African wild dogs for 2008–2018 in Angola in the Global Biodiversity Information Facility (GBIF, 2019).

Our findings indicate that the African wild dog's range as currently delimited (IUCN/SSC, 2015), should be extended c. 750 km further west-north-west from the Angolan/Namibian border, beyond the Cunene river and including Bicular National Park. As the species has been regularly detected in the Park since at least 2015, this complies with IUCN/SSC (2015) criteria as an area of African wild dog residency, with groups of ≥ 10 individuals and breeding confirmed through multiple observations of groups with pups, made by park rangers in 2016 (Fabiano *et al.*, 2017, Overton *et al.*, 2017). It is likely that

other large extents of good quality habitat in Angola also harbour resident populations, and further monitoring to assess presence and residency status are required. Cheetahs have been observed regularly in the lower Angolan range of the Cubango river, and also in south-eastern, south-western and central-eastern Angola in the provinces of Namibe, Cuando-Cubango and Moxico (Marker *et al.*, 2010, Funston *et al.*, 2017, Taylor *et al.*, 2018; Fig. 3.1). These reports suggest that IUCN's classification of the south-western Angolan range for the cheetah should be changed from Possibly Extant to Extant.

Our findings will support the new political willingness in Angola to invest in wildlife conservation strategies and will help to unlock conservation funding for the cheetah, African wild dog and other carnivores. Given that the majority of the distribution of these two species potentially falls outside protected areas where they are more susceptible to anthropogenic threats, we emphasize the urgency of identifying remnant populations in Angola and quantifying any threats to the species.

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Chapter 4

Understanding top-down and bottom-up processes in an ungulate community to define conservation priorities in a desert environment

4.1 Abstract

Deserts are typically governed by bottom-up forces and are predicted to be further depleted of their resources, exacerbating extinction risk for local wildlife populations. Additionally, human populations living in these ecosystems are predicted to increase, exposing wildlife to additional human-induced top-down constraints and intensifying human-wildlife conflicts.

We aim to investigate how surface water availability, forage availability and other landscape factors shape the spatial arrangement of large herbivore populations in a desert region, and to explore wildlife-livestock co-occurrence patterns to inform coexistence strategies that maximize conservation outputs.

We fitted Bayesian zero-inflated binomial N-mixture models (Kéry and Royle 2015) to group count data collected over a 4-year period in the northern Namib desert (Iona National Park, Angola), and found that Hartmann's mountain zebra and gemsbok preferentially forage in suboptimal low productivity flat areas, away from human activities. Conversely, springbok preferentially occurred in more productive and relatively rugged terrain. We also found a reliance of Hartmann's mountain zebra on natural water sources ($\beta_{DistWater} = -1.04 \pm 0.26$ and $\beta_{DistWater} = -0.77 \pm 0.20$, for dry and wet seasons, respectively), and a weaker reliance by gemsbok ($\beta_{DistWater} = 0.20 \pm 0.10$ and $\beta_{DistWater} = -0.15 \pm 0.10$, respectively for dry and wet seasons). Conversely, we found springbok to forage further from available water ($\beta_{DistWater} = 0.43 \pm 0.05$ and $\beta_{DistWater} = 0.26 \pm 0.06$, for dry and wet seasons, respectively), suggesting this species may be able to balance hydric requirements from dietary water.

Our results support that human activities (inc. livestock herding) induce broad scale top-down regulation in landscape use by our target species, which are then susceptible to resource-driven bottom-up forces at a finer scale. These constraints reflect differences between the realized and expected conservation value of Iona National Park, because human-occupied areas force wildlife to suboptimal habitats. Additionally, we found significant stretches of the landscape to be co-occupied by wildlife and livestock, increasing competition for already limited resources.

Our results are useful for informing conservation actions, namely through protected area zonation. Securing exclusive access to key resources by wildlife could be of utmost importance to ensure the long-term survival of these species, and to foster sustained human-wildlife coexistence.

Keywords: Bottom-up regulation; Surface water dependency; Hartmann's mountain zebra; Human-wildlife coexistence; climate change; Namib desert

4.2 Introduction

Deserts are defined as “any area of land that receives less rain than it loses through evaporation and transpiration”, and such areas occupy one third of the earth’s land surface (Purcell, 2018). Hot deserts are particularly challenging for local wildlife populations because of rainfall unpredictability (Ward, 2016), albeit their extreme conditions facilitate biodiversification and speciation (Brito *et al.*, 2014), generating endemic species (Brito and Pleguezuelos, 2019, Gurera and Bhushan, 2020). The current climate change scenario is expected to have dramatic effects on desert biomes, mostly due to an above-average increase mean temperature and, more importantly, by changing precipitation patterns, which are expected to become less frequent but with more extreme events (Thomas and Nigam, 2018, U. N. Environment, 2019). These changes could have profound effects on the conservation of desert-dwelling species, many of which already occur at suboptimal conditions and/or have unfavourable conservation status (Vale and Brito, 2015, Fuller *et al.*, 2016, Thomas and Nigam, 2018, Brito and Pleguezuelos, 2019).

Body fluid homeostasis is achieved through a trade-off between water intake and prevention of water loss. Either of these processes can be made efficient through ecological, behavioural and physiological adaptations each species has developed, hence shifting the relative importance of drinking for their fitness and survival. Water dependency, i.e. the total amount of water intake needed to maintain fluid homeostasis, is achieved through a combination of surface water and dietary water consumption, and by balancing water loss (Fuller *et al.*, 2016). Desert-adapted species developed different strategies to prevent water loss, despite potentially having different drinking needs (Kihwele *et al.*, 2020). From a physiological perspective, ungulates adapted to dry environments developed compensatory mechanisms to prevent the reduction of plasma fluid and circulatory failure by taking water from the rumen and other body tissues, and by reducing their basal metabolic rate (Cain III *et al.*, 2006, Boyers *et al.*, 2019, Kihwele *et al.*, 2020). From a behavioural perspective, when predation risk and/or competition are not sufficient to constrain behavioural decisions (Sirot, Renaud and Pays, 2016, Veldhuis *et al.*, 2020), herbivores tend to coincide their activity peaks with the coolest times of the day (Nagy and Knight, 1994, Cain III *et al.*, 2006, Boyers *et al.*, 2019) and

to use the shade of trees and shrubs, which offer cooler microenvironments (Boyers *et al.*, 2019).

The scarcity of food and water typical of deserts suggests that wildlife communities should be mainly governed by bottom-up processes, i.e., constrained by resource availability. However top-down forces, mostly mediated by predators and humans may also play an important role in wildlife dynamics (Meserve *et al.*, 2003, Hopcraft *et al.*, 2010). The optimal foraging theory (OFT) postulates that animals maximize fitness by adopting foraging strategies that provide the most benefit (energy) for the lowest cost (Pyke *et al.*, 1977). However, environmental constraints (e.g. predation risk) can shape animals' ability to maximize their access to resources, hence the optimal decision rule becomes the one that maximizes caloric intake under the constraints of the environment (Sinervo, 1997). Under these assumptions, one would expect a species' spatiotemporal patterns of landscape use to be the result of behavioral decisions made over three processes: i) necessity or level of requirement of a given resource, ii) accessibility and iii) relative risk of accessing that resource. Therefore, optimal foraging in a given landscape is only achieved if top-down constraints are not efficiently imposed, or if the resource in question is of vital importance such that animals have no choice but to expose themselves to high risk situations in order to access it (Lima and Bednekoff, 1999, Valeix *et al.*, 2009, Thaker *et al.*, 2011).

The shared use of natural landscapes by wildlife and humans in natural systems adds additional top-down pressures on the former, namely on herbivores, which are often targeted for trophy and/or bushmeat hunting (Vinks *et al.*, 2020). Therefore, humans impose a super-predator effect on wild populations, and its influence exacerbates already existing constraints posed by natural top-down forces (Darimont *et al.*, 2015, Smith *et al.*, 2017), potentially inducing changes in space use (Gaynor *et al.*, 2021c), diel activities (Gaynor *et al.*, 2018) and behaviour of wildlife populations, ultimately affecting its fitness and population trends (Tablado and Jenni, 2017).

Deserts are frequently inhabited by human populations, which frequently subsist on livestock herding. If the human presence *per se* may be a limiting factor for some wild species (Wilson and Mittermeier, 2011, Tablado and Jenni, 2017), it poses additional negative effects for wildlife when associated with livestock. The scarcity of fundamental resources, such as food and water, and the demand of livestock to access them, increase interspecific competition with wildlife (Prins, 2000).

Here we investigate how surface water dependency and forage availability shapes the local abundance and space use by wild and domestic herbivores in a desert environment and how the availability of these resources could inform conservation strategies. Particularly, we aim to identify the co-occurrence patterns between wild and domestic species and define the most important areas for wildlife in a landscape shared with human and livestock. We expect a pattern by which species with higher surface water dependency exhibit constrained distribution patterns, mainly clustered near water sources. Conversely, species able to fulfil their water requirements through foraging activities should have their spatial distribution mainly constrained by the availability of high-quality vegetation. We further hypothesize that human-mediated top-down effects could limit the access of wildlife to otherwise suitable areas. The spatial configuration of limited resources should shape the distribution not only of wild ungulates but also of livestock, potentially leading to conflicts over limited resources.

4.3 Methods

4.3.1 Study area

The Iona National Park (INP) is located in the Namib desert, southwest Angola (N: -15° 43' 31"; E: 11° 44' 06" to N: -17° 17' 17"; E: 13° 20' 29") (Appendix 4: Fig. S.4.1). The Namib is classified as a hot arid desert (Beck *et al.*, 2018) hosting multiple endemic species (Gurera and Bhushan, 2020). INP ranges over ca. 15000 km², from the sea level at the Atlantic coast to a rugged 2041 m.a.s.l. in the eastern part. INP receives a mean annual rainfall of 82.1 mm (<http://www.sasscalweathernet.org/index.php>), which plays a fundamental role for vegetation growth (Li *et al.*, 2016). Water is also available as night fog and dew, originated from the ocean (Mendelsohn and Mendelsohn, 2018, Wang *et al.*, 2019).

INP is divided in three main habitats: i) mobile sand dunes, broadly at the northwest; ii) arid savannah, occupying the central plains; and iii) mountainous bushland and dry mopane forests, mostly at the east and at higher elevations (Appendix 4: Fig. S.4.1 C). Several species of meso and large herbivores occur, of which the most iconic are the springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazella*) and Hartmann's mountain zebra (*Equus zebra hartmannae*; hereafter zebra). The INP zebra population is threatened by hybridization with domestic donkeys (*Equus asinus*), where phenotypically-identified zebra-donkey hybrids (zonkeys) are estimated to account for ca. 5% of the zebra population and dwell together with its wild ancestor (Chicomo, 2021).

In fact, zonkeys comprise individuals of all age classes, suggesting that the interbreeding is a continuous and ongoing process (Chicomo, 2021). Other species include steenbok (*Raphicerus campestris*), dik-dik (*Madoqua kirkii*), black-faced impala (*Aepyceros melampus petersi*) and greater kudu (*Tragelaphus strepsiceros*), but with limited distributions. Large mammalian carnivores include cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*) and brown hyaena (*Parahyaena brunnea*).

Several villages are enclosed within INP boundaries and surroundings at the northeast to southeast, where ca. 3300 people live. Most villagers belong to the OvaHimba tribe, leading a semi-nomadic life, highly dependent on livestock herding. Although they use settlements, herders make seasonal movements with the livestock in search of the grazing areas and water (Mendelsohn and Mendelsohn, 2018). There are 15,000 cattle and 31,800 goats inside INP borders (De Cauwer and Lages, 2018).

4.3.2 Target species

Our target species are the springbok, gemsbok and zebra, three ungulate species which have the Namib desert of SW Angola as the northwesternmost limit of their range (IUCN SSC Antelope Specialist Group, 2016a, b, Gosling *et al.*, 2019). Mountain zebras are currently classified as “Vulnerable” due to population fragmentation, habitat loss, poaching and sensitivity to droughts (Gosling *et al.*, 2019). The zebra population in INP is geographically isolated (Gosling *et al.*, 2019) and their numbers are low (ca. 480 individuals; Chicomo 2021). Despite being classified as “Least Concern” (IUCN SSC Antelope Specialist Group, 2016a, b), gemsbok and springbok populations also suffered significant declines during the Angolan civil war, with important ecosystem-level consequences as they constitute the staple prey for large carnivores (Durant *et al.*, 2015, Wiesel, 2015, Stein *et al.*, 2016). Springbok and gemsbok abundance in INP is unknown.

4.3.3 Animal counts

Wildlife and livestock observation data were collected opportunistically during daily activities of the INP manager, from a four-wheel drive vehicle during daytime between October 2013 and September 2017. Despite the absence of a systematic sampling design, all park regions were surveyed at least once per month. Transect tracks were systematically recorded using a Garmin Montana 680 GPS Unit, as a measure of survey effort. All animal sightings were recorded, including geographic coordinates, time, species and group size. The INP area was divided into a 5 km × 5 km grid, to which all daily group observations and survey effort were aggregated (Appendix 4: Fig. S.4.2).

Daily survey data was classified as belonging to one of two different periods: dry season, from May to October; or wet season, from November to April (<http://www.sasscalweathernet.org/index.php>).

4.3.4 Covariates

Bottom-up related covariates consisted of surface water and forage availability, whereas top-down related covariates comprised the human-induced disturbance on wildlife populations. We used the proportion of grassland cover as a surrogate for forage availability and enhanced vegetation index (EVI) as an indicator for the primary productivity. Yearly proportion of grassland cover was obtained with 100m resolution from Copernicus Global Land Service (<https://land.copernicus.eu/global/products/lc>), while EVI was derived from the MODIS – Terra Moderate Resolution Imaging Spectroradiometer, with a 250 m resolution, and obtained from NASA's EarthDATA (<https://search.earthdata.nasa.gov/>). Pixel values for these covariates were averaged within each respective 5 km × 5 km grid square. We tested for the linear and quadratic effects of EVI on species' abundance to allow identifying local maxima in resource selection. Surface water availability was estimated by calculating the Euclidean distance from each grid-square centroid to the nearest water source. We considered natural water sources (e.g., rivers and springs) for our target wildlife species, whereas artificial water sources (e.g., solar water pumps) were also considered for domestic species, since they were built in the vicinity of human settlements and livestock grazing areas.

Human-induced disturbance was estimated as the Euclidean distance from each grid-square centroid to the nearest known human settlement. Although predator presence and abundance are potential top-down constrainers (Valeix *et al.*, 2009), such data was not available.

Additional landscape configuration preferences included topographic and soil type-related features, and were considered as follows: i) mean altitude, calculated from a 90 m resolution digital elevation model (DEM), obtained from the Shuttle Radar Topography Mission Grid version 2 (SRTM) dataset at NASA's EarthDATA website (Farr *et al.*, 2007); ii) topographic ruggedness index (TRI), expressed the amount of elevation difference between adjacent cells of a DEM (Reilly, DeGloria and Elliot, 1999); iii) proportion of arenosols (i.e. sandy soils), obtained from SoilGrids classifications with 250 m resolution (Hengl *et al.*, 2017).

The species-specific covariates were chosen considering the previous knowledge of the species and the expected influence of each covariate. The covariates tested for springbok and gemsbok were distance to water, distance to human settlements, topographic ruggedness index (TRI), altitude, enhanced vegetation index (EVI) and proportion of grassland cover. For zebra, apart from the covariates considered for the other species, we also included the proportion of sandy soils. The hypothesis description, reasoning and expected responses can be found in Table 4.1. For domestic species, the tested covariates were distance to water, topographic ruggedness index (TRI) and enhanced vegetation index (EVI). All covariates were standardized to z-scores to avoid data dispersion bias and facilitate model numeric convergence (Shiffler, 1988, MacKenzie *et al.*, 2017).

Multicollinearity among continuous covariates was assessed through a nonparametric Spearman's correlation analysis using the psych R package (Revelle, 2020). Among correlated covariates ($|\rho| \geq 0.5$; Zuur *et al.* 2009), the covariate less correlated with the species abundance or for which the predicting hypothesis had less biological relevance for this study's goals was excluded from the subsequent modelling procedure.

Table 4.1 - Covariates used for the modelling, rationale and underlying hypothesis of how each covariate would influence the herbivores' landscape use.

Species	Variable	Range	Hypothesis	References
Springbok	Distance to water	0.1 – 31.4 km	Springboks are well adapted to arid environments and have low surface water dependency. We hypothesize springbok is little affected by distance to surface water sources.	Jackson, Skinner and Richardson (1993), Nagy and Knight (1994), Ritter and Bednekoff (1995), Kihwele <i>et al.</i> (2020)
	Distance to human settlements	0.8 – 83.7 km	Springboks are sensitive to human disturbance, therefore should avoid areas closer to human settlements and with higher disturbance.	Parris and Child (1979), Verlinden (1997)
	TRI	0 – 317	Springboks are a plains species. We hypothesize that they preferentially occur in the lower altitude flatter areas.	Burger, Safina and Gochfeld (2000) Kingdon (2015)
	Altitude	0 – 1802 m	As plains species, springbok should be negatively affected by altitude.	Burger <i>et al.</i> (2000) Kingdon (2015)
	EVI	Dry: 559 – 201,570 Wet: 896 – 294,544	Springboks are variable browsers; hence we hypothesize that they will use areas with higher primary productivity.	Nagy and Knight (1994), Hofmann, Knight and Skinner (1995), Hempson <i>et al.</i> (2015)
	Proportion of grassland in land cover	0 – 91 %	Springboks are variable browsers, with preference for mixed savannas with low grass; hence we hypothesize that they will use areas with relatively small grass cover.	Nagy and Knight (1994), Hofmann <i>et al.</i> (1995), Hempson <i>et al.</i> (2015)

<i>Gemsbok</i>	Distance to water	0.1 – 31.4 km	Gemsbok is well adapted to arid environments with no water dependency. However, being grazers, their ability to obtain dietary water is limited. Therefore, we hypothesize they will be more reliant on surface water than springbok, especially in dry season.	Hempson <i>et al.</i> (2015), Boyers <i>et al.</i> (2019), Kihwele <i>et al.</i> (2020)
	Distance to human settlements	0.8 – 83.7 km	Gemsbok is sensitive to human disturbance, therefore should avoid areas closer to human settlements and with higher disturbance.	Parris and Child (1979), Verlinden (1997)
	TRI	0 – 317	Gemsbok prefers stony plains but can subsist in dunes and rocky mountainous areas. Hence, they can have some tolerance to rugged areas.	IUCN SSC Antelope Specialist Group (2016b)
	Altitude	0 – 1802 m	Although adapted to plains, gemsbok may use rocky mountainous areas, especially to visit springs and salt licks	IUCN SSC Antelope Specialist Group (2016b)
	EVI	Dry: 559 – 201,570 Wet: 896 – 294,544	Gemsbok is variable grazer; therefore, we hypothesize they should use areas with relatively low primary productivity (i.e., grassland areas).	Hempson <i>et al.</i> (2015), Relton (2015)
	Proportion of grassland in land cover	0 - 91 %	Gemsbok is variable grazer; and its preferential habitat are wooded grasslands and acacia bush. Therefore, we hypothesize they should use areas with intermediate values of grassland cover.	Hempson <i>et al.</i> (2015), Relton (2015)
<i>Zebra</i>	Distance to water	0.1 – 31.4 km	Mountain zebras are highly water dependent and are grazers, which limits their ability to obtain dietary water. Therefore, we hypothesize they will be highly reliant on the proximity to surface water	Hempson <i>et al.</i> (2015), Muntifering <i>et al.</i> (2019), Kihwele <i>et al.</i> (2020)
	Distance to human settlements	0.8 – 83.7 km	Mountain zebra are highly sensitive to human activity, consequently they avoid areas with human activity.	Muntifering <i>et al.</i> (2019); Wilson and Mittermeier (2011)
	TRI	0 – 317	Although zebra may use the foothills of mountains or plateaus, are typically found in rugged, broken mountainous and escarpment areas with a rich diversity of grass species and perennial water sources.	Wilson and Mittermeier (2011) Penzhorn (2013)
	Altitude	0 – 1802 m	Zebra can use areas with low altitude, in the foot of the mountains or plateaus, so we hypothesize some flexibility of the species to the altitude	Wilson and Mittermeier (2011)
	EVI	Dry: 559 – 201,570 Wet: 896 – 294,544	Zebra is a variable grazer; therefore, we hypothesize they should use areas with relatively low primary productivity (i.e., grassland areas).	Hempson <i>et al.</i> (2015), Muntifering <i>et al.</i> (2019)
	Proportion of grassland cover	0 - 91 %	Zebras is variable grazer and use areas of grassland or in shrub communities with high biomass of grass (> 50% grass cover); therefore, we hypothesize they	Hempson <i>et al.</i> (2015), Muntifering <i>et al.</i> (2019)

		should use areas with relatively high grassland cover.	
Proportion of sandy soils	Relative frequency (0 – 1)	The foot morphology of zebras is not adapted to locomotion in soft sands. Therefore, we predict zebra distribution to be limited by soil amount of sand in the soil.	Zhang, Ding and Xu (2015) Bruce Bennett (personal experience)

4.3.5 Modelling approach

We built group count matrices on single-day sampling occasions from our drive counts. The gregarious nature of our target species makes the detection of individuals dependent, deeming the detection of an individual within a social group more likely upon the detection of another one. However, although spatially converging under certain conditions, groups of animals are statistically independent of each other, as supported by the scarcity of large group sizes (Appendix 4: Figure S.4.3). Hence encounter histories consisted of the number of groups of each species observed per day in each grid square. The set of covariates included in each species' model was defined based on our above-described *a priori* hypotheses regarding our target species' expected biological requirements (Table 4.1). We included sampling effort, defined as the total transect length, as a detection (p) covariate for all target species, under the assumption that longer sampling transects would increase the probability of group detection within a grid square. We set the minimum threshold effort of 2km/day in each grid cell for it to be considered as sampled. Therefore, cells with sampling effort lower than 2 km were discarded.

Given the overabundance of zeros in the observed counts, we fitted Bayesian Zero-Inflated Poisson binomial N-Mixture models (Kéry and Royle, 2015) to our daily observation data to estimate the maximum expected number of groups using each 5 km × 5 km grid square. We defined s_i^A as discrete random variable describing the suitability ($s_i^A = 1$) or unsuitability ($s_i^A = 0$, the zero-inflation part) of grid square i for the species A , which was modeled as a Bernoulli random variable such that:

$$s_i^A \sim \text{Bernoulli}(\phi_i^A),$$

We then defined N_i^A as discrete random variable for the abundance state of groups, which was modeled as a Poisson random variable conditional on site suitability as:

$$N_i^A \sim \begin{cases} \text{Poisson}(\lambda_i), & \text{with probability } \phi_i^A \\ 0, & \text{with probability } 1 - \phi_i^A \end{cases},$$

where λ_i is the expected group abundance (Kéry and Royle, 2015). Finally, we defined $y_{i,j}^A$ as the group counts encounter history of the species A at site i across sampling occasion j , that was modeled as a Binomial random variable

$$y_{i,j}^A \sim \text{Binomial}(N_{i,j}^A, p_{i,j}^A),$$

where $p_{i,j}^A$ denotes the probability of detecting species A at site i on occasion j , given presence. $p_{i,j}^A$ was formulated as logit-scale and the baseline detectability (α_0) was assumed to be constant between years but varied seasonally according to effort, such that:

$$\text{logit}(p_{i,j}^A) = \alpha_0 + \alpha_{1,j} * \text{effort}$$

The effects of site-specific covariates on abundance (λ^A) were formulated as log-scale parameters and year-specific baseline abundance as random intercepts such that

$$\log(\lambda_{i,k}^A) = \beta_{0,k} + \beta_1 * \text{Cov1}_i + \beta_2 * \text{Cov2}_i + \dots,$$

where $\beta_{0,k}$ denotes the log-scale baseline abundance on year k and follows a normal distribution, and $\beta_1, \beta_2, \dots, \beta_n$ denote the effect of covariates on the log expected abundance. Each season was modelled independently allowing species responses to each specific covariate to vary between dry and wet seasons.

Under this modelling framework, imperfect detection is accounted for by within-site temporal replication under the assumption that survey duration occurs within a period (one season) over which it is reasonable to assume that the number of groups is constant. However, although it is reasonable to assume demographic closure at the superpopulation level (i.e., over the total sampling area), this assumption is not met across sampling units because animals are expected to move across grid squares between sampling occasions (days). If N varies, then the variability attributed to the binomial component of the model is overstated, leading to an underestimation of p and overestimation of N . As proposed by Kéry and Royle (2015), this violation of the closure assumption is handled simply by changing the interpretation of the abundance parameter so that it describes the total number of groups ever associated to a site during the primary survey period, while the obtained detection histories predictably result from the same state process of habitat selection.

Models were fit in JAGS (version 4.3.0), executed from R (version 3.6.2; R Core Team, 2021) using R2Jags (Su and Yajima, 2015) through rjags (Plummer, 2016). We ran three

Markov Chain Monte Carlo (MCMC) chains with 100,000 iterations after a 50,000 iteration burn-in and thinned by 30. Prior distributions for each of our model parameters is presented in Appendix 4: Table S.4.1. We assessed model convergence from a visual inspection of chain trace plots and from the Gelman-Rubin statistic (i.e. R-hat), where values <1.1 suggested reliable convergence (Gelman and Rubin, 1992). Goodness-of-fit was assessed by calculating the Bayesian p-value (BPV, Gelman et al. 1996) and by visual inspection of the distribution of residuals, whereas overdispersion was evaluated using the overdispersion parameter (i.e. c-hat) (Kéry and Royle, 2015). The relative importance of each covariate was assessed by inspecting the probability posterior distribution of corresponding coefficients. All results are presented as mean [95% Posterior Credible Intervals], unless explicitly stated otherwise.

The outputs of our species-specific models were used to calculate the expected local group abundance across the landscape as derived from the posterior predictive mean, whereby the estimated value is conditional on the data, but prediction is made via parameter effects. These predictions were then combined to achieve an estimation of realized conservation value, i.e., the most important areas for our set of target wild species given their expected distribution under the actual conditions. The cell-specific realized conservation value was calculated by integrating the expected abundance of the target species following:

$$Realized\ Conservation\ Value = 1 - \prod_{A=1}^k \left(1 - \frac{\lambda^A_i}{\lambda^A}\right),$$

Where k is the number of target species considered, λ^A_i is the expected abundance of the species A at site i , and λ^A is the maximum local abundance of the species A . This metric ranges from '0', corresponding to areas not expected to be used by any of our target species, to '1' in areas where the predicted abundance is the highest for at least one of the target species. Prediction maps were downscaled to a resolution of 250 meters for graphical representation purposes through spatial interpolation from grid cell centroids. Likewise, co-occurrence probability between wild animals and livestock was calculated for dry and wet season by multiplying the standardized expected abundance of wildlife and livestock, calculated following the same equation used to estimate realized conservation value. The values for the co-occurrence range from '0', when the expected abundance of one or both groups is 0; to '1', when the expected abundance for both groups is the highest. We defined as areas of likely co-occurrence those with the 25% highest co-occurrence probability. This threshold provided a reliable representation of

the expected co-occurrence based on our field experience and knowledge of the study area.

4.4 Results

We obtained a total of 4,666 observations of 23 wildlife species (Appendix 4: Table S.4.3). A total of 2,507 observations were groups of springboks ($n_{dry} = 1,498$; $n_{wet} = 1,009$); 1,447 groups of gemsboks ($n_{dry} = 733$; $n_{wet} = 714$); and 202 groups of zebras ($n_{dry} = 114$; $n_{wet} = 88$) (Appendix 4: Table S.4.3). Out of 1,899 livestock observations 1,004 were groups of cattle ($n_{dry} = 650$; $n_{wet} = 354$); 535 were groups of sheep and goats ($n_{dry} = 351$; $n_{wet} = 184$); and 360 were groups of donkeys ($n_{dry} = 175$; $n_{wet} = 185$).

Among the target wild species, gemsbok was the species with the smallest group sizes (presented as median [quantiles 2.5%, 97.5%]): $\tilde{x}_{dry} = 2$ [1; 46]; $\tilde{x}_{wet} = 2$ [1; 46]), whereas zebra exhibited the largest ($\tilde{x}_{dry} = 5$ [1; 16]; $\tilde{x}_{wet} = 5$ [1; 19]). Springbok exhibited intermediate median group size values, although occasionally occurring in much larger groups ($\tilde{x}_{dry} = 3$ [1; 69]; $\tilde{x}_{wet} = 4$ [1; 100], Appendix 4: Fig. S.4.3). The most frequent observations (mode) of springbok and gemsbok consisted of a single individual ($Mo_{dry} = 1$ and $Mo_{wet} = 1$), while the most common group size for zebra was $Mo_{dry} = 4$ and $Mo_{wet} = 5$, respectively for dry and wet seasons. Among domestic species, the smallest group size was exhibited by donkeys ($\tilde{x}_{dry} = 2$ [1; 8]; $Mo_{dry} = 2$; $\tilde{x}_{wet} = 3$ [1; 16]; $Mo_{wet} = 2$), followed by cattle ($\tilde{x}_{dry} = 15$ [2; 85]; $Mo_{dry} = 8$; $\tilde{x}_{wet} = 15$ [1; 101]; $Mo_{wet} = 3$). Sheep & goats were the species with the largest herds ($\tilde{x}_{dry} = 50$ [4; 300]; $Mo_{dry} = 50$; $\tilde{x}_{wet} = 60$ [3; 250]; $Mo_{wet} = 50$; Appendix 4: Fig. S.4.3).

Annual variation of baseline abundance varied with species: it was relatively constant for zebra (between 1.2 and 1.6 groups/cell), gemsbok (between 1.5 and 2.5 groups/cell) and domestic species (between 1.2 and 2.2 groups/cell). However, it exhibited higher variation (between 13.2 and 49.0 groups/cell) for springbok (untransformed values in Appendix 4: Table S.4.4).

4.4.1 Landscape effects on wildlife spatial abundance

The exploratory analysis showed multicollinearity among some of the suggested covariates, of which EVI, distance to water, TRI and proportion of sand were retained for subsequent analyses (detailed information in Appendix 4: Appendix 4.1).

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All models for zebra and for livestock (except for cattle in the dry season) presented a good goodness-of-fit, with BPV values ranging from 0.37 to 0.48. The models for springbok ($BPV_{dry} = 0.19$; $BPV_{wet} = 0.06$), gemsbok ($BPV_{dry} = 0.24$; $BPV_{wet} = 0.18$) and cattle ($BPV_{dry} = 0.18$; Appendix 4: Table S.4.4) exhibited low BPVs, suggesting model lack-of-fit. However, upon visual inspection of their residuals, the apparent lack-of-fit revealed to be unstructured noise due to the large variance, common in count data (Kéry and Royle, 2015). All models revealed a c-hat of ca. 1 (Appendix 4: Table S.4.4).

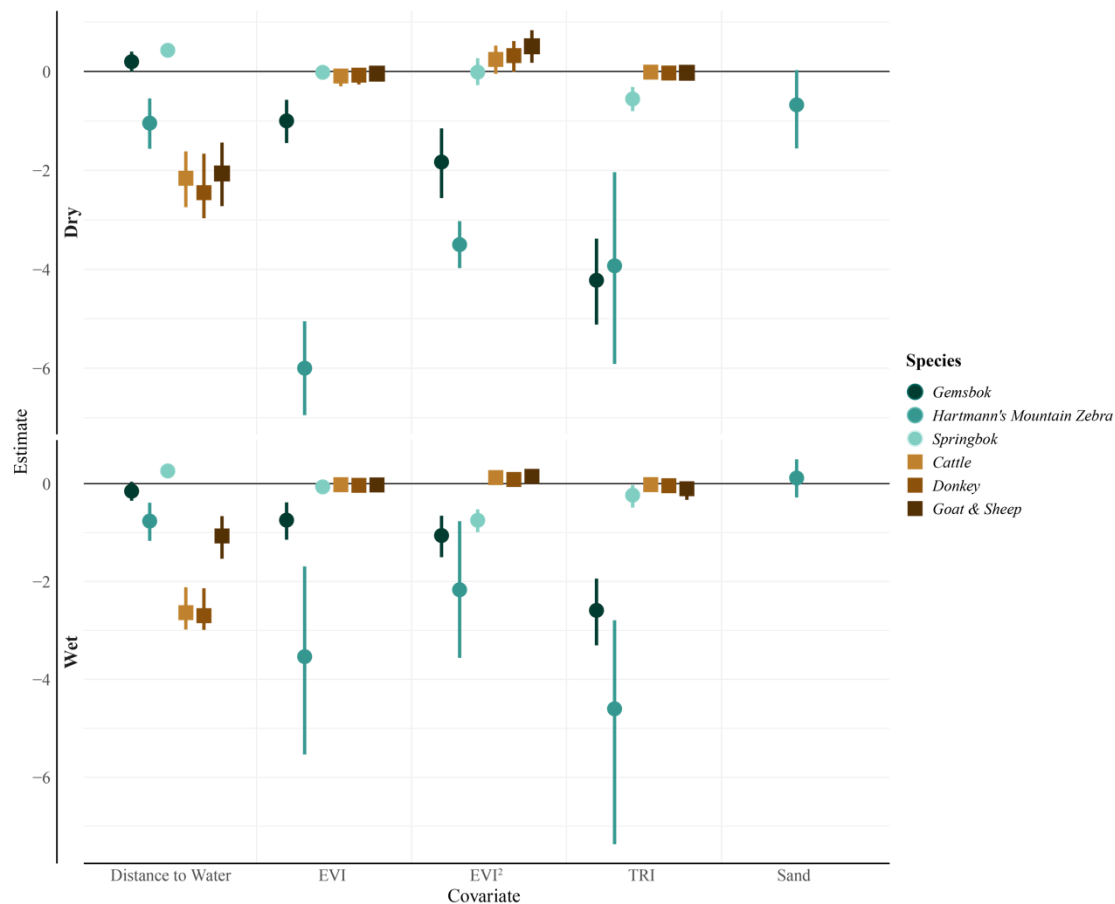


Figure 4.1 - Covariate effects with respective 95% posterior credible intervals on the log abundance of target wildlife species (round dots) and livestock (square dots) during dry and wet seasons, as obtained from our modelling results. Distance to water - Euclidian distance from cell centroid to the nearest natural water source; EVI - Enhanced Vegetation Index, a proxy for food availability; TRI - topographic ruggedness index; Sand - proportion of sand in the soil.

Distance to the nearest natural water source revealed a strong and consistent negative effect on the abundance of zebra groups across seasons ($\hat{\beta}_{dry} = -1.04 [-1.56; -0.55]$; $\hat{\beta}_{wet} = -0.77 [-1.17; -0.39]$; Figs. 4.1 and 4.2), supporting a tendency to remain closer to water sources. Conversely, we found the inverse pattern for springbok groups, which were positively correlated with distance to natural water sources, a relationship that was particularly strong during the dry season ($\hat{\beta}_{dry} = 0.43$ $CI_{95}: [0.32; 0.53]$; $\hat{\beta}_{wet} = 0.26 [0.15; 0.37]$; Figs. 4.1 and 4.2). Similar to springboks, gemsbok groups also responded positively to distance to natural water during dry season ($\hat{\beta}_{dry} = 0.20 [-0.01; 0.40]$), although the strength of this effect was considerably smaller. During wet season, gemsbok group abundance was negatively influenced by distance to water ($\hat{\beta}_{wet} = -0.15$ $CI_{95}: [-0.35; 0.04]$; Figs. 4.1 and 4.2).

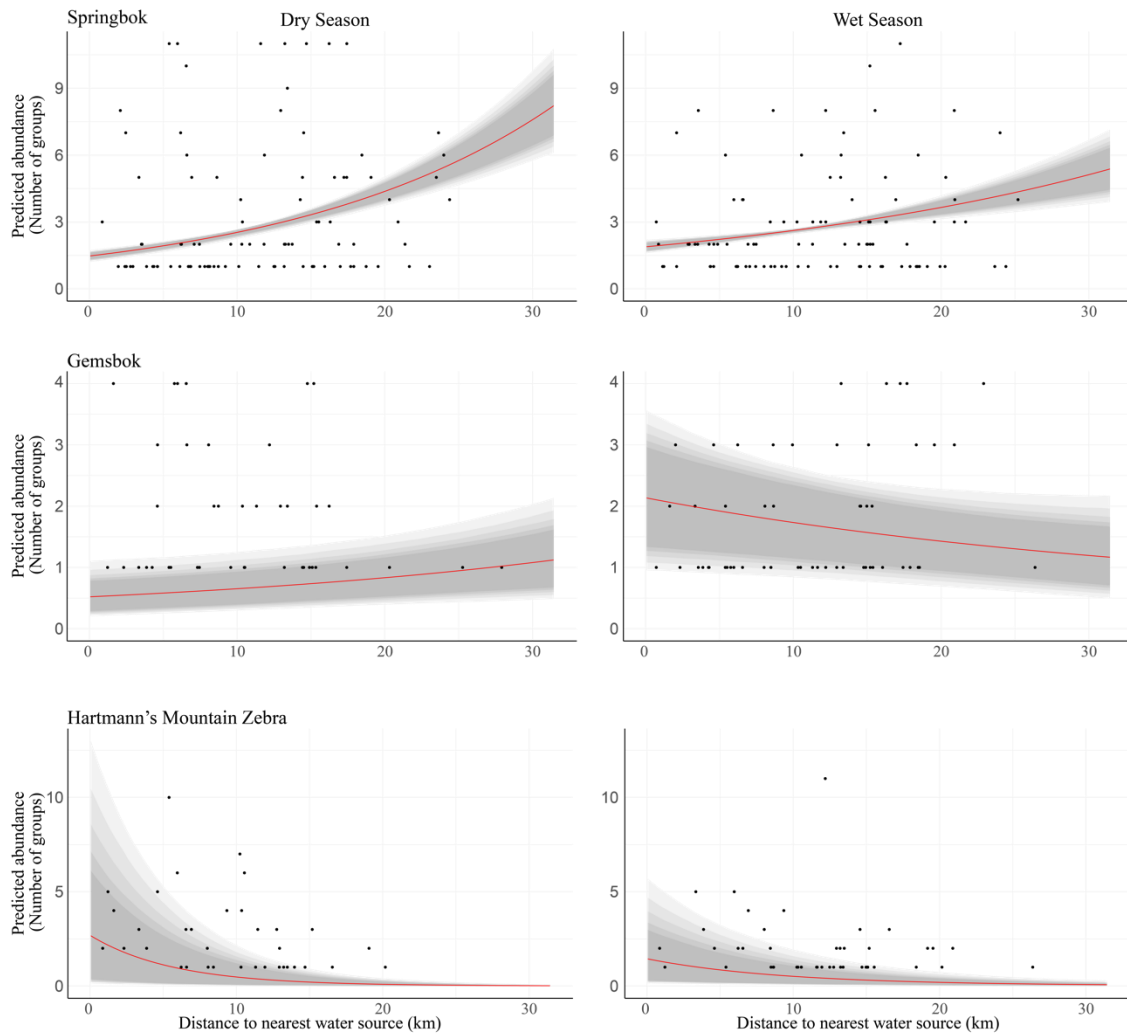


Figure 4.2 - Maximum expected group abundance of our target wildlife species in response to the distance to the nearest water source (km), during dry and wet seasons. The different shades of grey represent the 95%, 90%, 85%, 80% and 75% posterior credible intervals, while the black dots stand for the observed data.

The response we found by zebras to water availability matched what was previously described in the literature (Table 4.2). Conversely, gemsbok's response to the same covariate was below previously published descriptions of water dependency. Based on the literature, springbok's abundance should be independent of distance to water, but our results showed avoidance of this resource (Table 4.2).

Table 4.2 - Expected and observed effect of each covariates, categorized as: i) strong negative effect if estimate for both seasons is <-1 (- -), ii) negative effect if estimate ≥ -1 and <0 (-); iii) no effect if estimate ≈ 0 and varies between seasons (0); iv) positive effect if estimate ≥ 0 and <1 (+); v) strong positive effect if estimate is for both seasons is >1 (+ +). NA – Not evaluated (see methods section).

	Distance to water		TRI		EVI		Proportion of sandy soils	
	Expected Effect	Categorized Influence	Expected Effect	Categorized Influence	Expected Effect	Categorized Influence	Expected Effect	Categorized Influence
<i>Springbok</i>	0	+	--	-	+	0	NA	NA
<i>Gemsbok</i>	-	0	-	--	-	-	NA	NA
<i>Zebra</i>	--	-	-	--	--	--	--	0

We found EVI to have a negligible influence on springbok during dry season ($\hat{\beta}_{EVI_{dry}} = -0.02 [-0.07; 0.00]$; $\hat{\beta}_{EVI^2_{dry}} = -0.01 [-0.28; 0.27]$). However, they tended to occur in higher numbers at intermediate EVI values during wet season ($\hat{\beta}_{EVI_{wet}} = -0.07 [-0.2; 0.00]$; $\hat{\beta}_{EVI^2_{wet}} = -0.75 [-0.99; -0.53]$; Figs. 4.1 and 4.3). Conversely, gemsbok ($\hat{\beta}_{EVI_{dry}} = -1.00 [-1.45; -0.57]$; $\hat{\beta}_{EVI^2_{dry}} = -1.83 [-2.56; -1.15]$; $\hat{\beta}_{EVI_{wet}} = -0.75 [-1.15; -0.38]$ and $\hat{\beta}_{EVI^2_{wet}} = -1.06 [-1.50; -0.66]$) and zebra ($\hat{\beta}_{EVI_{dry}} = -6.00 [-6.95; -5.05]$; $\hat{\beta}_{EVI^2_{dry}} = -3.50 [-3.97; -3.03]$; $\hat{\beta}_{EVI_{wet}} = -3.54 [-5.54; -1.69]$ and $\hat{\beta}_{EVI^2_{wet}} = -2.17 [-3.56; -0.77]$) exhibited a selection optimum at the lower half of the EVI distribution, indicating a preference for areas with lower primary productivity (Figs. 4.1 and 4.3). This pattern was consistent for both species across seasons, although the range of preferred EVI values during the wet season was wider (Fig. 4.3).

The response found for zebra and gemsbok with regard to EVI matched their expected response as described in the literature. Conversely, we found springbok to use areas with lower primary productivity than expected (Table 4.2).

Our models showed a negative influence of the TRI on all target wild species (Figs. 4.1 and 4.4), which was particularly pronounced for gemsbok ($\hat{\beta}_{dry} = -4.22 [-5.12; -3.38]$; $\hat{\beta}_{wet} = -2.59 [-3.31; -1.94]$) and zebra ($\hat{\beta}_{dry} =$

$-3.93 [-5.91; -2.04]$; $\hat{\beta}_{wet} = -4.60 [-7.37; -2.79]$). Springbok appeared to be relatively more tolerant to some level of topographic ruggedness although the effect of this covariate remains negative ($\hat{\beta}_{dry} = -0.56 [-0.80; -0.31]$; $\hat{\beta}_{wet} = -0.24 [-0.49; -0.03]$). These results contrast with what is reported for these species in specialized literature, which describes some tolerance to rugged terrain by zebra and gemsbok and a strong avoidance of such areas by springbok (Table 4.2).

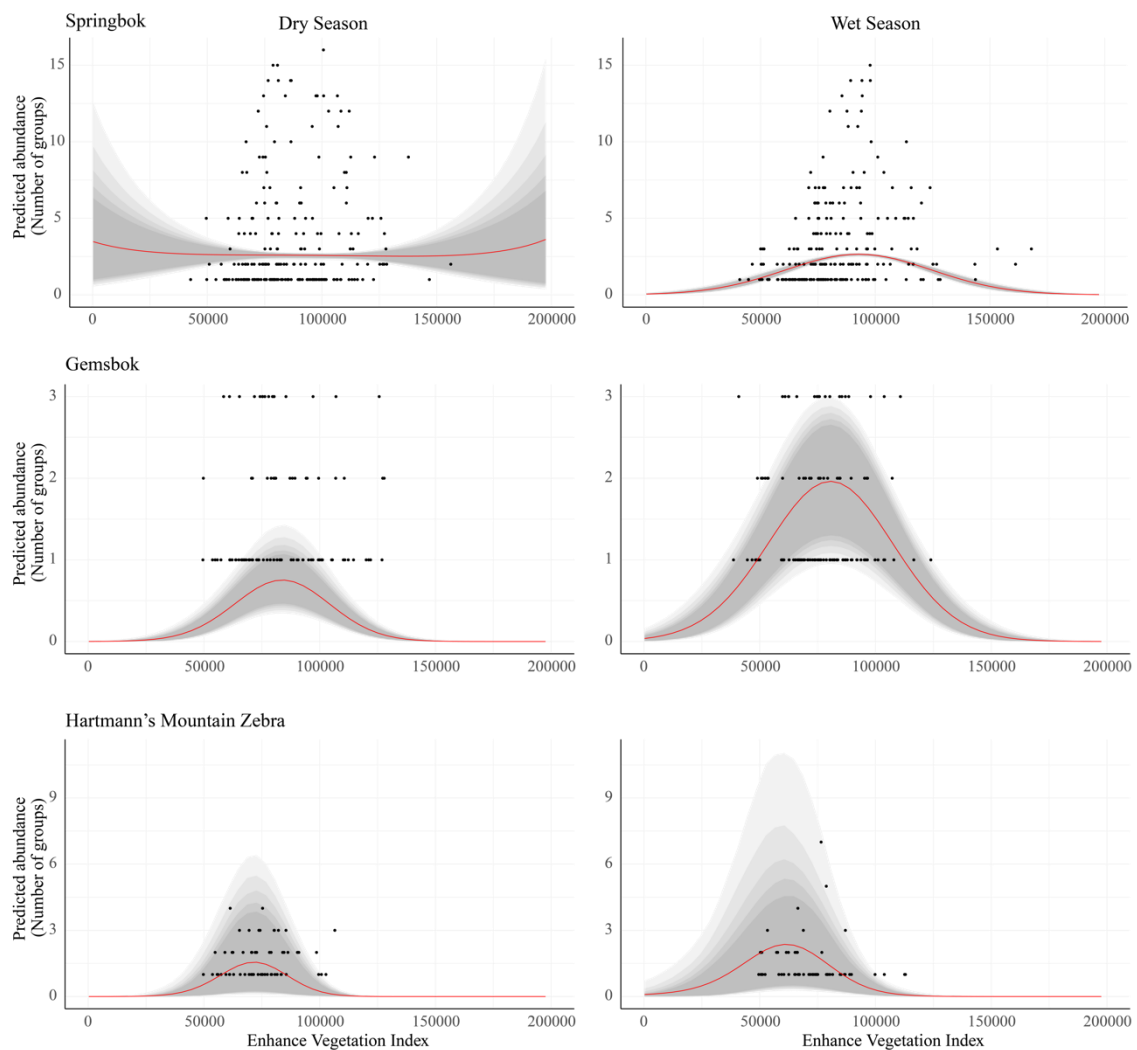


Figure 4.3 - Maximum expected group abundance of our target wildlife species in response to EVI during dry and wet seasons. The different shades of grey represent the 95%, 90%, 85%, 80% and 75% posterior credible intervals, while the black dots stand for the observed data.

Zebra avoided sandy soils during the dry season ($\hat{\beta}_{dry} = -0.68 [-1.55; 0.03]$), but their abundance was relatively independent of this covariate during the wet season ($\hat{\beta}_{wet} = 0.12 [-0.28 - 0.50]$; Fig. 4.1).

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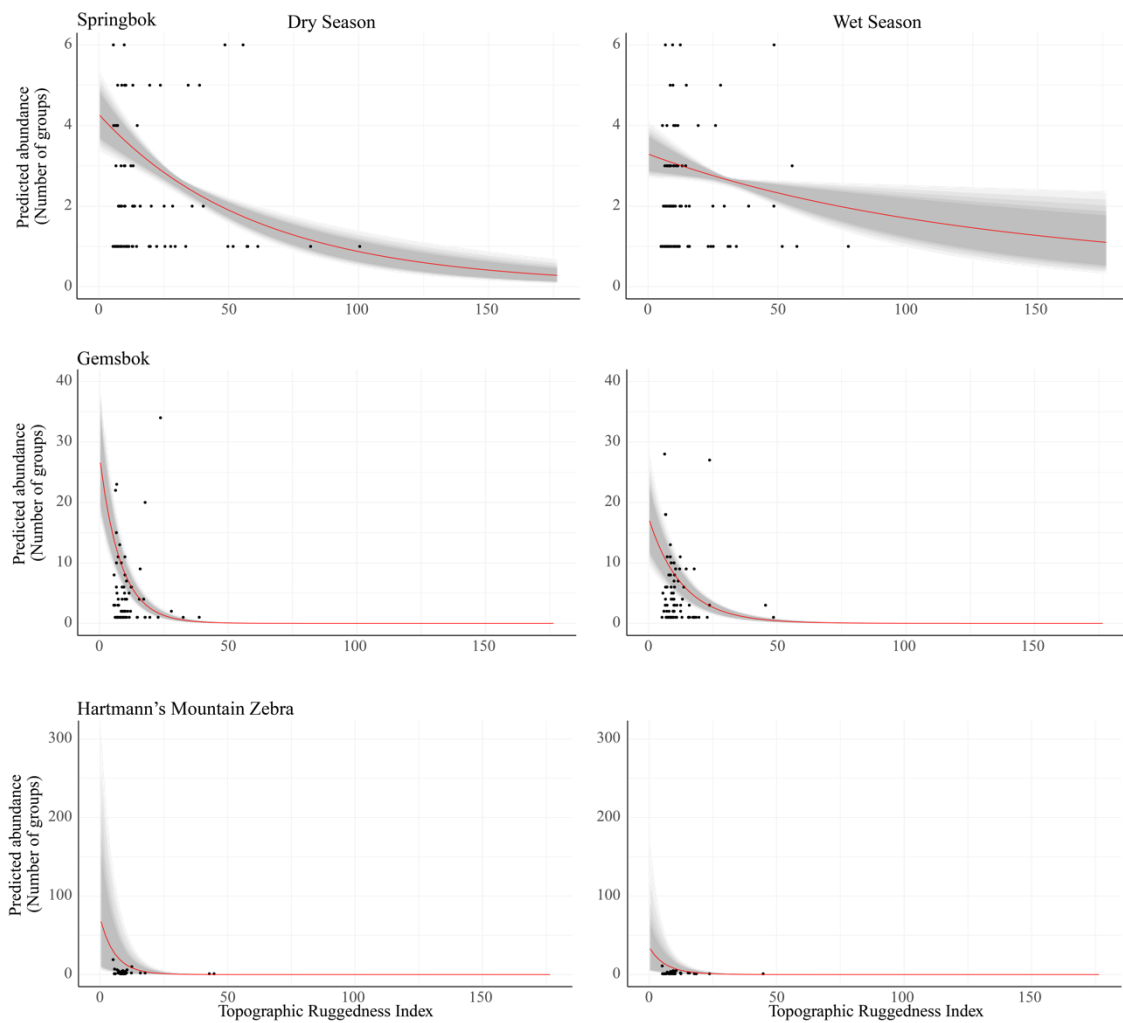


Figure 4.4 - Maximum expected group abundance of our target wildlife species in response to Topographic Ruggedness Index (TRI) during dry and wet seasons. The different shades of grey represent the 95%, 90%, 85%, 80% and 75% posterior credible intervals, while the black dots stand for the observed data.

According to our models' predictions, the median number of springbok, gemsbok and zebra groups associated to each cell was $\tilde{x}_{springbok} = 3$; $range: [0, 12]$, $\tilde{x}_{gemsbok} = 4$; $range: [0, 40]$ and $\tilde{x}_{zebra} = 4$; $range: [0, 200]$, respectively (Fig. 4.5; Appendix 4: Table S.4.4).

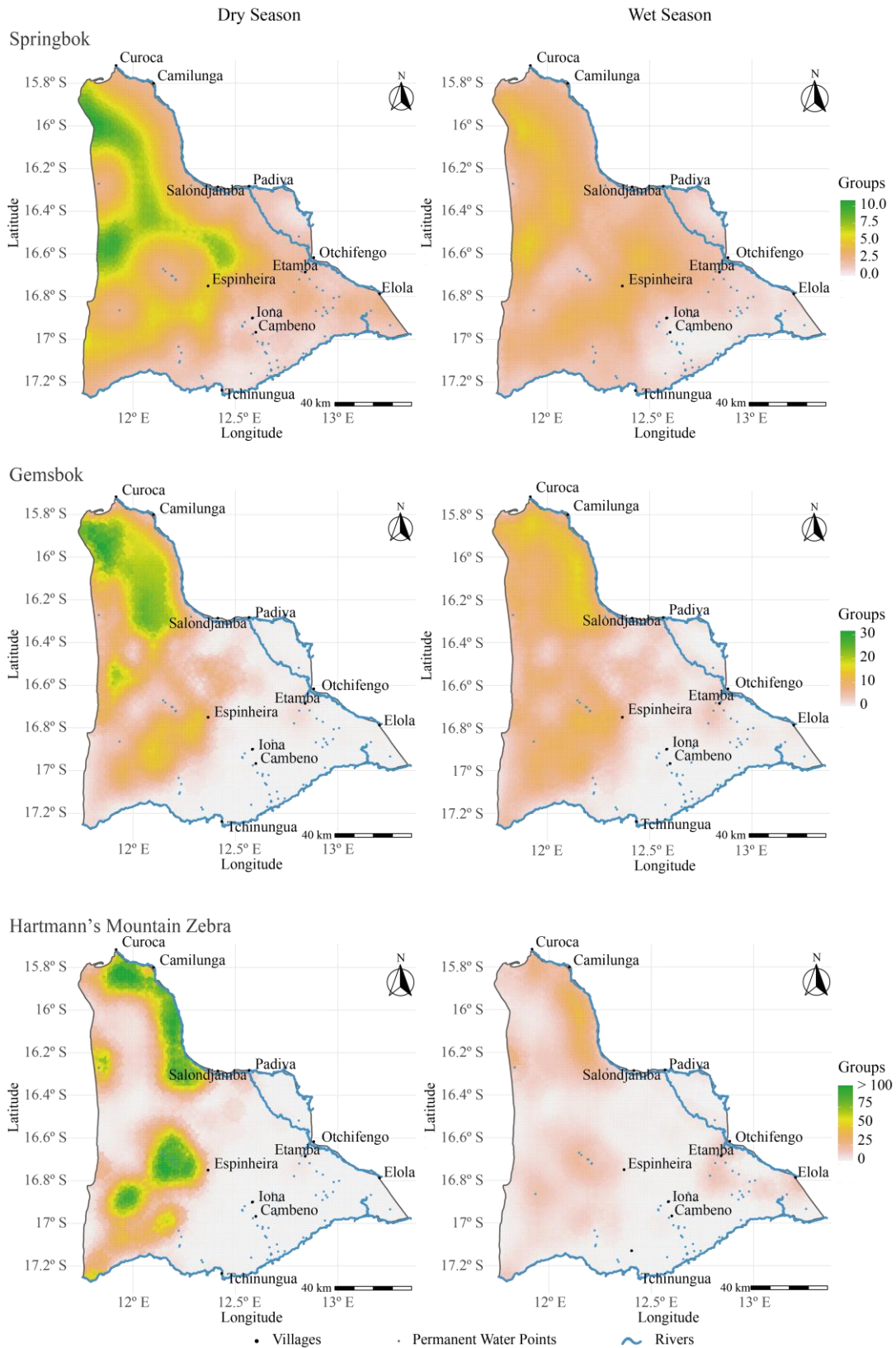


Figure 4.5 - Maximum expected number of groups associated to each site of our target wildlife species in Iona National Park.

4.4.2 Landscapes of coexistence and core conservation areas

We found distance to permanent water sources to be a strong predictor for water dependence by all livestock species during dry ($\hat{\beta}_{Cattle} = -2.16 [-2.74; -1.62]$, $\hat{\beta}_{Donkey} = -2.45 [-2.97; -1.66]$ and $\hat{\beta}_{Sheep \& Goats} = -2.06 [-2.72; -1.44]$) and wet seasons ($\hat{\beta}_{Cattle} = -2.64 [-2.98; -2.12]$, $\hat{\beta}_{Donkey} = -2.70 [-2.99; -2.14]$ and $\hat{\beta}_{Sheep \& Goats} = -1.07 [-1.53; -0.67]$) (Table 4.3, Fig. 4.1 and Appendix 4: Fig. S.4.5). Conversely, we found EVI and TRI to have little influence on livestock spatial abundance (Table 4.3, Fig. 4.1, and Appendix 4: Figs. S.4.6 and S.4.7).

Table 4.3 - Effect of the modelled covariates in the abundance and distribution of the domestic species in INP.

Species	Covariate	Dry Season	Wet Season
<i>Sheep & Goats</i>	EVI	-0.04 ± 0.04	-0.03 ± 0.03
	EVI ²	0.51 ± 0.17	0.15 ± 0.04
	Distance to Water	-2.06 ± 0.33	-1.07 ± 0.22
	TRI	-0.03 ± 0.03	-0.10 ± 0.09
<i>Cattle</i>	EVI	-0.09 ± 0.08	-0.02 ± 0.02
	EVI ²	0.24 ± 0.15	0.12 ± 0.03
	Distance to Water	-2.16 ± 0.29	-2.64 ± 0.23
	TRI	-0.01 ± 0.01	-0.02 ± 0.02
<i>Donkey</i>	EVI	-0.08 ± 0.07	-0.04 ± 0.03
	EVI ²	0.32 ± 0.16	0.08 ± 0.03
	Distance to Water	-2.45 ± 0.36	-2.70 ± 0.24
	TRI	-0.03 ± 0.03	-0.04 ± 0.04

Our estimates of realized conservation value revealed the highest values across the western section of INP (Fig. 4.6A). Overall, we found areas of higher realized conservation value to correspond mostly to areas with predicted low abundance or near absence of livestock (Appendix 4: Fig. S.4.8). However, we predict potentially co-suitable areas in the central plains surrounding existing springs as well as along the western stretches of the Curoca river (Fig. 4.6B).

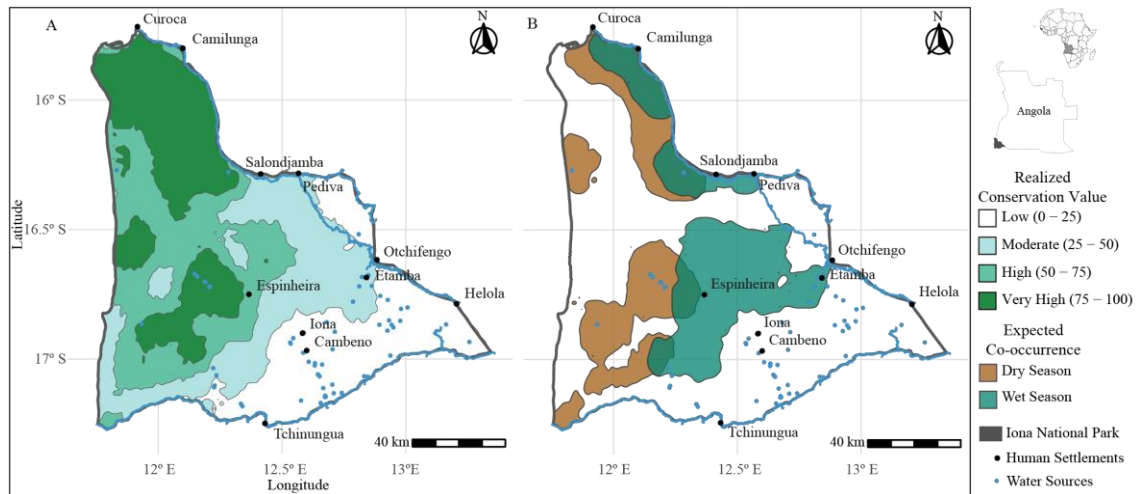


Figure 4.6 - A - Geographic representation of the realized conservation value (i.e., remaining strongholds for our target wildlife species) in INP, according to our modelling results. The realized conservation value categories were defined from quartiles so that low realized conservation value correspond to values in the first quartile until the very high conservation values comprising the values in the fourth quartile. B - Map depicting the highest potential co-occurrence areas between our target wildlife species and livestock, during dry (brown) and wet (green) seasons.

4.5 Discussion

Hot deserts are among the most sensitive biomes to climate change, and global drylands are predicted to increase by 7% until 2100, with a human population of 3.3 to 5.2 billion projected to live in these challenging environments (Koutroulis, 2019). The impacts of climate change are expected to be extensive both on wild and domestic plants and animals, and to threaten the food security of subsistence-oriented communities (Thornton *et al.*, 2008, Savo *et al.*, 2016). Therefore, local-scale studies are cornerstone for understanding the pervasiveness of climate change effects on ecosystem functioning, wildlife conservation and human livelihoods (Savo *et al.*, 2016). Using the northern Namib desert as a model system, we evaluated how surface water dependency and forage availability shape the spatial patterns of wild ungulates' abundance in a hot desert environment. Our results suggest that water dependency may not be a surrogate for drinking requirements. Although described as being more water dependent than gemsbok (Kihwele *et al.*, 2020), we found springbok to reach higher abundances in areas far from natural water sources. This finding is concordant with studies elsewhere showing that water dependent species could occur independently of surface water availability (e.g. Veldhuis *et al.*, 2019). Furthermore, we found the spatial patterns of abundance of wild ungulates to be regulated by the availability of resources but their broad distribution patterns to be constrained by anthropogenic factors, suggesting that our herbivore community is likely broadly constrained by human-related top-down effects, but

governed by bottom-up processes in undisturbed areas (e.g. Hopcraft *et al.*, 2010, Schuette, Creel and Christianson, 2016).

We hypothesized that species with higher surface water dependency would preferentially occur near available water sources. Zebra, described as a variable grazer with high water dependency (Hempson *et al.*, 2015, Kihwele *et al.*, 2020), was assumed to fit this criterion. Coherently, we found a strong negative effect of the distance to the nearest natural water sources on zebra abundance (Fig. 4.5). This pattern was consistent across seasons, suggesting that this species is not able to meet its hydric needs from dietary water alone, even during periods with higher primary productivity. Our findings are consistent with those found in NW Namibia, where zebras tended to select areas with higher forage quality and nearby water sources (Muntifering *et al.*, 2019), which are key resources for this aridity-adapted species (Gosling *et al.*, 2019). However, opposite to the findings of Muntifering *et al.* (2019), our results show that zebra preferentially use areas with lower primary productivity. Hartmann's mountain zebra are typically found in rugged, broken mountainous and escarpment areas with a rich diversity of grass species and perennial water sources (Penzhorn, 2013), but may expand into new, sometimes lowland, areas if water sources are available (Novellie *et al.*, 2002, Wilson and Mittermeier, 2011). Interestingly, our results conflict with the topographic preferences described for the species, as they were found to strictly avoid rugged areas at INP, where the highest primary productivity and number of natural springs are found. We suggest that the strong human disturbance occurring in the mountainous areas of INP are perceived as top-down constraints preventing zebras from occupying its preferred habitats (Wilson and Mittermeier, 2011, Muntifering *et al.*, 2019). The recent history and contemporary hunting practices in INP may have led to this scenario, as the persistence of these activities may shift the species' behaviour through learning (Crosmar *et al.*, 2012). Moreover, livestock can act as dominant competitors for the best grazing areas (Sirot *et al.*, 2016), relegating zebras to suboptimal habitats. Therefore, given the absence of most zebra predators or dominant competitors in INP, it is reasonable to assume that the broad scale distribution patterns of zebra are shaped by top-down interference, whereas the optimal decision in unconstrained areas is to secure access to drinking water with low energetic costs (i.e. not dispersing further from water sources), rather than securing access to high-quality forage.

Although well adapted to arid environments and regarded as having little water dependence (Kihwele *et al.*, 2020), gemsbok require access to surface water to maintain their body fluid homeostasis (Boyers *et al.*, 2019). However, we found surface water

availability to have little influence in how gemsbok use INP's landscapes. Conversely, our results suggest that gemsbok uses areas with higher primary productivity than those used by zebra (Fig. 4.3). As a variable grazer (Hempson *et al.*, 2015) that may browse in the absence of good-quality grass (Kingdon, 2015), and known to travel $ca. 5.65 \pm 0.42$ km/day (Keeping and Pelletier, 2014), gemsbok's physiological adaptations to water retention allow the species to reduce the drinking frequency (Boyers *et al.*, 2019) and to concentrate efforts into foraging through large areas in search for better quality food (Knight, 2013, Kingdon, 2015). We argue that gemsbok's physiology allows it to forage across INP's forage-poor central plains, while still maintaining enough access to natural water sources (Appendix 4: Fig. S.4.1). These movements may become wider during dry season, time when forage quality and quantity decreases, requiring wider ventures to fulfil their energetic demands. Conversely, gemsbok may fulfil their energetic demands closer to water sources during wet season, time when forage quality increases, hence optimizing energetic balance. A similar pattern was found by Boyers *et al.* (2019), who reported gemsbok to be mostly found within 20 km from water sources, and spending more time around these features during the wet season. We expected some tolerance of rugged terrains by gemsbok since the species is known to move across mountains to visit springs and salt licks (IUCN SSC Antelope Specialist Group, 2016b). However, our models showed a strong avoidance of the most rugged areas of INP. In an analogous situation to that found for zebra, we argue that anthropogenic disturbance mostly caused by the presence of humans and livestock may push gemsbok away from favourable habitats (Tablado and Jenni, 2017), relegating them to the central plains and mobile dune habitats of INP. Therefore, our combined results of seasonal use of surface water, grazing areas and topography support a hypothesis by which human-induced top-down forces constrain gemsbok from efficiently foraging across otherwise suitable landscapes, and the optimal decision becomes to forage in the best available feeding patches while maintaining a reasonable ability to access drinking in unconstrained areas.

Subordinate species, such as the springbok in INP, tend to be more susceptible to wildlife-based top-down constraints that shape their behavioral decisions. Being a staple prey for many mammalian predators still occurring in INP (Owens and Owens, 1978, Hayward *et al.*, 2006a, Hayward *et al.*, 2006b, Chicomo, 2021, Freixial, 2021), predation pressure could play an important role in springboks' behavioural decisions. This assertion is further supported by the springbok's unexpected tolerance to terrain ruggedness (Burger *et al.*, 2000), suggesting the species may use humans as 'shields' against predators (Gaynor *et al.*, 2019). The shielding against predators offered by

humans could outweigh anthropogenic disturbance effects. We expected springboks to occur in the landscape irrespective of surface water sources. However, our results revealed them to be less abundant near natural waterbodies, and preferentially occur in areas with higher primary productivity than those used by gemsbok or zebras throughout the year. Springbok has lower surface water dependence than grazer species (Kihwele *et al.*, 2020), and are described as being able to balance their hydric needs if they can obtain plant food containing at least 67% water (Nagy and Knight, 1994). Additionally, in dry regions, waterholes are areas of predictable high predation risk, which constrain access to and behaviour at these sources of surface water (Valeix *et al.*, 2008, Crosmar *et al.*, 2012, Davidson *et al.*, 2013). Taken together, these patterns suggest that springbok might be able to meet their nutritional and hydric requirements across large segments of INP's landscape, even tolerating some level of human disturbance, therefore they tend to use the space according to top-down constraints potentially imposed by competitors and/or predators (Valeix *et al.*, 2008, Sirot *et al.*, 2016). Therefore, this species is likely able to avoid areas with the highest risk without significant loss of its basic needs. We propose that the optimal decision for springboks in INP is to concentrate their efforts in finding good-quality forage that simultaneously meets their nutritional and hydric requirements, limiting their need to access surface water.

4.5.1 Implications for conservation

Our results suggest that the spatial patterns of abundance of Hartmann's mountain zebra and gemsbok in INP are governed, at the broader scale, by anthropogenic top-down forces, but spatially shaped by bottom-up processes via availability of nutritional and hydric resources in unconstrained areas. Conversely, springbok's patterns of abundance appear to be broadly determined by bottom-up processes, but their access to the highly valued natural water sources constrained by natural top-down forces. As a result, our target large herbivores tend to spatially segregate from livestock and human-disturbed areas, and efficiently exploit only a fraction of otherwise good quality habitats in INP. Given the recent and continued human expansion towards INP's core, we predict important areas of potential co-occurrence in the remaining strongholds for wildlife conservation. Human population growth within park boundaries, and their need to secure enough resources to meet their livelihoods, could further limit the availability of suitable habitat for wild species, increase competition, and facilitate hybridization and disease transmission, ultimately undermining the park's conservation goals.

The areas we identified as having higher realized conservation value should be considered as of top priority to implement strategies targeted at limiting the contact between wild and domestic animals, hence contributing to the safeguard the sanitary status and demographic sustainability of the wild counterparts. Given the strong bottom-up regulation we identified in the remnant landscapes, the exclusive access by wildlife to remaining important resources with few human and/or livestock pressure, such as natural waterholes and surrounding grazing zones in areas defined as having high conservation value, could be of utmost importance in the current climate change scenario (Thomas and Nigam, 2018, Koutroulis, 2019). Moreover, active conservation actions may be needed to reclaim currently human-exploited areas exclusively for wildlife use allowing to secure key resources for wild species and releasing them from anthropogenic top-down constraints. The management of protected areas that host human populations within their boundaries is particularly challenging and costly (Armsworth *et al.*, 2018), deeming authorities to be reluctant in implementing exclusively wildlife-directed conservation measures. However, zonation strategies could allow it to be more effectively managed, contributing to foster wildlife populations in the long term.

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Chapter 5

Unveiling the impacts of fire severity in herbivore occupancy patterns in disrupted communities

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5.1 Abstract

Fire is part of the savannah ecosystem and has been frequently used by managers to produce nutritious fresh grass to promote herbivore abundance. Counterintuitively, more frequent and severe fires induce the growth of tall grass, which, especially in scenarios of low herbivore density, is recognized to induce landscape homogeneity, creating undesirable habitat for herbivores. However, there is no empirical research to confirm the negative effect of fire in herbivores' occupancy patterns.

We used dynamic occupancy models applied to herbivore camera-trapping data in two southern Angola conservation areas, to estimate the periodic occupancy probability of herbivores of different dietary guilds during ca. 6 months after a fire. We also assessed the effects of distance to unburned areas and regrowth of vegetation (variation in Enhanced Vegetation Index (EVI) in two consecutive periods) in species' local re-colonization. We tested the effects of three different fire severity categories: 'mild fires', 'severe fires' and adjacent 'no fire' areas.

Although our results show an increase in the occupancy probability of grazer species and elephants of burned areas during ca. 2 months, at the end of study period the levels of occupancy are lower than before the fire. Grazer species' occupancy is higher in 'no fire' and 'severe fire' areas than in 'mild fire' zones, as opposed to mixed-feeders, generalists and browser species that show higher use of 'mild fire' areas. Our results suggest that grazer species' re-colonization is positively influenced by plant regrowth, while it has negligible effect on mixed-feeders, generalists and browser species. In this work we demonstrate the negative effect of fire in herbivore occupancy in two mammals communities, regardless the guild and fire severity. Our results support that, in systems with of reduced populations, fires may not be a good measure to promote herbivore abundance.

Keywords: Angola, Reduced mammal communities, Effects of fire, Fire severity, Herbivore guilds, Herbivore occupancy

5.2 Introduction

Fire is an integral part of the seasonal dynamics of savanna ecosystems and has important consequences for structuring the landscape and vegetation communities (e.g. Archibald and Hempson, 2016, Hempson *et al.*, 2018, Rouet-Leduc *et al.*, 2021, Meller *et al.*, 2022). Consequently, fire also has the potential to influence the dynamics of space use by wildlife, particularly that of mammalian herbivores (both grazers and browsers), which strictly depend on green vegetation to meet their energetic and hydric demands, but also on the landscape structure to cope with predation risks (Gaynor *et al.*, 2019), leading to cascading consequences for predator space use (Geary *et al.*, 2020, Gigliotti *et al.*, 2022). Although fire is a natural process in savanna ecosystems, humans have altered fire pervasiveness, extent, and seasonality (Archibald and Hempson, 2016). Among other reasons (Eriksen, 2007), humans have altered fire regimes because of its importance for nutrient recycling, such as copper, potassium, magnesium, and nitrogen of senescent tall grass and woody plants, promoting the growth of small and highly-nutritious fresh grass that can be consumed by grazers (Eby *et al.*, 2014). For this reason, fire has been used as a management tool to renew grasslands for livestock (Augustine and Derner, 2014) and wild grazer populations (Fynn *et al.*, 2019).

Several studies have proven that the benefits to herbivores are not a result of fire alone, but from the pyrodiversity (Beale *et al.*, 2018, Hempson *et al.*, 2018), i.e. from the 'variety in interval between fires, seasonality, dimensions and fire characteristics' (Martin and Sapsis, 1992). There is a well described feedback mechanism between natural fire regimes, vegetation and herbivores that keep ecosystems in balance (Fig. 5.1). Fire and herbivores act as competing forces that consume and control plant communities (Archibald *et al.*, 2005, Archibald and Hempson, 2016, Donaldson *et al.*, 2018), however to different extents. Fire consumes mostly dry matter of tall and less nutritious grass (Fig. 5.1F; Veen *et al.*, 2008). Faster growing plants benefit from a reduced fire interval, leading to reduced grass diversity and dominance of tall grass species (Fig. 5.1G), which are less palatable for herbivores (Archibald *et al.*, 2005, Veen *et al.*, 2008, Donaldson *et al.*, 2018), creating undesirable habitats for these animals (Fig. 5.1I). Conversely, herbivores (especially grazers) feed mostly on short and more nutritious grass (Anderson *et al.*, 2007), promoting the creation of grazing lawns (Fig. 5.1J; Veldhuis *et al.*, 2014) that control fires (Fig. 5.1H; Rouet-Leduc *et al.*, 2021). Browser species' effect on vegetation cannot be excluded from the cycle, because they regulate the growth of

woody vegetation and the expansion of forests (Fig. 5.1C), controlling fires' intensity (Fig. 5.1A and D; Daskin *et al.*, 2016).

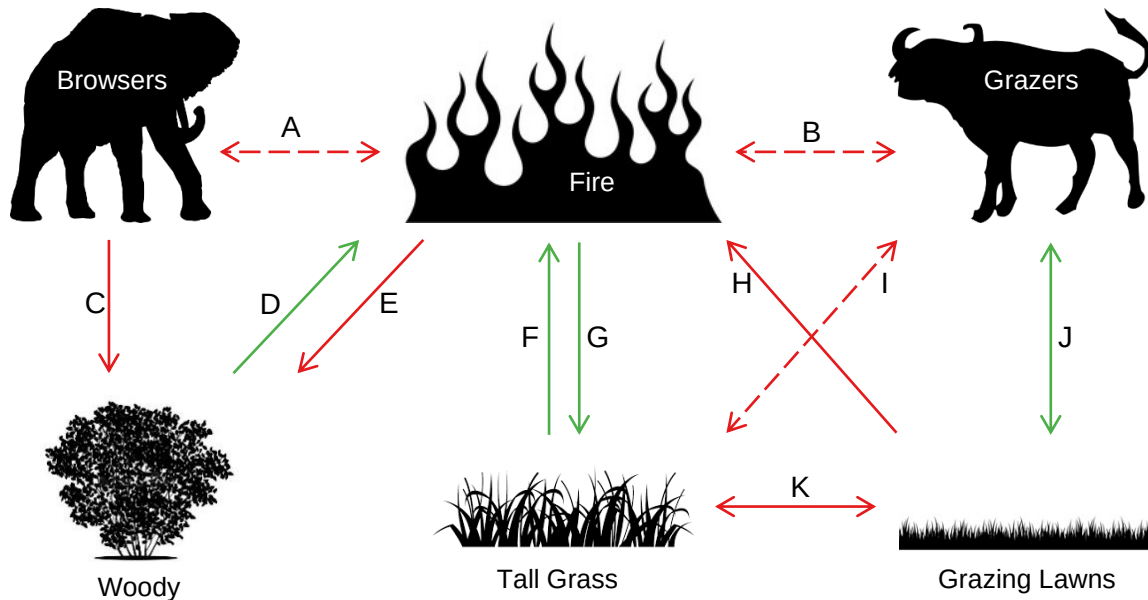


Figure 5.1 – Feedback mechanism between fire, herbivores (grazers and browsers) and vegetation. Green and red arrows represent, respectively, positive and negative feedbacks, while full and dashed lines indicate direct or indirect associations, respectively. Herbivore species have indirect negative effects on fire (A and B) in different extents: while browser species regulate the growth of woody vegetation (C) which are one of the biggest sources of fuel for fires (D), grazer species promote the generation of short grass (J), hence preventing the tall grass to grow (I and K) decreasing fuel loads for fire (H). On the other hand, fire controls the growth of all types of vegetation (E, G and H), potentially leading to the temporal extinction of herbivore species (A and B). However, long-term frequent fires promote homogeneous grasslands of tall grass (G), which is less palatable for grazer species (I) and preclude the growth of short grass (K), potentially indirectly affecting grazer species (I).

The consequences of fire for each herbivore functional group (i.e. grazers, mixed-feeders/generalists and browsers (Hempson *et al.*, 2015)) change with fire severity, i.e. ‘the loss of or change in organic matter aboveground and belowground’ (Keeley, 2009). Early dry season fires are frequently less severe than late dry season fires due to the higher vegetation moisture content, lower air temperature and wind speed. In these conditions, fires are less powerful, consuming mostly herbaceous vegetation (Smit *et al.*, 2016). Conversely, as the dry season progresses, the scarcity of water reduces vegetation moisture, which, combined with the high air temperature, creates favorable conditions for severe fires. These have significantly higher impacts on the ecosystem, decimating grasslands, woodlands and forests (Werner and Prior, 2013, Smit *et al.*, 2016). As such, grazer species may be impacted by all fires, while mixed-feeders, generalist and browser species should be mostly affected by more severe fires (Table 5.1; Smit *et al.* (2016)).

Despite the frequent reports of short-term herbivore use of burned areas (Beale *et al.*, 2018, Dlamini *et al.*, 2020), fire causes an immediate depletion of vegetation availability. This potentially leads to herbivore migrations to areas with higher food availability and consequent local extinctions (i.e. the local extirpation of herbivores, but with potential to return (Smith-Patten *et al.*, 2015)) at burned areas (Anderson *et al.*, 2016). The vegetation regrowth depends on ground-water availability (Beale *et al.*, 2018, Dlamini *et al.*, 2020). Consequently, early dry-season fires are likely to facilitate accelerated vegetation regrowth, making them more favorable for herbivores. In contrast, the low soil water availability during the late dry season results in a delay of vegetation regrowth until the subsequent rainy season.

Protected areas and game reserve managers, frequently use early dry season fires to produce fresh grass for herbivores (Fynn *et al.*, 2019), and, coherently several studies report short-term increases in herbivore use of burned areas driven by the temporary increase in nutrient levels and decrease in vegetation height and live : dead biomass in the new vegetation (Eby *et al.*, 2014). However, there is no clear understanding of the long-term efficiency of this measure, especially because of fire-driven changes in vegetation structure (Hempson *et al.*, 2018, Nieman *et al.*, 2022). This is even more relevant in the current context of mammals' decline (Ripple *et al.*, 2015), since the reduction of herbivory increases fuel loads (Rouet-Leduc *et al.*, 2021) and, consequently, creates more frequent and severe fire regimes (Daskin *et al.*, 2016). Similar effects happened as a consequence of large mammal extinction during the Pleistocene (Gill *et al.*, 2009), and have currently been documented in depleted mammal populations (Donaldson *et al.*, 2018).

Angola is, together with Zambia, classified as the southern African country with most fire activity (Archibald *et al.*, 2009). An increase in the extent of uncontrolled burning and fire intensity (Mendelsohn, 2019) has been documented in Angola in this millennium. Roughly 30% of Angola's surface burns every year, with the highest percentage of annual burnt area in the Northeast and Southeast (Catarino *et al.*, 2020). Some protected areas have experienced alarming increases in the trends of burned area, such is the case of Bicuar National Park (Catarino *et al.*, 2020). Moreover, Angolan Civil War (1975-2022) is argued to have decimated wildlife populations (Chapter 2) and changed people's livelihoods, increasing the rural populations in Angola (Huntley, 2017). Angolan rural people are largely dependent on subsistence activities such as traditional slash-and-burn agriculture, and commercial logging, hunting and agriculture. As a result of food insecurity and poor subsistence conditions experienced by nearly all inhabitants may

have a major influence on long-term fire regimes by altering the seasonality of fires and increasing its frequency, size and intensity (Stellmes *et al.*, 2013, Schneibel *et al.*, 2016).

Here we used two areas in southern Angola with similar fire regimes to investigate how specific herbivore functional groups respond to fire events, particularly which characteristics of fire may lead to local extinction of species and the factors involved in its recolonization. We hypothesize that (H1) the reduction in food availability after a fire leads to an immediate local extinction of herbivores (both grazers and browsers) in burned areas (Fig. 5.1 A and B). However, the likelihood of extinction will depend on the dimension and severity of the fire, and on the distance to the fire perimeter. (H2) Browsers should be the first functional group to recolonize burned areas, especially in low-severity fires, while (H3) grazers should only recolonize burned areas after the first rains, following the recovery of grass (Table 5.1).

5.3 Methods

5.3.1 Study area

This study was carried out in two areas in southern Angola: Bicuar National Park (BNP) and Cuatir Conservation Area (CCA). BNP (S 15.1°, E 14.8°; Huíla Province) spans over 6,900 km² in the transition between the Angolan Miombo Woodland, Zambezian *Baikiaea* Woodland and Angola Mopane Woodland ecoregions (Huntley *et al.*, 2019b). The core area of BNP remains largely intact and constitutes a mosaic of miombo woodland, *Baikiaea-Burkea* woodland, shrub/thicket vegetation and seasonally flooded grasslands (Godlee *et al.*, 2020). The altitude ranges between 1200 and 1400 m.a.s.l., the mean temperature is ca. 21.8°C, with mean minimum temperature of 4°C and mean maximum temperature of 33°C (Brun *et al.*, 2022a, Brun *et al.*, 2022b). The annual rainfall reaches 857 mm, usually between November and April (i.e. wet season; <http://www.sasscalweathernet.org/>). Despite the loss of species during the Angolan Civil War (Chapter 2), BNP maintains stable populations of common duiker (*Sylvicapra grimmia*, hereafter duiker), bushpig (*Potamochoerus larvatus*), warthog (*Phacochoerus africanus*), greater kudu (*Tragelaphus strepsiceros*, hereafter kudu), roan antelope (*Hippotragus equinus*, hereafter roan), common eland (*Taurotragus oryx*, hereafter eland), African savannah elephant (*Loxodonta Africana*, hereafter elephant), leopard (*Panthera pardus*), African wild dog (*Lycaon pictus*) and spotted-hyaena (*Crocuta crocuta*). Large predator density in BNP is considered low (Monterroso, unpublished data).

The CCA (S 16.5°, E 18.2°; Cuando-Cubango Province) is a ca. 100 km² section along the Cuatir riverbed. It is located in the Zambezian *Baikiaea* Woodland ecoregion (Huntley *et al.*, 2019b), and is dominated by *Baikiaea-Burkea* woodlands, with a ca. 1 km wide grasslands and floodplains along the Cuatir (a tributary of the Okavango river) and Luatuta Rivers. CCA is ca. 1140 m.a.s.l., and accounts for a mean temperature of ca. 21.9°C, with mean maximum temperature of ca. 30°C and a mean minimum temperature of ca. 9° to 12°C. Rainfall can reach 819 mm during the wet season (Brun *et al.*, 2022a, Brun *et al.*, 2022b). CCA retains stable populations of steenbok (*Raphicerus campestris*), duiker, reedbuck (*Redunca arundinum*), bushpig, warthog, and roan (Chapter 2), while the population of kudu was re-stocked in 2020 together with the reintroduction of impala (*Aepyceros melampus*), plains zebra (*Equus quagga*), eland and Angolan giraffe (*Giraffa giraffa angolensis*). Similar to BNP, CCA's large predators populations are low-abundant (Monterroso, unpublished data), but there are resident populations of cheetah (*Acinonyx jubatus*) and leopard, and transient populations of African wild dog and spotted-hyaena (Monterroso *et al.*, 2020b).

Both areas use prescribed early dry season fires in grasslands to produce fresh food for herbivorous and to mitigate the risk of uncontrolled fires from the edge reaching the center of the areas. These human-induced fires occur any time during dry season, and especially in the late dry season these fires invade the conservation areas, when the fires are more severe and progress through the woodlands.

5.3.2 Data acquisition and covariates

We conducted systematic camera trap surveys to assess the structure of the mammal communities of BNP and CCA. An equivalent sampling design was set up in both study areas, allowing for direct comparability: camera stations (one camera per station) were uniformly deployed, following a grid-sampling scheme at a ca. 2 km inter-camera distances. Cameras were deployed on trees approximately 0.6 m off the ground without any lures or attractants, but some were installed next to trails. Cameras were set to shoot a burst of 3 (ScoutGuard), 5 (Cuddeback) or 10 (Reconyx) photos when triggered, without any time delay (0 s), to maximise the number of photos taken per activation. Camera stations were serviced every 4 months for maintenance.

The surveys in BNP occurred in two different periods: i) July 2017 through June 2018, with 51 camera stations of three different models: Cuddeback C1 Strobe Flash (n=11; Cuddeback, Green Bay, Wisconsin, USA), Reconyx Hyperfire HC600 (n=32; Reconyx, Holmen, Wisconsin, USA) and ScoutGuard SG570 (n=8, HCO Outdoor

Products, Norcross, Georgia, USA); and ii) November 2018 through November 2021, with an expanded sampling grid of 91 camera stations, all Reconyx Hyperfire 2 (n=91; Reconyx, Holmen, Wisconsin, USA). Whereas, in CCA the field sampling started in July 2018 until October 2021, with a total of 70 camera traps from three different models: Cuddeback C1 Strobe Flash (n=10; Cuddeback, Green Bay, Wisconsin, USA), Reconyx Hyperfire HC600 (n=27) and Reconyx Hyperfire 2 (n=33; Reconyx, Holmen, Wisconsin, USA). The processing of camera trapping data was performed using the “camtrapR” v.2.0.2 R package (Niedballa *et al.*, 2016).

Our study focused on the most common herbivore species in BNP and CCA, of which species from different dietary types (Hempson *et al.*, 2015) and body size (Jones *et al.*, 2009) were chosen (Table 5.1). We built detection/non-detection matrices on single-day sampling occasions from each species’ detection records. Encounter histories consisted of station- and species-specific records whereby 1 denotes at least one detection of the target species during a given sampling occasion, and 0 denotes non-detection (MacKenzie *et al.*, 2017). The detection histories used for the posterior analysis was generated using a stacked approach. For each fire event were selected all the cameras located in the fire area and in a 5 km buffer around the fire perimeter. A period of 240 days was analyzed for each fire, this period was split in a primary period of 64 days before the fire and 11 periods of 16 days after the fire.

The perimeter of the fires occurred in the study areas during the sampling period was retrieved from Mahood *et al.* (2022) database and validated with camera trapping images. For the entire area of each fire we calculated its severity according to the index suggested by Zheng *et al.* (2016): , which is the difference between the ratio of Land Surface Temperature (LST) and Enhanced Vegetation Index (EVI) after and before the fire, considering the following equation:

$$Fire\ Severity\ Index\ (FSI) = \frac{LST_{post}}{EVI_{post}} - \frac{LST_{pre}}{EVI_{pre}}$$

The fires were separated in two different categories of severity, i.e. “Mild Fires”: $FSI \leq 1.25$, “Severe Fires”: $FSI > 1.25$. A third category, called “No fire”, was used for the cameras within a buffer of 5 km from the fire perimeter.

The LST and EVI were retrieved from MODIS—Terra Moderate Resolution Imaging Spectroradiometer products MOD11A2 and MOD13Q1, respectively, and obtained from NASA’s EarthDATA (<https://search.earthdata.nasa.gov/>).

Besides the calculation of the fire severity, EVI variation (ΔEVI) was also used as a proxy for the evolution of forage availability for herbivores. For each period, we calculated the standardized ΔEVI , according to:

$$\Delta EVI_t = \frac{EVI_t - EVI_{t-1}}{EVI_{t-1}}$$

Where $EVI_t - EVI_{t-1}$ denotes the difference of mean EVI values in a buffer of 1 km around each camera station (Rich *et al.*, 2016) between the two consecutive time periods mentioned above.

Table 5.1 - Distribution of the target species in the guilds and the rationale behind the expected response of each guild to fire events. Herbivores were distributed in guilds following the classification of Hempson *et al.* (2015), i.e. Grazers: > 60 % of their diet is compound by monocots; mixed-feeders: 30-70% of their diet is plants and < 20% fruit; generalists: >20% of all food types; browsers: > 70% of consumed plants are dicots.

Diet type	Species	Rationale
Grazers	Warthog	Grazers feed mostly on herbaceous vegetation, which is also the most affected group in a fire event. Grazers should be the most affected group by fire and should only return when the herbaceous vegetation regrows, responding positively to the enhanced vegetation index (EVI) variation.
	Roan antelope	
Mixed-feeders	Steenbok	Generalists and mixed-feeders should be at an intermediate state between grazers and browsers. This group should not be much affected by fire because their diet plasticity allows shifts in their diet towards woody plants that remain available after less severe fires. Accordingly, mixed-feeders should not be very sensitive to variations of EVI.
	Common eland	
	Elephant	
Generalists	Bushpig	
	Greater kudu	
Browsers	Common duiker	Browsers should only be affected by the most severe fires that burn woody vegetation. Coherently, they should experience little influence of EVI variation.

References: Hempson *et al.* (2015), Archibald and Hempson (2016), Nieman *et al.* (2022)

We also considered the distance to the fire perimeter as possibly influencing the probability of colonization after a fire. To assess that, we calculated the Euclidian distance between each camera station within a fire perimeter and the closest fire border. For the cameras outside the fire perimeter, we considered the distance as 0.

Multicollinearity among continuous covariates was assessed through a nonparametric Spearman's correlation analysis using the "psych" R package, v.2.2.5 (Revelle, 2020). Among correlated covariates ($|\rho| \geq 0.5$; Zuur *et al.* (2009b)), the covariate correlated with

more covariates or for which the predicting hypothesis had less biological relevance for this study's goals was excluded from the subsequent modelling procedure.

All continuous covariates were standardized to z-scores to avoid data dispersion bias and facilitate the numeric convergence of our models (MacKenzie *et al.*, 2017).

5.3.3 Data analysis

We used dynamic occupancy models (DOM; MacKenzie *et al.* (2003)) to estimate the occupancy (ψ), the colonization (γ) and extinction (ε) probabilities for each species in each primary period.

Under the ecological sub-model, the initial state is denoted by z_{i1} and represents true occurrence state at site i during period 1, which is described by a Bernoulli trial governed by the occupancy probability in the first season, (ψ_{i1}):

$$z_{i1} \sim \text{Bernoulli}(\psi_{i1})$$

For all subsequent periods, occurrence probability is a function of occurrence at site i at time $t - 1$ and one of two parameters that describe the colonization-extinction dynamics of the system. These dynamic parameters are the probability of local survival ($\phi_{i,t}$), probability of local extinction ($\varepsilon = 1 - \phi_{i,t}$), and the probability of colonization ($\gamma_{i,t}$).

$$z_{i,t} \sim \text{Bernoulli}(z_{i,t-1}\phi_{i,t-1} + (1 - z_{i,t-1})\gamma_{i,t})$$

Likewise, occupancy probability $\psi_{i,t}$ at all later periods t is computed from:

$$\psi_{i,t} = \psi_{i,t-1}\phi_{i,t-1} + (1 - \psi_{i,t-1})\gamma_{i,t-1}$$

The observation sub-model describes the observation process, and accounts for the observation error (specifically, false-negative observations), under a conventional Bernoulli detection process, such that:

$$y_{i,j,t} \sim \text{Binomial}(z_{i,t}p_{i,j,t})$$

Here, $p_{i,j,t}$ is the detection probability at site i during survey j and period t , where detection is conditional on occurrence and multiplying $p_{i,j,t}$ with $z_{i,t}$ ensures that occurrence can only be detected where in fact a species occurs.

The above-described model formulation assumes the detection and occupancy as constant across sites. Spatial and temporal heterogeneity in the state and detection processes can be modelled as a function of site- and sampling-specific covariates, under the form of linear regressions using a logit-link function as follows:

$$\text{logit}(\phi_{i,t}) = \beta_{0\phi}$$

$$\begin{aligned}
 \text{logit}(\gamma_{i,t}) = & \beta_{0\gamma} + \beta_1 \times \text{Trend}_{i,t} + \beta_2 \times \text{fireClass}_{i,t} + \beta_3 \times \text{dEVI}_{i,t} \\
 & + \beta_4 \times \text{dist to fire perimeter}_{i,t} + \beta_5 \times \text{StudyArea}_{i,t} \\
 & + \beta_6 \times \text{Trend}_{i,t} \times \text{dist to fire perimeter}_{i,t} + \beta_7 \times \text{Trend}_{i,t} \times \text{dEVI}_{i,t} \\
 \text{logit}(p_i) = & \alpha_0 + \alpha_1 \times \text{trail}_i
 \end{aligned}$$

Where $\beta_{0\phi}$, $\beta_{0\gamma}$ and α_0 denote the baseline probabilities of local survival, colonization, and detection, respectively, β_{1-7} represent the effect of site- and sampling-specific covariates in the colonization probability, and α_1 is the site-specific effect of trail on detection probability of a species. ‘fireClass’ and ‘StudyArea’ were modelled as categorical variable, where the comparative levels are ‘No Fire’ and ‘BNP’, respectively. The covariate ‘StudyArea’ was only included in the models of species that exist in both study areas and whose we obtained sufficient detections to inform the model, i.e. warthog, roan, bushpig, kudu and duiker, while for steenboks’ model we considered only data from CCA and for elephant’s and eland’s models data from BNP.

Models were fit in JAGS v.4.3.0, executed from R v.4.2.0 (R Core Team, 2021) using “jagsUI” v.1.5.2 (Kellner and Meredith, 2019). We ran three Markov Chain Monte Carlo (MCMC) chains with 50,000 iterations after a 10,000 iteration of adaptative phase, 20,000 iteration burn-in and thinned by 10. Prior distributions for each of our model parameters followed a uniform distribution between -5 and 5. Model convergence was assessed from a visual inspection of chain trace plots and from the Gelman-Rubin statistic ($\hat{R}$), where values < 1.1 suggested reliable convergence (Gelman and Rubin, 1992). Goodness-of-Fit was assessed by calculating the Bayesian p-value (BPV, Gelman *et al.* (1996)) in the open and closed parts of the model. In the open part we used only the χ^2 test, while for the closed part we used χ^2 and Freeman-Tuckey tests (Kéry and Royle, 2021). The relative importance of each covariate was assessed by inspecting the probability posterior distribution of corresponding coefficients. All results are presented as mean [95% Bayesian Credible Intervals] and associated probability for a non-zero effect (f), unless explicitly stated otherwise.

5.4 Results

During the sampling period 24 fires deflagrated in the study areas, of which 8 were in BNP (5 “mild” and 3 “severe” fires) and consumed a total of 333 km² (84 km² burned in mild fires, while 249 km² in severe fires) and 16 in CCA (12 “mild” and 4 “severe”) burning a total of 568 km² (526 km² burned in mild fires, while 42 km² in severe fires).

Our camera trapping surveys represented an effort of 78016 trap-days in BNP, collecting 60807 independent records of 35 mammal species. At CCA, the effort was 41906 trap-days, with the detection of 13151 independent records of 38 mammal species (more details in the Appendix 5: Table S.5.1).

5.4.1 Effect of fire severity in species occupancy

Our results demonstrated that fires have different impacts in the occupancy of different guilds, with an increase in the occupancy in the first ca. 30 to 60 days after the fire in grazer species and elephants, followed by a decrease during the rest of the tested period (Fig. 5.2 Aggregate). Conversely, the other guilds showed a decrease in occupancy immediately after fires (Fig. 5.2 Aggregate). Only generalist species and elephants exhibited some recovery in occupancy patterns ca. 90 days after fires (Fig. 5.2 Aggregate). In general, we observed that all the species showed lower occupancy 6 months after fire when compared to the levels before. Moreover, fire influence is not restricted to the burned area, but it is expanded to the surroundings, since we observe a reduction in the occupancy of species in the unburned area within 5 km around the fire perimeter (Fig. 5.2 No Fire). Despite the general negative trend in the occupancy after 6 months, our results depicted an increase in the occupancy of grazer species and elephants in unburned and severe fire areas, while the remaining mixed-feeders, kudu and browser species presented a continuous decrease in occupancy after a fire (Fig. 5.2 No Fire and Severe Fire). Concerning mild fires, all species showed a reduction in the occupancy after the fire which continued throughout the tested period for grazer species and elephant. Conversely, the occupancy of the remaining mixed-feeders, generalist and browser species stabilized or increased after the initial reduction (Fig. 5.2 Mild Fire). Consequently, the occupancy probability of grazer species in unburned and severe fire areas is higher than in mild fire zones, while the occupancy of mixed-feeders, generalists and browser species is similar in the three areas or is higher in areas of mild fires, than in unburned and severe fire areas. Elephants present a unique pattern of occupation dynamics, since their occupancy is higher in burned areas (either mild or severe fires) in the first ca. 3 months, but then the pattern shifts for a higher use of unburned areas (Fig. 5.2).

Rediscovering Angolan Biodiversity: Patterns and regulation processes underlying large mammal community structure across South Angola

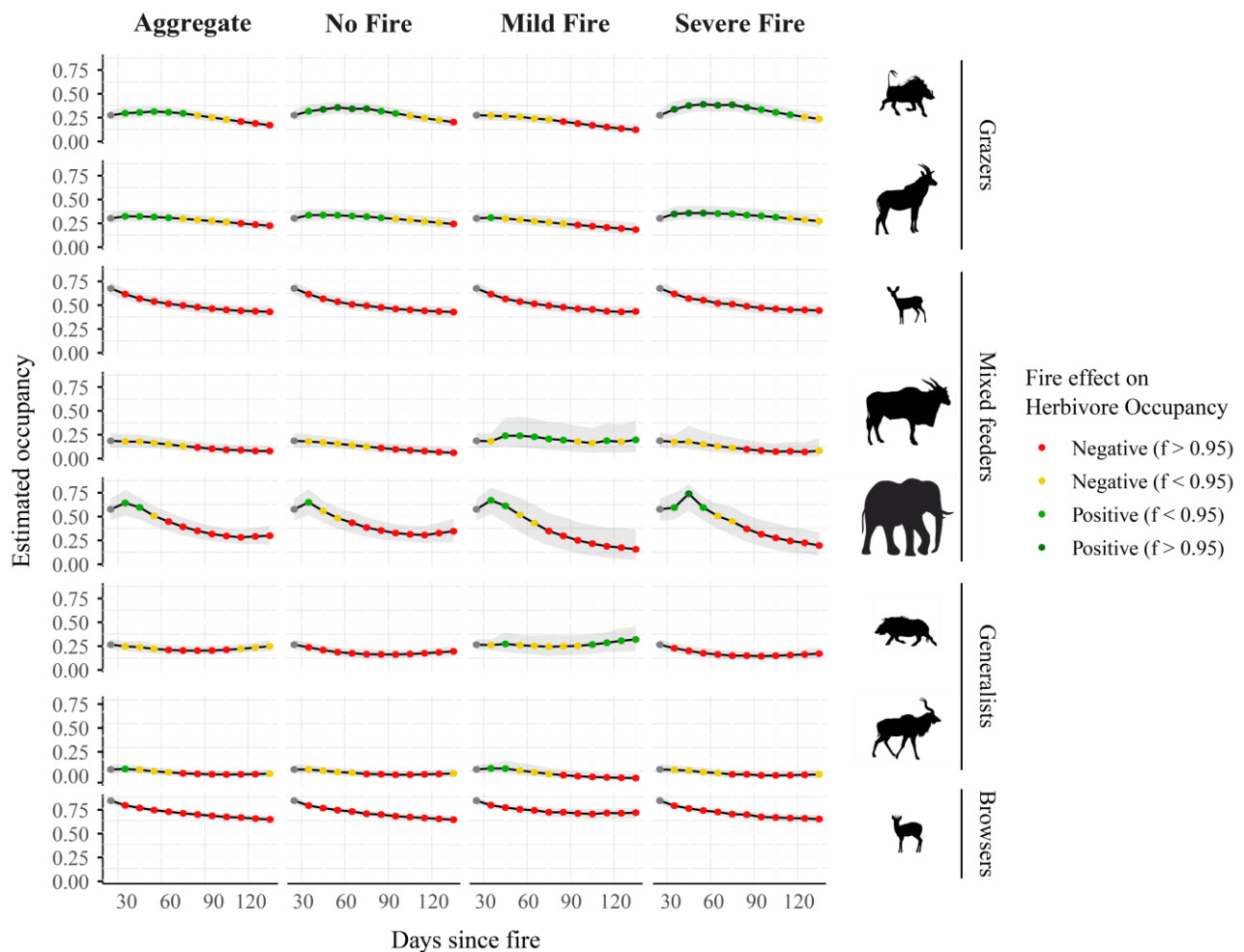


Figure 5.2 – Evolution of the occupancy of each target species in the 6 months after a fire event in camera stations located within a 5 km buffer around fire perimeter, in areas that burned with mild and severe fires and the aggregated results. The species are organized by dietary type (grazers, mixed-feeders, and browsers), and by body weight. The color coding indicates the modeling support for the difference between the estimated mean occupancy before the fire and each subsequent primary period. Modeling support (f) was measured as the proportion of the posterior distribution that is negative or positive, depending on whether the mean occupancy decreases or increases, respectively, compared to the period before the fire. The shadow colors around the lines show the 95% posterior confidence intervals.

5.4.2 Influence of fire area and distance to fire perimeter on herbivore re-colonization

Multicollinearity analysis showed that fire area and distance to the fire perimeter covariates are collinear ($\rho = 0.55$; $p - value = 0.01$). We decided to proceed only with distance to the fire perimeter because the covariate fire area is also collinear with fire severity ($\rho = 0.59$, $p - value < 0.01$).

Our results showed little influence of distance to unburnt on colonization probability of most species (Appendix 5: Table S.5.2). Nevertheless, a tendency for a negative influence was observed for eland ($\beta_4 = -0.37 [-1.76, 1.33]$; $f = 0.74$) and duiker ($\beta_4 = -0.21 [-0.60, 0.15]$; $f = 0.86$), while the remaining species showed no influence (warthog: $\beta_4 = 0.00 [-1.07, 1.05]$; $f = 0.52$) or a positive effect (roan: $\beta_4 =$

0.27 [−0.57, 1.19]; $f = 0.74$, steenbok: $\beta_4 = 0.12$ [−0.51, 0.72]; $f = 0.66$, elephant: $\beta_4 = 1.07$ [−0.32, 2.57]; $f = 0.93$, bushpig: $\beta_4 = 0.29$ [−0.32, 0.92]; $f = 0.81$ and kudu: $\beta_4 = 0.69$ [−1.20, 1.93]; $f = 0.84$; Fig. 5.3; Appendix 5: Table S.5.2).

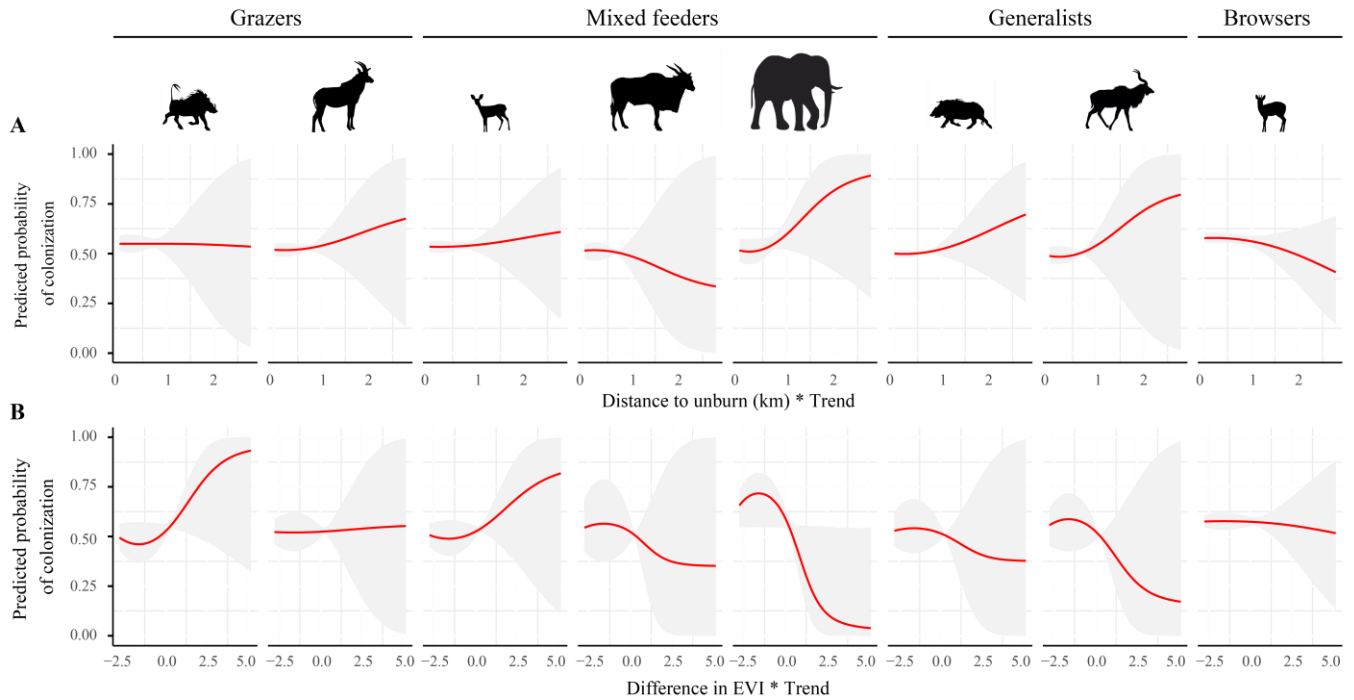


Figure 5.3 – Predicted values of the effects of the interaction between the covariates "Distance to the fire perimeter" (A) and "EVI variation" (B) with trend in the species colonization. In (A) we show how the colonization probability varies with the increase distance to the fire perimeter, while in (B) we show how the colonization probability is affected by EVI variation, from a reduction ($\Delta EVI < 0$) to an increase in primary productivity ($\Delta EVI > 0$). Species are organized by dietary type, i.e. grazers, mixed-feeders, generalists, browsers, and by body weight. The grey shaded area represents 95% posterior confidence intervals.

5.4.3 Influence of primary productivity recovery in herbivore re-colonization

Similarly, to distance to unburnt areas, our results do not show significant influence of ΔEVI in the species re-colonization (Fig. 5.3; Appendix 5: Table S.5.2). However, we depict a general pattern for grazer species and steenbok to respond positively to the ΔEVI (warthog: $\beta_3 = 0.97$ [−0.21, 1.95]; $f = 0.98$, roan ($\beta_3 = 0.05$ [−1.08, 1.09]; $f = 0.55$ and steenbok: $\beta_3 = 0.53$ [−0.51, 1.45]; $f = 0.85$; Fig. 5.3). Conversely, the remaining mixed-feeders, generalists and browser species have higher colonization probability in places with no difference or reduction of primary productivity (eland: $\beta_3 = 0.97$ [−0.21, 1.95]; $f = 0.65$, elephant ($\beta_3 = 0.05$ [−1.08, 1.09]; $f = 0.98$, bushpig: $\beta_3 = 0.97$ [−0.21, 1.95]; $f = 0.62$, kudu $\beta_3 = 0.05$ [−1.08, 1.09]; $f = 0.88$ and duiker: $\beta_3 = 0.53$ [−0.51, 1.45]; $f = 0.59$; Fig. 5.3).

5.4.4 Effect of study area in herbivore re-colonization

Our results highlight differences between guilds, since grazer species are more likely to re-colonize an area after fires in BNP (warthog: $\beta_2 = -1.88 [-2.73, -1.19]$; $f = 1.0$, roan: $\beta_2 = -1.21 [-2.20, -0.52]$; $f = 1.0$; Appendix 5: Table S.5.2), whereas for generalist and browser species the colonization is more likely at CCA, although the effect is more pronounced for bushpig (bushpig: $\beta_2 = 0.83 [0.38, 1.31]$; $f = 1.0$, kudu: $\beta_2 = 0.25 [-0.51, 1.01]$; $f = 0.75$, duiker: $\beta_2 = 0.20 [-0.11, 0.51]$; $f = 0.90$; Appendix 5: Table S.5.2).

5.5 Discussion

Fire is an important component of savanna ecosystems, but the regimes have been altered with the expansion of human populations. Fire has also been used as a management tool to create fresh short grass for herbivores, which would assume an increase in the use of burned areas after a fire (Nieman *et al.*, 2022). Our results partly agree with that premise for grazer species and elephants, but not for the remaining guilds, which tend to decrease in occupancy probability in the study areas throughout the study period. Moreover, the positive effect of fire on grazer species and elephants is temporary, and at the end of the study period the occupancy levels are lower than before fire, which agree with patterns found elsewhere (van Dyke and Darragh, 2007, Green *et al.*, 2015, Eby and Ritchie, 2016, Roerick, Cain and Gedir, 2019). Additionally, our results report that the negative effect of fire in the herbivore occupancy is not restricted to burned areas, but the surroundings of the fire perimeter also suffer declines in herbivore occupancy probability.

We hypothesized that (H1) herbivores (both grazers and browsers) would become locally extinct after a fire event. Although our results show an important reduction in the occupancy probability of most mixed-feeders, generalist and browser species, none become locally extinct after a fire. Conversely, we report a short-term increase in occupancy of burned areas by grazer species and elephants during ca. 2 months. The observed temporal increase in the use of burned area coincides with the period of greater concentration of copper, nitrogen, magnesium and potassium in green leaf tissues (Van de Vijver, Poot and Prins, 1999), as well as the lower live : dead ratio observed after a fire (Eby and Ritchie, 2016). These changes in vegetation nutritional value and live matter lead to increases in primary productivity and, coherently, our results suggest higher colonization probability of grazer species as the primary productivity increases

(H3). Similar patterns have been found in other African savannas (Eby and Ritchie, 2016, Nieman *et al.*, 2022) and in other ecosystem around the world, such as Australia (Lindenmayer *et al.*, 2016) and North America (van Dyke and Darragh, 2007). However, consistently with the temporary increase in occupancy we report, most of these studies refer that the benefits of fire for herbivore populations are limited and, after a period that may vary between 2 month to 1 year, mammal species use of burned areas decreases (van Dyke and Darragh, 2007, Green *et al.*, 2015, Eby and Ritchie, 2016, Roerick *et al.*, 2019), arguably because of a decrease of fire effects on vegetation nutrients and live : dead ratio along with an increase in the size of the grass (Green *et al.*, 2015).

Our results support different spatial responses according to fire severity classes by different guilds. Grazer species revealed higher occupancy probability in the surrounding unburned areas than in burned zones, arguably to forage on the vegetation available there, without the need to move much further. Additionally, the higher use of the edge of the fire perimeter can also be justified by the proximity to fresh and nutritive vegetation that presumably grow in burned areas (Allred *et al.*, 2011), arguably leading to the observed increase in colonization probability of grazer species following the re-growth of the vegetation (i.e. a positive effect of the ΔEVI). Contrarywise, we did not expect grazer species to have higher occupancy in areas after severe fire than in areas of mild fires. Although unexpected, high burn severity stimulates photosynthesis, vertical growth and biomass accumulation of vegetation (Wan, Rhodes and St. Clair, 2014), and consequently a higher increase in forage availability than areas that burnt with mild fires.

Consistent with our hypothesis for browsers, generalists and mixed-feeders (H2; Table 5.1), the avoidance of duiker, bushpig and eland is less pronounced in areas affected by mild fires, compared to areas affected by severe fires and unburned areas, that may be explained by the limited impact of mild fires in woody vegetation (Werner and Prior, 2013, Smit *et al.*, 2016) likely remaining sufficient food available in these areas. Unexpectedly we found a short increase in the occupancy trends observed for elephant in burned areas, especially areas that suffer severe fires where the vegetation was most affected. We propose three plausible explanations for the increased occupancy of burned areas by elephants: (i) elephants may use these areas to forage on fresh shoots that grow on the remnant vegetation, although this alternative is unlikely since few vegetation remains after a severe fire. However, elephants may (ii) forage on the highly nutritious post-fire roots (Anderson *et al.*, 2007), which density is promoted by fire to facilitate plant regeneration (Bombo, Siebert and Fidelis, 2022). The use of burned shrubland to forage on roots has been observed in other species, for instance in grizzly

bear (*Ursus arctos*; Pengelly and Hamer (2006)), and given the importance of roots in the diet of elephants (Kingdon, 2015), this hypothesis cannot be excluded. Additionally, (iii) elephants may use burned areas to move across the landscape, since the reduction in the vegetation by fires facilitates the movement of animals (Nimmo *et al.*, 2019).

We expected that browser, mixed-feeders and generalist species would be the first post-fire colonizers, especially for mild fires (H2) due to its limited effect on woody vegetation. Coherently, our results suggest that, all species of this guild except steenbok, have higher probability of colonizing areas with a small decrease in primary productivity, which correspond to areas of mild fires, where the woody vegetation and especially the green leaves (responsible for the photosynthesis) are less affected (Hempson, Archibald and Staver, 2019).

Our models failed to detect significant influence of distance to unburned areas on species colonization probability, possibly because of the small Euclidean distance between our sampling sites and the edge of burned areas ($\bar{x} = 0.68 \pm 0.61$ range: [0.01, 2.78] km), which may not be enough to capture an effect on the target species. Accordingly, other studies that have reported negligible effects of distance to unburned areas on species' space use also support this pattern, particularly considering the relatively small fire patches relevant to the target species. For instance Cohen *et al.* (2019) detected an impact of the distance to unburned areas on the space use of Eastern wild turkeys (*Meleagris gallopavo silvestris*) only when the distance exceeded 250 meters. This threshold distance may be even greater for intermediate and large mammals. The dilution of the effect may result from the movements between burned areas, where herbivores find nutritious vegetation for foraging, and unburned areas, which offer cover for concealment from predators and thermoregulation (Allred *et al.*, 2011, Cohen *et al.*, 2019). On the other hand, some authors (e.g. García, Castellanos and Pausas, 2016) have attributed the limited effect of distance to unburned areas on arthropod space utilization to a reduced probability of detection following a fire. However, in our study, although we observe an overall reduction in occupancy patterns, this explanation seems unlikely to apply because even species showing temporary increases in occupancy do not demonstrate a significant effect of distance to unburned areas.

The influence of the distance to unburned areas may change over time since a fire event. Nevertheless, the interaction between the trend (time since fire) and distance to unburned areas is only statistically significant for elephants and duikers (Appendix 5: Table S. 5.2). In the case of elephants, the effect of distance to unburned areas weakens as the time since the fire event increases. This suggests that immediately after the fire,

they tend to utilize areas in the center of burned regions, likely for movement and foraging on roots, as previously described. Conversely, the effect of distance to unburned areas on duiker colonization probability strengthens as the time since the fire event increases. Longer periods after a fire, a tendency to stay closer to fire perimeter becomes more pronounced, maybe coinciding with newly sprouted forbs that typically grow in burned areas around four months after a fire (Klop, van Goethem and de longh, 2007)

Longer sampling periods are required to assess the time until the full recovery of wild herbivores occupancy standards and accurately address the main drivers for herbivore recolonization after fire. Nevertheless, we report important negative consequences of fire for herbivore species, which may be related to short inter-fire intervals observed in the study areas (2.08 ± 1.46 years), which may be promoting the growth of tall and less nutritious grass (Fig. 5.1; Archibald and Hempson, 2016). Frequent fires and reduced herbivory, caused by the depletion of the population of large herbivores (Chapter 6), jointly contribute to changes in the vegetation structure, leading to the prevalence of less palatable plants and producing undesirable habitat for herbivores (Archibald *et al.*, 2005, Archibald and Hempson, 2016), which may justify the observed reductions in occupancy patterns in burned areas. Similar patterns have been observed in other systems, for instance in Kruger National Park (South Africa) where frequent fires are reported to limit herbivore numbers (Donaldson *et al.*, 2018). Herbivore species prefer areas where fires occur irregularly with longer intervals between them (Dlamini *et al.*, 2020). With this work, we suggest that fire may not be a good measure to promote herbivores abundance in reduced mammal communities, as has been already postulated by other authors (e.g. Archibald *et al.*, 2005, Donaldson *et al.*, 2018), but largely ignored by managers (van Wilgen, 2009). Instead, it may be more beneficial to promote pyrodiversity, with changes in fire periodicity and severity (Beale *et al.*, 2018, Hempson *et al.*, 2018, Meller *et al.*, 2022), because it promotes habitat heterogeneity and more foraging opportunities for herbivores (Souza, Lourenço and Vieira, 2023). The preference of herbivores for areas with higher fire heterogeneity is likely related to bottom-up processes related to increase in food resources (Lewis *et al.*, 2022) and is recognized to have positive effects on herbivore species richness and abundance (Beale *et al.*, 2018, Cherry *et al.*, 2018).

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Chapter 6

Landscape use by prey: Bottom-up regulation
prevails under reduced perception of risk

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6.1 Abstract

Resource specialist herbivores may suppress antipredator strategies to access scarcely available key resources, while proactive antipredator behaviours should be privileged by generalists or when resources are abundant. We quantified the relative effects of predation- (top-down) and resource-driven (bottom-up) constraints to spatiotemporal patterns of landscape use by a prey community in a dynamic system under low predator abundance, and investigated how prey manage the risk posed by predators with different hunting strategies. We fitted Royle-Nichols co-abundance models to camera trapping data collected between 2017 and 2019 in Bicular National Park (Angola) to assess spatial association/segregation across predator-prey dyads, while accounting for the effects of water and food availability during dry and wet seasons. We further estimated pairwise seasonal differences in diel activity overlap between predator and prey. We failed to detect spatiotemporal proactive antipredator responses either towards the cursorial or ambush predator. The community-wide predator-prey association patterns we found support that predation pressure is insufficient to displace prey from their preferred habitats or to adjust their endogenous clock, and support predominantly bottom-up regulated behaviours. We suggest that, in landscapes where predator density is low, limited perception of risk may prevent the employment of proactive antipredator behaviour.

Keywords: Bottom-up; Control of Risk; Landscape of Fear; Low predator density; Predator's hunting mode; Top-down.

6.2 Introduction

Over recent decades, multiple theories have tried to explain how trophic levels interact with each other to maintain ecosystem balance. Seminal examples include 'Resource-Based Hypothesis', which postulates that organisms are limited by resource availability that determines the shape of the ecological pyramid (Lindeman, 1942). Conversely, the 'Green World Hypothesis' proposes that predators are the main drivers of ecosystem balance through regulating herbivore populations (Hairston *et al.*, 1960), hence indirectly controlling grazing intensity. This theory evolved into the 'Exploitation

Ecosystem Hypothesis' (Oksanen *et al.*, 1981), which theorizes that, in productive terrestrial ecosystems, primary production is high enough to support three trophic levels: plants, herbivores and predators. In less productive ecosystems, however, herbivore populations are too small to support predator populations, so there are only two trophic levels, with herbivores regulating plant biomass. In extremely unproductive ecosystems, the productivity is too low to support more than the plant trophic level. All these theories describe functional relationships whereby prey populations can be regulated by the availability of required resources – bottom-up processes – or by the pressure imposed by carnivores at the top levels of the food chain – top-down processes (Preisser *et al.*, 2005, Hopcraft *et al.*, 2010).

Top-down constraints imposed by predators have been widely described as producing two types of effects on prey: i) 'consumptive' or 'lethal', resulting in the removal of individuals from the population, therefore directly influencing prey population demography (Preisser *et al.*, 2005); and ii) 'non-consumptive', which lead to changes in behavioural and physiological prey traits, driven by the risk of predation (Lima and Dill, 1990, Say-Sallaz *et al.*, 2019, Wirsing *et al.*, 2021). Recent studies have suggested that the importance of non-consumptive effects may rival or even exceed those of lethal effects in wildlife communities (Lima and Dill, 1990, Preisser *et al.*, 2005, Wirsing *et al.*, 2021). Non-consumptive effects are reflected in prey's antipredator response which has been described by Creel (2018) as the 'Control of Risk Hypothesis', and can be classified as: i) reactive, when predation risk is unpredictable or uncontrollable; or ii) proactive, when prey are able to anticipate predation risk. On the latter, one of the proposed prey survival mechanisms entails the mental mapping of the spatial variation of risk – the 'Landscape of Fear' (Laundré *et al.*, 2001, Gaynor *et al.*, 2019). This strategy allows individuals to use the landscape in a way that minimizes the risk of an encounter with a predator. However, whether these theories apply across systems and species remains poorly understood. For example, when prey species acquire a signal of a cursorial predator presence they may alter their spatiotemporal dynamics to avoid predation (Latombe, Fortin and Parrott, 2014), but prey may not perceive variation in predation risk in landscapes where cursorial predator density is low (Middleton *et al.*, 2013). Regardless, prey face a continuous trade-off between the need of acquiring resources while managing the risk of being preyed upon (Hopcraft *et al.*, 2010). The 'Optimal Foraging Theory' (OFT) (Sinervo, 1997) attempts to tackle this trade-off by proposing that animals maximize fitness by securing the highest benefit (energy) for the lowest cost, while avoiding predation (Pyke *et al.*, 1977). Hence, prey species more susceptible

to predation (primary prey) should be more constrained by the predator's activity and space use than less important prey species (secondary prey) (Valeix *et al.*, 2009, Thaker *et al.*, 2011, Tambling *et al.*, 2012).

Predator species may be classified as either ambush or cursorial, according to their preferred predation strategy. When hunting, ambush predators tend to use areas with high likelihood of meeting prey and with sufficient vegetation concealment that allows approaching without being noticed (Preisser, Orrock and Schmitz, 2007). This spatial pattern should promote proactive predator avoidance (Makin *et al.*, 2017b) as prey are able to avoid areas with perceived high risk of an ambush (Thaker *et al.*, 2011), or temporal avoidance of predators in high risk areas (Tambling *et al.*, 2012). Conversely, cursorial predators' distribution in the landscape is generally less predictable because cues of their presence tend to be more dispersed, and because of their lower dependency on specific landscape features to hunt (Makin *et al.*, 2017b). This behaviour should limit prey's ability to anticipate predation risk (Preisser *et al.*, 2007), relegating antipredator behaviours to reactive responses (Wirsing *et al.*, 2021). Therefore, risk perception by prey should be a mental construct derived from the abundance of predators, how they are distributed in the landscape, their diel activity patterns and from their preferred hunting strategy (Creel, 2018, Gaynor *et al.*, 2019, Wirsing *et al.*, 2021). In summary, the spatial behaviour exhibited by prey should be shaped by resource availability and perceived risk. When resources are limited, prey are expected to prioritize meeting nutritional and hydric needs, and therefore tolerate higher predation risk (Owen-Smith, 2015, Riginos, 2015, Davies *et al.*, 2021). Contrariwise, prey should exhibit stronger antipredator responses when resources are widely available (Hopcraft *et al.*, 2010). Under this reasoning, we hypothesize that spatial patterns of landscape use by prey should be mainly governed by bottom-up (resource-based) processes in resource depleted scenarios, whereas top-down (predation-related) processes should increase their relative importance in constraining landscape use by prey in resource-rich contexts (Owen-Smith, 2015). Furthermore, we hypothesize that under similar resource availability circumstances, proactive antipredator spatial behaviour is stronger towards ambush than for cursorial predators.

Using a protected area in Southern Angola with low predator abundance as a case study, we investigate the effects of top-down and bottom-up processes in shaping spatiotemporal patterns of prey species in a dynamic system. We hypothesize that: H1 - Top-down responses are more pronounced during wet season, whereas bottom-up processes increase during dry season, especially for predominantly grazers and water-

dependent species; H2 - primary prey employ stronger proactive antipredator behaviour towards a predator than secondary prey; H3 - ambush predators induce proactive antipredator responses, limiting prey's access to resource-rich areas either spatially or temporally; and H4 - cursorial predators induce limited spatial nor temporal responses on prey, because risk unpredictability lead prey to rely mainly on reactive responses.

6.3 Methods

6.3.1 Study area

This study was carried out in Bicular National Park (BNP) (S 15.1°, E 14.8°), Angola (Fig. 6.1). The area expands over 6 900 km² and altitude ranges between 1200 and 1400 m.a.s.l., with a mean annual temperature of ca. 20.5°C and mean annual precipitation of 857.4 mm (<http://www.sasscalweather.net.org/>). BNP lies in the transition between the Angolan miombo woodland, Zambezian *Baikiaea* woodland and Angola mopane woodland ecoregions (Huntley *et al.*, 2019b). The largely intact core area of BNP is comprised of a mosaic of miombo woodland, *Baikiaea-Burkea* woodland, shrub/thicket vegetation and seasonally flooded grasslands (Godlee *et al.*, 2020). Rains are concentrated between November and April, providing food and water, while during dry season from May to October, the availability of water and the quantity and quality of vegetation gradually reduces.

BNP hosts a rich wildlife diversity, including resident populations of African elephant (*Loxodonta africana*), common eland (*Taurotragus oryx*), roan antelope (*Hippotragus equinus*, hereafter roan), greater kudu (*Tragelaphus strepsiceros*, hereafter kudu), bushpig (*Potamochoerus larvatus*), warthog (*Phacochoerus africanus*), common duiker (*Sylvicapra grimmia*, hereafter duiker), steenbok (*Raphicerus campestris*), Malbrouck-monkey (*Chlorocebus cynosuros*, hereafter monkey), scrub hare (*Lepus saxatilis*, hereafter hare), leopard (*Panthera pardus*), spotted-hyaena (*Crocuta crocuta*), African wild dog (*Lycaon pictus*), serval (*Leptailurus serval*) and caracal (*Caracal caracal*) (Beja *et al.*, 2019, Monterroso *et al.*, 2020b).

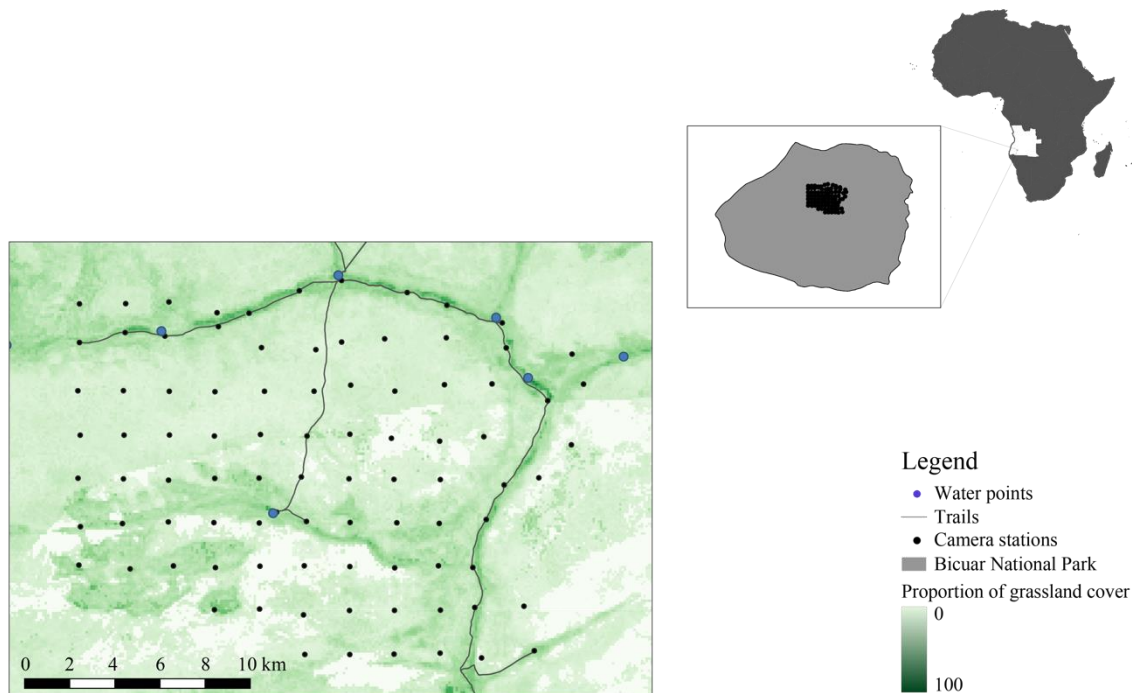


Figure 6.1 - Study area location and camera trapping stations in BNP. The background describes the proportion of grassland cover across the sampled areas, along with the location of the permanent water sources and trails.

6.3.2 Data collection

Camera trapping stations were uniformly deployed, following a grid-sampling scheme at a ca. 2 km inter-camera distance, ensuring spatial independence (Monterroso *et al.*, 2013, Fig. 6.1). Field sampling occurred in two different periods: i) July 2017 through June 2018, with 51 camera stations of three different models: Cuddeback C1 Strobe Flash (n=11; Cuddeback, Green Bay, Wisconsin, USA), Reconyx Hyperfire HC600 (n=32; Reconyx, Holmen, Wisconsin, USA) and ScoutGuard SG570 (n=8, HCO Outdoor Products, Norcross, Georgia, USA); and ii) November 2018 through November 2019, with an expanded sampling grid of 91 camera stations, all Reconyx Hyperfire 2 (n=91; Reconyx, Holmen, Wisconsin, USA).

Cameras were deployed on trees approximately 0.6 m off the ground without lures or attractants and were set to shoot a burst of 3 (ScoutGuard), 5 (Cuddeback) or 10 (Reconyx) photos when triggered without delay time (0 s). We sampled continuously, during both dry (May-October) and wet (November-April) seasons. Camera stations were serviced every 3-4 months.

6.3.3 Detections and covariates

Initial data processing was carried out using the *camtrapR* v.2.0.2 R package (Niedballa *et al.*, 2016) and included tagging each file with identifiers for camera station, date, time and detected species in each detection record.

Our study focused on two of BNP's apex predator species with different hunting strategies - the leopard (density: 2-3 ind/100km²; Monterroso, unpublished data) and the spotted-hyaena (density: 0.7 ind/100km²; Monterroso, unpublished data). Insufficient data on wild dogs precluded their inclusion in the analysis. We selected a suite of locally relevant prey for each of the predators (Bacchiocchi, 2020, Jesus, 2021). Following Trites and Joy (2005) prey were classified as primary for a predator whenever their frequency of consumption in BNP exceeds 5% of its diet, otherwise the species is classified as secondary prey. Using this reasoning duiker, bushpig, kudu and monkey were considered as primary prey species for leopard, while duiker and bushpig were considered as primary prey for spotted-hyaena. Hare, warthog and roan were classified as secondary prey for both predators, whereas kudu and monkey were considered as secondary prey for spotted-hyaena only.

We built detection/non-detection matrices on single-day sampling occasions from each species' detection records. Encounter histories consisted of station- and species-specific records whereby 1 denotes at least one detection of the target species during a given sampling occasion, and 0 denotes non-detection (MacKenzie *et al.*, 2017).

The set of state covariates for each target species was defined based on *a priori* hypotheses on their feeding and water requirements, as assessed from the literature (Table 6.1). The location of water sources was digitized from Google Earth® Satellite imagery and ground validated, and water accessibility was estimated as the Euclidean distance (km) from each camera-trap station to the nearest water body. The mean proportion of grassland and shrubland cover in a 1 km buffer around each station (Rich *et al.*, 2017b) were calculated as a proxy for food availability according to each species' dietary preferences (Table 6.1), and obtained from the Copernicus Global Land Cover raster with a 100 m resolution (<https://land.copernicus.eu/global/products/lc>).

All continuous covariates were standardized to z-scores to avoid data dispersion bias and facilitate the numeric convergence of our models (MacKenzie *et al.*, 2017).

Table 6.1- Description of a priori hypotheses based on target species' ecological traits, and respective covariates, including their mean, standard deviation (SD) and range of values.

Covariate	Mean±SD [range]	Ecological Trait	Species	Hypothesis	References
Proportion of grassland cover	22.1 ± 8.8 % [0.0 - 43.0]	Predominantl y Grazers	Scrub hare Roan Antelope Warthog	During dry season, the lower quality of available vegetation forces grazers to expose themselves to a higher predation risk while foraging. Prey species are expected to prioritize food acquisition over predator avoidance	(Valeix <i>et al.</i> , 2009, Thaker <i>et al.</i> , 2011, Hempson <i>et al.</i> , 2015, Wirsing <i>et al.</i> , 2021)
		Generalists	Malbrouck monkey Bushpig	Generalist species are usually associated with shrubland areas. However, due to their unspecialized dietary requirements, these species are expected to be less restricted to shrubland areas than browser species	(Thaker <i>et al.</i> , 2011, Hempson <i>et al.</i> , 2015)
Proportion of shrubland cover	32.2 ± 8.2 % [17.3 - 53.4]	Predominantl y Browsers	Greater Kudu Common Duiker	Predominantly browsers are expected to use areas with increased shrubland cover, which offers food opportunities as well as shelter against predators	(Thaker <i>et al.</i> , 2011, Hempson <i>et al.</i> , 2015, Wirsing <i>et al.</i> , 2021)
		High	Roan Antelope Warthog	Species with higher surface water dependency are expected to be spatially constrained by water availability. Predator abundance is not expected to restrict prey species' access to water sources	(Périquet <i>et al.</i> , 2010, Valeix, 2011, Kihwele <i>et al.</i> , 2020)
Water Dependency	4.6 ± 2.6 km [0.2 - 12.5]	Low	Greater Kudu Bushpig Common Duiker Scrub hare	Less water-dependent prey species will not prioritize access to water over safety. The abundance of these prey species is expected to be more influenced by the abundance of predator species than by the availability of surface water	(Périquet <i>et al.</i> , 2010, Valeix, 2011, Kihwele <i>et al.</i> , 2020)

6.3.4 Data analysis

We used Bayesian two-species co-abundance models (Brodie *et al.*, 2018) to estimate the influence of the local abundance of a predator on the local abundance of a prey while accounting for the effect of resource-related covariates. The abundance component formulation of our models follows the Royle-Nichols (RN) parameterization (Royle and Nichols, 2003), based on observed species-specific detection histories of our target prey and predator species. We assumed local abundance as being influenced by 'habitat' and 'distance to water', and detection by whether a camera trap is set on a trail or otherwise. We independently modelled each season (wet and dry) for each year, such that populations were considered closed within a season, but abundance was allowed to

change across seasons and years. We assumed constant covariate effects among years for the same season. Model formulation for predators was:

$$\begin{aligned} N_{i,k}^{Pred} &\sim \text{Poisson}(\lambda_{i,k}^{Pred}) \\ \log(\lambda_{i,k}^{Pred}) &= \beta_{0,k}^{Pred} \\ y_{i,j,k}^{Pred} | N_{i,k}^{Pred} &\sim \text{Poisson}(N_{i,k}^{Pred}, \phi_{i,j,k}^{Pred}) \\ \text{logit}(\phi_{i,j,k}^{Pred}) &= \alpha_{0,k}^{Pred} + \alpha_1^{Pred} \times \text{trail}_i \end{aligned}$$

Where $\lambda_{i,k}^{Pred}$ denotes the mean local abundance of the predator at the site i in year k , $\phi_{i,j,k}$ is the individual detection probability at site i , occasion j and year k , $N_{i,k}^{Pred}$ is the local abundance of the predator at the site i in year k , and $y_{i,j,k}$ is the observed detection/non-detection at the site i , occasion j and in year k . The model formulation for prey species is similar to predators', except for the sub-model explaining the spatial heterogeneity in abundance:

$$\log(\lambda_{i,k}^{Prey}) = \beta_{0,k}^{Prey} + \beta_1^{Prey} \times \text{habitat}_{i,k} + \beta_2^{Prey} \times \text{DistWater}_i + \gamma \times N_{i,k}^{Pred}$$

Where $\beta_{0,k}$ is the baseline abundance in year k , β_1 and β_2 are the coefficients for the effect of each state covariate, and γ is the coefficient for the influence of predator abundance on prey abundance at the site i .

Occupancy ($\psi_{i,k}$) was defined as the probability that a species uses a particular camera trapping site in a specific year, despite potentially not being detected (MacKenzie *et al.*, 2017). Following Royle and Nichols (2003), we modelled occupancy as a function of abundance as:

$$\psi_{i,k} = 1 - \exp(-\lambda_{i,k}).$$

Models were fit in JAGS v.4.3.0, executed from R v.4.1.2 (R Core Team, 2021) using *R2Jags* v.0.7-1 (Su and Yajima, 2015) through *rjags* v.4-12 (Plummer, 2016). We ran three Markov Chain Monte Carlo (MCMC) chains with 150,000 iterations after a 50,000 iteration burn-in and thinned by 30. Prior distributions for each of our model parameters followed a uniform distribution between -10 and 10. Model convergence was assessed from a visual inspection of chain trace plots and from the Gelman-Rubin statistic ($\hat{R}$), where values < 1.1 suggested reliable convergence (Gelman and Rubin, 1992). Goodness-of-Fit was assessed by calculating the Bayesian p-value (BPV, Gelman *et al.*, 1996) and by visual inspection of the distribution of residuals, whereas overdispersion was evaluated using the overdispersion parameter ($\hat{c}$; Appendix 6: Table S.6.2) (Kéry

and Royle, 2015). The relative importance of each covariate was assessed by inspecting the probability posterior distribution of corresponding coefficients. All results are presented as mean $\pm$ posterior standard deviation [95% Bayesian Credible Intervals], unless explicitly stated otherwise.

We assessed the relative importance of predator abundance (top-down process) and resource availability (bottom-up process) on spatial abundance of prey using a contrast measure between the parameter estimates obtained in the RN models, following $\log \frac{|\gamma|}{|\beta|}$. Under this rationale, $\log \frac{|\gamma|}{|\beta|} > 0$ indicates a stronger effect of predators on prey spatial behaviour, whereas $\log \frac{|\gamma|}{|\beta|} < 0$ suggests a stronger effect of resource availability.

The activity overlap (AO) between predator and prey species is the proportion of time that the activity of each predator and prey species pair overlapped within their diel cycle, and was calculated using non-parametric circular kernel density functions (Ridout and Linkie, 2009). This method considers that a species' trap rate at a given time of day is proportional to the level of activity of its population at that time, and the total amount of activity is proportional to the area under the trap rate curve (Ridout and Linkie, 2009). For each focal species, the time of independent records (i.e. time between consecutive detections of the same species >30 min (Monterroso *et al.*, 2013)) were converted in radians, where 0 or 2π correspond to midnight and π to noon. Mathematically, the calculation of AO required a previous calculation of the activity pattern of each species, which was assumed to be described by a circular distribution defined as a nonparametric Von Mises kernel probability density function: $f(x) = \frac{1}{n} \sum_{i=1}^n \frac{e^{K \cos d_i}}{2\pi I_0(K)}$, where the Von Mises concentration parameter (K) defines the degree of smoothing and $I_0()$ is the modified Bessel function of order 0 (Ridout and Linkie, 2009, Linkie and Ridout, 2011). Lastly, for each predator-prey species pair, the AO was calculated as the intersection of the proportion of time when both species are active within their diel cycle (Ridout and Linkie, 2009). We used empirical bootstrap resampling with 1000 iterations to generate 95% confidence intervals. All activity-related calculations were performed using the R package *overlap* v.0.3.4 (Ridout and Linkie, 2009).

6.4 Results

Sampling effort comprised 19,068 trap-days during dry season (2017: 4,495; 2019: 14,573) and 21,376 during wet season (2017-2018: 7,961; 2018-2019: 13,415). We

collected 6,004 and 6,018 independent detections of our target species during dry and wet seasons, respectively. An overview of the number of occasions with detection and non-detections of each target season is provided in the Appendix 6: Table S.6.3.

Although the estimates indicate lower density of spotted-hyaena (0.7 ind/100km²; Monterroso, unpublished data) than leopard (2-3 ind/100km²; Monterroso, unpublished data) in BNP, the first exhibited a wider occupancy ($\hat{\psi}_{hyaena} = 0.47 \pm 0.06[0.34; 0.59]$ vs. $\hat{\psi}_{leopard} = 0.38 \pm 0.07[0.25; 0.53]$). Among prey species, duiker exhibited the highest mean local abundance and was the most widely distributed, followed by bushpig, roan, hare and monkey. Warthog and kudu were the species displaying the lowest mean local abundance and occupancy (Table 6.2).

Table 6.2 - Estimates of covariate effects – Habitat (grassland/shrubland), distance to water, predator abundance (Gamma) – on each prey species' local abundance, occupancy and mean local abundance. Results are presented as mean estimated parameter $\pm$ posterior standard deviation [95% Bayesian credible intervals].

Prey	Predator	Parameter	Dry	Wet
Roan antelope	Leopard	Habitat	0.34 $\pm$ 0.27 [-0.19; 0.87]	1.11 $\pm$ 0.15 [0.83; 1.41]
		Distance to Water	-0.18 $\pm$ 0.29 [-0.76; 0.38]	-0.09 $\pm$ 0.12 [-0.32; 0.13]
		Gamma	1.43 $\pm$ 0.36 [0.82; 2.33]	0.31 $\pm$ 0.11 [0.08; 0.54]
	Spotted hyaena	Habitat	0.48 $\pm$ 0.20 [0.11; 0.90]	1.12 $\pm$ 0.16 [0.82; 1.44]
		Distance to Water	-0.16 $\pm$ 0.24 [-0.65; 0.30]	-0.13 $\pm$ 0.12 [-0.36; 0.09]
		Gamma	1.07 $\pm$ 0.25 [0.62; 1.58]	0.11 $\pm$ 0.07 [-0.02; 0.26]
	-	Occupancy	0.47 $\pm$ 0.10 [0.31; 0.68]	0.43 $\pm$ 0.04 [0.35; 0.51]
		Mean Local Abundance	2.64 $\pm$ 1.67 [0.93; 7.24]	1.12 $\pm$ 0.17 [0.85; 1.5]
Greater kudu	Leopard	Habitat	0.04 $\pm$ 0.29 [-0.57; 0.58]	-0.64 $\pm$ 0.27 [-1.22; -0.16]
		Distance to Water	-1.04 $\pm$ 0.47 [-2.02; -0.21]	-0.95 $\pm$ 0.31 [-1.58; -0.38]
		Gamma	-0.27 $\pm$ 0.35 [-1.05; 0.31]	-0.69 $\pm$ 0.40 [-1.59; 0.01]
	Spotted hyaena	Habitat	0.00 $\pm$ 0.29 [-0.61; 0.55]	-0.59 $\pm$ 0.25 [-1.12; -0.14]
		Distance to Water	-1.13 $\pm$ 0.5 [-2.21; -0.21]	-1.00 $\pm$ 0.33 [-1.66; -0.40]
		Gamma	-0.42 $\pm$ 0.43 [-1.36; 0.31]	-0.40 $\pm$ 0.23 [-0.91; 0.01]
	-	Occupancy	0.26 $\pm$ 0.11 [0.09; 0.51]	0.16 $\pm$ 0.04 [0.09; 0.25]
		Mean Local Abundance	0.41 $\pm$ 0.30 [0.15; 1.16]	0.22 $\pm$ 0.04 [0.16; 0.32]
Warthog	Leopard	Habitat	0.01 $\pm$ 0.29 [-0.58; 0.54]	0.17 $\pm$ 0.16 [-0.17; 0.48]
		Distance to Water	0.13 $\pm$ 0.27 [-0.41; 0.65]	-0.52 $\pm$ 0.23 [-0.99; -0.08]
		Gamma	0.41 $\pm$ 0.29 [-0.11; 0.98]	0.34 $\pm$ 0.2 [-0.05; 0.74]
	Spotted hyaena	Habitat	0.08 $\pm$ 0.28 [-0.48; 0.60]	0.18 $\pm$ 0.17 [-0.15; 0.50]
		Distance to Water	0.22 $\pm$ 0.29 [-0.35; 0.77]	-0.47 $\pm$ 0.24 [-0.94; -0.01]

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		Gamma	0.68 ± 0.28 [0.17; 1.29]	0.31 ± 0.12 [0.09; 0.54]
		Occupancy	0.27 ± 0.08 [0.13; 0.45]	0.23 ± 0.05 [0.14; 0.33]
		Mean Local Abundance	0.34 ± 0.12 [0.20; 0.63]	0.29 ± 0.04 [0.23; 0.38]
Bushpig	Leopard	Habitat	0.54 ± 0.18 [0.20; 0.89]	0.01 ± 0.10 [-0.20; 0.21]
		Distance to Water	-0.43 ± 0.23 [-0.90; 0.01]	0.06 ± 0.12 [-0.18; 0.30]
		Gamma	1.15 ± 0.30 [0.64; 1.82]	0.83 ± 0.14 [0.57; 1.12]
	Spotted hyaena	Habitat	0.57 ± 0.17 [0.24; 0.88]	-0.02 ± 0.11 [-0.24; 0.19]
		Distance to Water	-0.39 ± 0.24 [-0.84; 0.07]	0.05 ± 0.12 [-0.19; 0.28]
		Gamma	1.18 ± 0.27 [0.73; 1.73]	0.47 ± 0.07 [0.34; 0.62]
		Occupancy	0.56 ± 0.11 [0.36; 0.79]	0.66 ± 0.07 [0.53; 0.79]
		Mean Local Abundance	3.92 ± 5.49 [0.96; 19.8]	1.61 ± 0.34 [1.1; 2.40]
Common duiker	Leopard	Habitat	0.16 ± 0.08 [0.00; 0.30]	0.04 ± 0.05 [-0.07; 0.14]
		Distance to Water	-0.05 ± 0.09 [-0.24; 0.12]	0.12 ± 0.05 [0.01; 0.22]
		Gamma	0.24 ± 0.13 [0.01; 0.51]	0.28 ± 0.10 [0.10; 0.48]
	Spotted hyaena	Habitat	0.16 ± 0.08 [0.00; 0.31]	0.03 ± 0.05 [-0.08; 0.13]
		Distance to Water	-0.07 ± 0.09 [-0.25; 0.11]	0.09 ± 0.05 [-0.02; 0.20]
		Gamma	0.15 ± 0.09 [-0.03; 0.34]	0.08 ± 0.04 [0.00; 0.16]
		Occupancy	0.91 ± 0.03 [0.84; 0.96]	0.94 ± 0.01 [0.91; 0.97]
		Mean Local Abundance	2.82 ± 0.41 [2.17; 3.76]	3.06 ± 0.17 [2.74; 3.42]
Malbrouck monkey	Leopard	Habitat	-0.03 ± 0.23 [-0.51; 0.39]	-0.19 ± 0.24 [-0.68; 0.25]
		Distance to Water	-0.48 ± 0.31 [-1.10; 0.10]	-0.16 ± 0.24 [-0.65; 0.28]
		Gamma	1.00 ± 0.68 [0.20; 2.82]	1.56 ± 0.40 [0.90; 2.34]
	Spotted hyaena	Habitat	0.07 ± 0.20 [-0.34; 0.45]	-0.34 ± 0.25 [-0.85; 0.13]
		Distance to Water	-0.52 ± 0.28 [-1.08; 0.02]	-0.16 ± 0.24 [-0.63; 0.31]
		Gamma	0.83 ± 0.22 [0.42; 1.31]	0.86 ± 0.14 [0.60; 1.15]
		Occupancy	0.29 ± 0.06 [0.18; 0.42]	0.21 ± 0.04 [0.14; 0.29]
		Mean Local Abundance	0.86 ± 1.18 [0.35; 3.46]	0.58 ± 0.25 [0.32; 1.26]
Scrub hare	Leopard	Habitat	0.62 ± 0.24 [0.16; 1.10]	0.86 ± 0.23 [0.41; 1.30]
		Distance to Water	-0.05 ± 0.22 [-0.5; 0.37]	0.43 ± 0.14 [0.15; 0.70]
		Gamma	0.98 ± 0.29 [0.48; 1.59]	0.85 ± 0.26 [0.39; 1.41]
	Spotted hyaena	Habitat	0.66 ± 0.21 [0.27; 1.09]	0.95 ± 0.21 [0.54; 1.37]
		Distance to Water	-0.03 ± 0.22 [-0.47; 0.38]	0.32 ± 0.14 [0.03; 0.58]
		Gamma	0.80 ± 0.24 [0.39; 1.33]	0.24 ± 0.11 [0.04; 0.47]
		Occupancy	0.38 ± 0.07 [0.26; 0.53]	0.28 ± 0.04 [0.2; 0.37]
		Mean Local Abundance	1.14 ± 0.41 [0.64; 2.18]	0.53 ± 0.10 [0.37; 0.77]

6.4.1 Spatial response of prey to water availability

We found most prey species not to be spatially constrained by water availability (Table 6.2; Supporting Information: Fig. S.6.1). The kudu was the species most affected by distance to the nearest water source. Warthog was negatively influenced by distance to water only during wet season. Contrarywise, our results confirm that hare are more abundant further from the water points during wet season (Table 6.2; Supporting Information: Fig. S.6.1).

6.4.2 Spatial response of prey to feeding resources' availability

We found the strongest effect of feeding resource availability on two predominantly grazer species: the roan and the hare. We only observed a tendency for the warthog, the other grazer prey, to be more abundant in areas dominated by grasslands during wet season (Table 6.2; Supporting Information: Fig. S.6.2).

Generalists and predominantly browsers were not constrained by forage availability (Table 6.2; Supporting Information: Fig. S.6.2). The exceptions were the bushpig and the duiker, which responded positively to forage availability during dry season. Unexpectedly, we found the kudu to respond negatively to forage availability during wet season (Table 6.2; Supporting Information: Fig. S.6.2).

6.4.3 Spatial response of prey to the local abundance of predators

We found a consistent pattern of spatial association between prey and predators regardless of prey's importance in predators' diet. The only prey spatially avoiding predators was the kudu, although this effect was only tendential during dry season (Table 6.2 and Fig. 6.2).

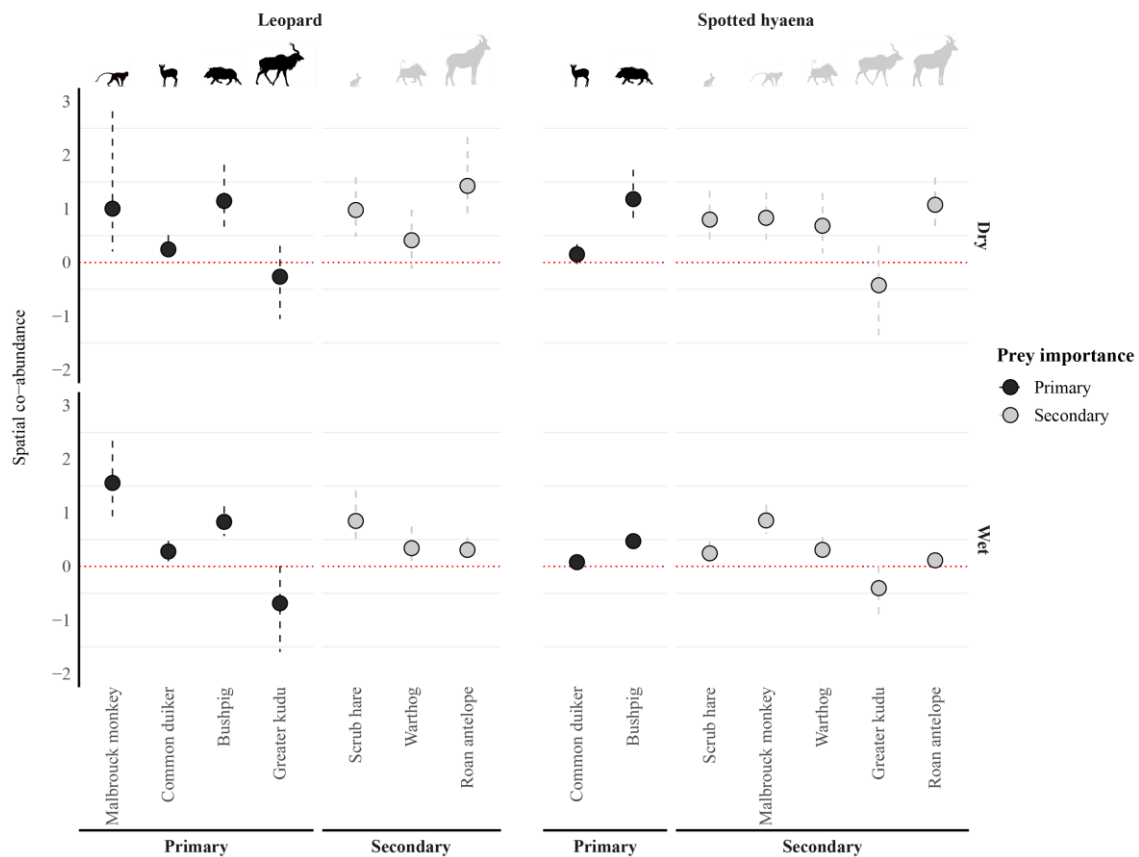


Figure 6.2 - Untransformed coefficient estimates (and respective 95% Bayesian credible intervals) of the effect of predators on prey species' local abundance (spatial co-abundance), based on leopard (left) and spotted-hyaena (right) dominance models for dry (top) and wet (bottom) seasons. Prey species are classified according to importance for each predator's diet – primary prey if the Frequency of Occurrence (FO) > 5%; secondary prey if $FO < 5\%$.

6.4.4 Contrast between resource availability and predator avoidance effects

Leopard's primary prey: we found local abundance of leopards to have a stronger effect on prey than resource availability. The pattern was most evident during wet season, with three out of four primary prey species for leopards – monkey, duiker and bushpig – exhibiting >95% contrast posterior distribution mass on the positive side (Figs. 6.3-6.4). Although less strong, the weight of evidence still supports stronger predator abundance effect is higher than bottom-up effects during dry season (Figs. 6.3-6.4). The positive contrast would only indicate predator avoidance if the model estimates for predator vs. prey co-abundance was negative. However, our results indicate co-abundance (positive effect), so predator abundance is not sufficient to displace prey. The kudu was the exception to the above-described pattern of primary leopard prey. We found water-related bottom-up effects on kudu to outweigh predator-related ones, particularly during wet season (Fig. 6.3). Access to forage and leopard abundance

revealed equally strong effects on three species during dry season – duiker, bushpig and kudu – and only on kudu during wet season (Fig. 6.4).

Leopard's secondary prey: we found a tendency for stronger predator co-abundance than water-related bottom-up effects in two out of three secondary prey species for leopard, as supported by >89% contrast posterior distribution mass on the positive side (Fig. 6.3). The exception was the warthog, for which predator abundance and water accessibility had near-similar importance (Fig. 6.3). Regarding food availability, we found an equivalent effect for top-down and bottom-up processes except for roan, which preferentially responded to leopard abundance during dry season, and to food availability during wet season (Fig. 6.4).

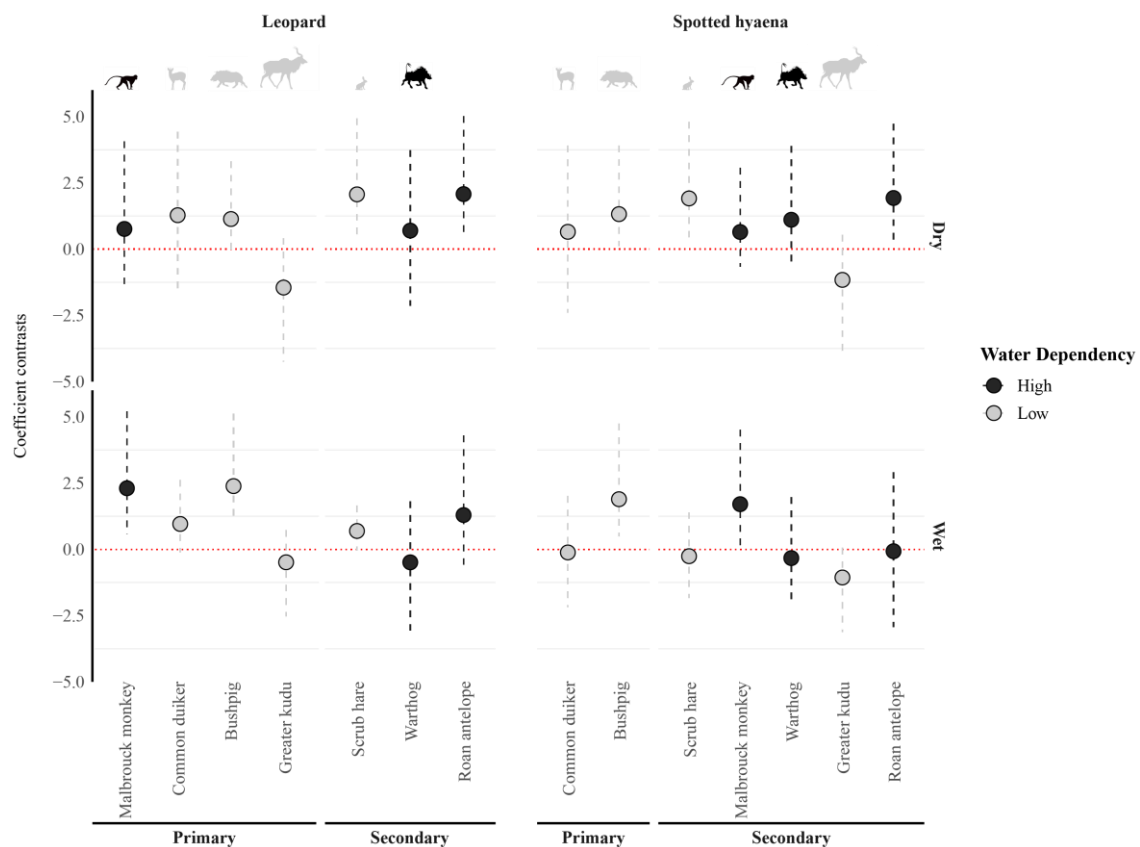


Figure 6.3 – Coefficient estimate contrasts (and respective 95% Bayesian credible intervals) between the effects of predator local abundance and of distance to the nearest water source, on prey species' local abundance, based on leopard and spotted-hyaena dominance models for dry (top) and wet (bottom) seasons. Prey species are classified according to: i) water dependency – high, if requiring near daily access to drinking water; low, if able to obtain sufficient water from forage or only requiring access to drinking water irregularly (Kihwele *et al.*, 2020); and ii) importance for each predator's diet – primary prey if the Frequency of Occurrence (FO) > 5%; secondary prey if FO < 5%.

Spotted-hyaena's primary prey: The bushpig was mostly influenced by spotted-hyaena abundance regardless of the resource (water or forage availability; Figs. 6.3-6.4), whereas the duiker exhibited equivalently strong response to spotted-hyaena and to resource availability (Figs. 6.3-6.4). These patterns were consistent across seasons.

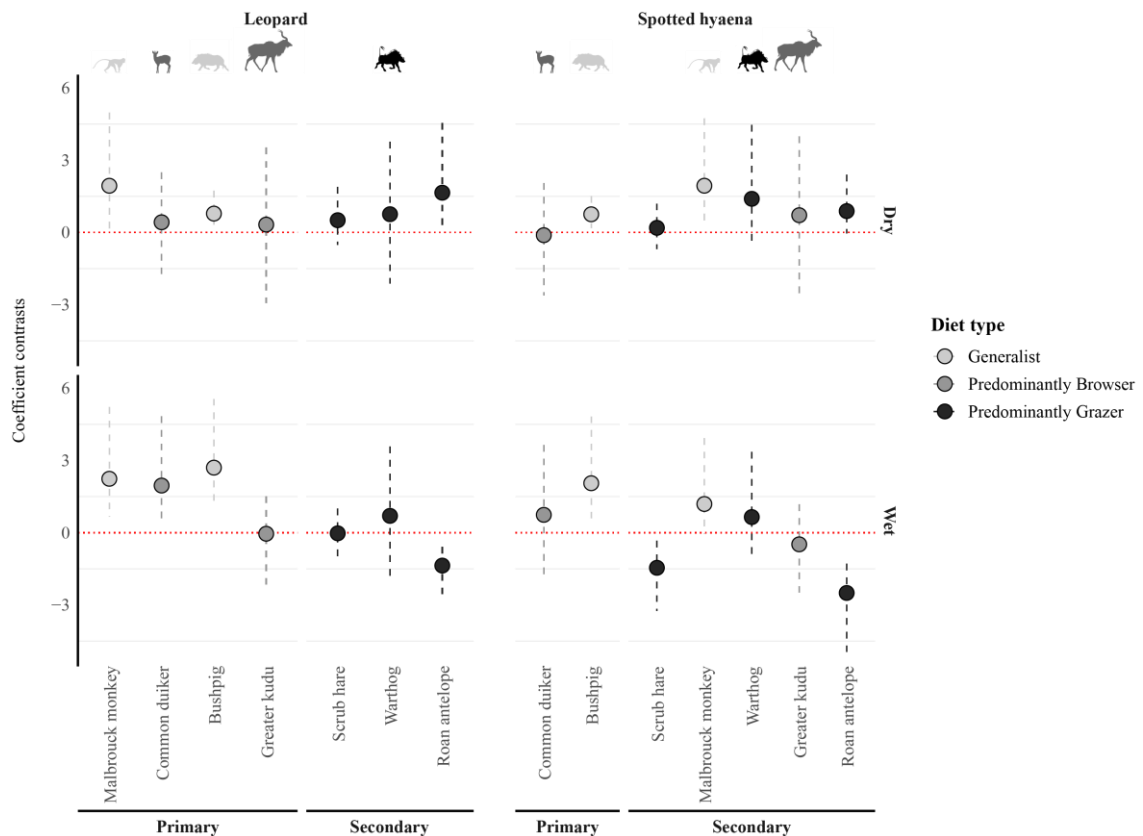


Figure 6.4 - Coefficient estimates contrast (and respective 95% Bayesian credible intervals) between the effects of predator local abundance and of habitat, on prey species' local abundance, based on leopard and spotted-hyaena dominance models for dry (top) and wet (bottom) seasons. Prey species are classified according to: i) diet type – predominantly grazer, if more than 60% of their diet is comprised by monocots; generalists, if they consume more than 20% of a variety of food, i.e. monocots, dicots or fruits; predominantly browser, if more than 70% of their diet is comprised by dicots (Hempson *et al.*, 2015); and ii) importance for each predator's diet – primary prey if the Frequency of Occurrence (FO) > 5%; secondary prey if FO < 5%

Spotted-hyaena's secondary prey: Regardless of their water dependency, secondary prey tended to exhibit stronger spatial responses to predator abundance than to resource availability during dry season when the resource in question was water accessibility (>90% contrast posterior distribution mass on the positive side). The disproportion of predator and resource-driven effects decreased during wet season, with three out of five species – hare, warthog and roan – exhibiting equivalent spatial response strengths to spotted-hyaena abundance and to water availability (Fig. 6.3). The exception was the kudu, which exhibited a consistently stronger spatial response to water availability than

to predator abundance (> 91% of the contrast posterior distribution mass with negative values; Fig. 6.3). The spatial response to forage availability also revealed a generalized shift in strength from predator to forage availability effect dominance from the dry to wet season: during dry season all but the hare exhibited a stronger spatial response to forage availability than to spotted-hyaena abundance, whereas the relative importance of both factors became more balanced or even shifted (for roan) during wet season (Fig. 6.4).

6.4.5 Temporal segregation with predators

Diel AO across predator-prey dyads averaged $\Delta_4 = 0.61 \pm 0.20$ [range: 0.25–0.92], and activity patterns significantly differed between predator and prey, except for the hare-spotted-hyaena dyad during dry season ($U^2 = 0.15, p\text{-value} > 0.10$). We found a general pattern of lower AO between prey species with spotted-hyaena ($\Delta_{4Dry} = 0.55 \pm 0.23$; $\Delta_{4Wet} = 0.53 \pm 0.23$), than with leopards ($\Delta_{4Dry} = 0.67 \pm 0.17$; $\Delta_{4Wet} = 0.68 \pm 0.15$).

Our results did not reveal changes in the AO between leopards and either prey group nor across seasons (primary prey: $\Delta_{4Dry} = 0.66 \pm 0.18$ vs. $\Delta_{4Wet} = 0.70 \pm 0.17$; secondary prey: $\Delta_{4Dry} = 0.67 \pm 0.18$ vs. $\Delta_{4Wet} = 0.66 \pm 0.16$; Fig. 6.5; Supporting Information: Table S.6.4). Concerning spotted-hyaena, our results revealed higher AO with primary prey than with secondary prey, regardless the season (primary prey: $\Delta_{4Dry} = 0.67 \pm 0.10$; $\Delta_{4Wet} = 0.68 \pm 0.18$; secondary prey: $\Delta_{4Dry} = 0.51 \pm 0.25$; $\Delta_{4Wet} = 0.48 \pm 0.24$; Fig. 6.5; Supporting Information: Table S.6.4).

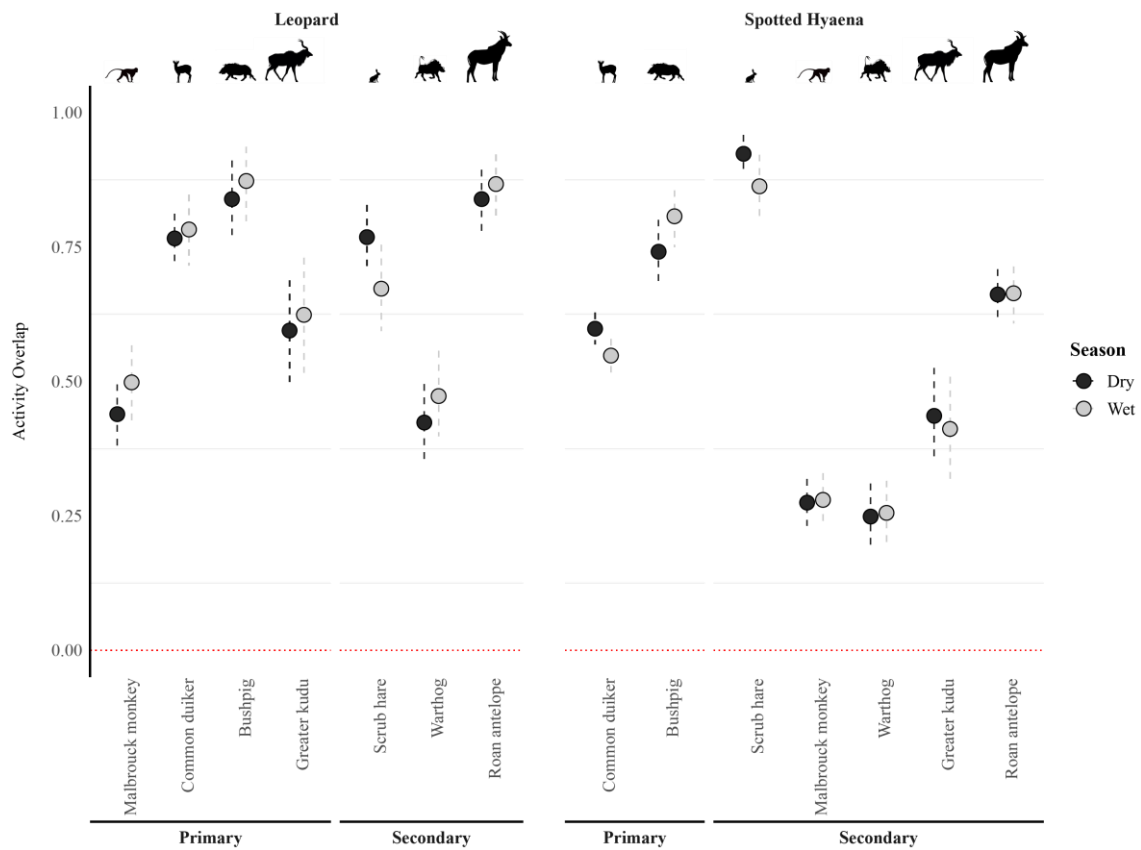


Figure 6.5 - Activity overlap (and respective 95% credible intervals) across predator-prey dyads during dry and wet season. Prey species are classified according to their importance for each predator's diet – primary prey if the Frequency of Occurrence (FO) $> 5\%$; secondary prey if $FO < 5\%$

6.5 Discussion

We found local co-abundance between prey and predator to be the rule in our study system, regardless of predator's hunting strategy and prey's importance in its diet. Our study suggests that under low predator density, prey may have limited perception of predation risk posed by both ambush and cursorial predators, which restricts the employment of spatiotemporal proactive antipredator strategies (Palmer *et al.*, 2022). These findings contribute to the understanding of how current ecological theories apply to a multi-predator multi-prey system with low predator abundance.

6.5.1 Spatial response of prey to water availability

Our results refuted the hypothesis that prey species with high water dependency would be consistently constrained by the distance to the nearest water source (Table 6.1). The warthog was the only water-dependent species (Kihwele *et al.*, 2020) constrained by water accessibility, and only during wet season. Other studies have also found that water-dependent herbivores may not be the most abundant around water

sources (e.g., Ogotu *et al.*, 2014). Regardless, the relatively short distance from sampling stations to the water sources ($\bar{x} = 4.6 \pm 2.7\text{km}$, range: 0.2 – 12.5; Table 6.1) could also have prevented us from fully capturing this effect, as surface water could be accessed from most sections of the landscape. For example, roan are known to forage up to 12 km from water (Havemann *et al.*, 2022), therefore water could have been accessed even from the furthest camera. Although unexpected, the absence of a clear hierarchy with respect to water accessibility from high to low water-dependent species suggests that other factors could be overriding prey's hydric needs in our study system. Factors potentially influencing these counterintuitive behaviours include interspecific competition (Valeix *et al.*, 2008), predation risk (Valeix *et al.*, 2008, Périquet *et al.*, 2010) and food availability (Ogotu *et al.*, 2014).

6.5.2 Spatial response of prey to feeding resources' availability

We found grazers to be spatially associated to grassland areas, where preferred forage availability is highest. The strength of this effect was highest during wet season, suggesting that these species may compensate or complement dry grass's lower nutritional value with alternative forage during dry season (Hempson *et al.*, 2015). Conversely, we hypothesized that generalists and browsers would be positively influenced by shrubland cover, but found most of these species to use shrublands as available. Shrublands are amongst the most widely available habitat type in our study area (mean cover: $32.2 \pm 8.2\%$; Table 6.1), therefore it is plausible to consider that forage is available such that it allows generalists and browsers to fulfil their energetic needs throughout the landscape. The reduced influence of shrubland cover during wet season could be related with incursions to open areas to access nutritious fresh shoots (Fynn *et al.*, 2019). Open areas are dominated by tall grass and scattered fern during wet season, hence also provide sufficient cover and escape routes (Abu Baker and Brown, 2014). Alternatively, these patterns could also be related with an increase in consumption of fresh herbaceous plants (Owen-Smith, Cooper and Novellie, 1983).

6.5.3 Spatial and temporal responses of prey towards the ambush predator

Contrary to our expectations, we found a general pattern of association between the ambush predator (leopard) and prey. Furthermore, we expected primary prey to exhibit a stronger proactive antipredator response than secondary prey (H2), but failed to detect a clear relationship between potential risk and predator avoidance. Rather, we found a general pattern of co-abundance between prey and predators, suggesting that local

abundance of the predator does not spatially constrain prey in our study system. Co-abundance between prey and ambush predators has been widely reported in other systems, such as between the Javan deer (*Rusa timorensis*) and leopard in South-East Asia (Pudyatmoko, 2019), or between the collared peccary (*Pecari tajacu*) and the agouti (*Cuniculus paca*) with jaguar (*Panthera onca*) in South America (González *et al.*, 2021). The Control of Risk Hypothesis (Creel, 2018) proposes that spatial co-abundance patterns may arise under two different scenarios: i) predator abundance is not enough to impose tangible predation risk on prey (Laundré *et al.*, 2001); or ii) the ambush predator is either ubiquitous leaving little refuge from predation pressure (Wirsing *et al.*, 2021), or is more efficient in spatially tracking its prey, which, in turn, is incapable (or unwilling) to avoid it (Owen-Smith, 2015, Wirsing *et al.*, 2021). The reduced predator abundance hypothesis cannot be excluded since leopard density in BNP (ca. 2-3 ind/100 km²; Monterroso, unpublished data) is at the lower end of leopards' known densities (e.g. Havmøller *et al.*, 2019, Davis *et al.*, 2021). Moreover, we found leopard occupancy to be < 0.5 , suggesting it is not ubiquitous across the landscape. Consequently, while it is reasonable to assume that prey species are not spatially constrained by this ambush predator, the homogeneity of the BNP's landscape may preclude perception of risk (Gaynor *et al.*, 2019). Spatial association between predators and prey have been reported in other homogeneous environments with chronic high predation risk (Schmidt and Kuijper, 2015). The mental mapping of a 'Landscape of Fear' implies perception and anticipation of risk, allowing proactive responses. However, limited perception of predation risk by prey in BNP may prevent such mental mapping. Moreover, spatial overlap alone may not be sufficient to predict predation risk, as a predation events require predator and prey to coexist in space and time (Suraci *et al.*, 2022).

Proactive temporal avoidance of leopards would be an alternative to spatial avoidance to prevent predation (H3). Coherently, we found significant differences between the activity patterns of leopards and all prey species, providing reasonable support to temporal segregation acting as an important strategy by which prey reduce the likelihood of agonistic encounters with the ambush predator (e.g. Palmer *et al.*, 2021). Activity pattern adjustments by prey have been reported elsewhere to avoid leopards (Hayward and Slotow, 2009, Havmøller *et al.*, 2020), but also other ambush predators such as clouded leopards (*Neofelis diardi*) (Ross *et al.*, 2013), tigers (*Panthera tigris*) (Linkie and Ridout, 2011), or pumas (*Puma concolor*) (Azevedo *et al.*, 2018). However, the AO overlap found between the leopard and its prey was high when compared to other ambush predator-prey systems, which are typically below 0.65 (Linkie and Ridout, 2011,

Ross *et al.*, 2013, Azevedo *et al.*, 2018, Havmøller *et al.*, 2020, Mills and Harris, 2020). Additionally, the similar levels of AO we found between leopards and its primary and secondary prey is indicative that temporal segregation is unlikely to be related to prey selection (Hayward and Slotow, 2009), and further contributes to refuting the hypothesis that the intensity of proactive antipredator responses would be a function of the consumption frequency of prey (H2). Changing the endogenous circadian clock entails costs related to potential exposure to other predators or humans, or to reduced physiological efficiency (Gaynor *et al.*, 2021c, Rocha *et al.*, 2022b). Therefore, the risk of predation should be high enough to compensate the negative effects of switching diel activity patterns (Monterroso *et al.*, 2013). Under this reasoning, perceived predation risk by the ambush predator in BNP may not be sufficient to compensate shifts in prey's diel activity and could justify higher than expected levels of AO between leopards and its prey.

Finally, we expected seasonal changes in spatiotemporal overlap levels between prey and its ambush predator because abundance and accessibility to resources during wet season could allow increased investment in anti-predator strategies (Riginos, 2015), while resource scarcity during dry season could force prey to devote more efforts to fulfilling their nutritional and hydric needs at the expense of safety (Hopcraft *et al.*, 2014). However, we failed to detect such adjustments, further supporting a hypothesis of low perceived predation risk. Therefore, coherently with the Optimal Forage Theory (Sinervo, 1997), it is reasonable to assume that in systems where prey are not able to perceive the risk of predation or are exposed to low predation risk, it may compensate to maximize resource acquisition (Palmer *et al.*, 2017), relegating antipredator behaviour to reactive responses to potential predatory events (Creel, 2018).

6.5.4 Spatial and temporal responses of prey towards the cursorial predator

Our results complied with the expectation of weak proactive antipredator responses towards the cursorial predator (H4) (Preisser *et al.*, 2007, Creel, 2018). Spatial association between prey and cursorial predators may result from a dilution of risk perception because of: (i) low predator abundance (Middleton *et al.*, 2013) or (ii) unstructured predator cues across the landscape (Makin *et al.*, 2017b). Under such circumstances it may be more beneficial for prey to rely on reactive antipredator responses because activities such as foraging are not limited, and hence have weaker effects on food security trade-offs (Creel, 2018). Spatial association between cursorial predators and prey has been reported elsewhere (Thaker *et al.*, 2011, Pudyatmoko,

2019, Davies *et al.*, 2021), namely between spotted-hyaena and its preferred prey (Davies *et al.*, 2021). Research focusing on antipredator responses towards spotted-hyaena are scarce, but suggest grouping (Moll *et al.*, 2016) and increased vigilance (Palmer and Packer, 2021) as key anti-predator strategies. Additionally, spotted-hyaena density in BNP (ca. 0.7 ind/100²; Monterroso, unpublished data) is low when compared to other studies across the species' range (Davis *et al.*, 2021, Vissia, Wadhwa and van Langevelde, 2021). Therefore, it is plausible to consider that such low spotted-hyaena density further contributes to low spatial avoidance response by prey. Similar patterns have been described towards another cursorial predator, the gray wolf (*Canis lupus*) which, when under low density, led to limited changes in elk (*Cervus elaphus*) behaviour that only respond to immediate risk (Middleton *et al.*, 2013). Nevertheless, while unstructured predator cues in the landscape could underlie the absence of spatial proactive antipredatory behaviour, prey could still limit predation risk through temporal segregation with the predator (Palmer *et al.*, 2017, Palmer *et al.*, 2022). Few studies have reported temporal segregation between prey and cursorial predators (Hayward and Slotow, 2009, Pudyatmoko, 2019, Mills and Harris, 2020). However, the generally strict nocturnal habits of spotted-hyaena could provide a predictable pattern by which prey could avoid predation. Coherently, we found significant differences in the activity patterns of prey and spotted-hyaena, and their AO was generally lower than observed in studies elsewhere (typically higher than 0.61) (Hayward and Slotow, 2009). Although these patterns apparently support temporal antipredator responses, they can also result from species' endogenous behaviour, since the activity patterns of predator and prey species in BNP are similar to those reported elsewhere (Estes, 2012). Moreover, predator mediated changes in preys' endogenous activity should lead to different levels of AO across seasons, because of different levels of tolerance to predation risk following seasonal variation in the availability of resources (Owen-Smith, 2015, Riginos, 2015, Davies *et al.*, 2021), which we failed to detect. So, our results are consistent with the idea that the limited perception of changes in predation risk attenuated the employment of spatiotemporal proactive responses.

6.5.5 Top-down vs. bottom-up ecological structuring

In spite of a stronger influence of predator abundance than resource availability on prey's spatial behaviour, the predominant pattern is of spatial association indicating that prey prioritize access to required resources (Riginos, 2015, Davies *et al.*, 2021). Our results suggest that poorly enforced of top-down forces may give rise to a generalized

pattern among prey species by which their spatiotemporal behaviour is mostly governed by bottom-up processes, even when the resources are not limited (Letnic and Ripple, 2017). We propose that this pattern is likely driven by generalized low predator density rather by resource limitation (Laundré *et al.*, 2014), as supported by consistent bottom-up regulation across seasons regardless of prey dietary type and water dependency (H1). Further, we suggest that in systems with low predator density such as ours, predator hunting strategy does not lead to different antipredator strategies. The spatiotemporal perception of risk informs about the antipredator strategy adopted by prey (Creel, 2018) such that if the risk is loosely perceived, prey cannot proactively respond to it (Palmer *et al.*, 2022). Moreover, under such conditions, it may be more profitable for prey to rely on responses to short-term predation risk towards both cursorial and ambush predators (Middleton *et al.*, 2013, Creel, 2018, Palmer *et al.*, 2022).

Spatial and temporal relationships among species have been widely used to explore intraguild interactions in carnivore communities (Brodie *et al.*, 2018, Pudyatmoko, 2019, Monterroso *et al.*, 2020a). However, this analytic framework is seldomly used to investigate predator-prey relationships, or mostly implemented to investigate single predator-prey dyads (Say-Sallaz *et al.*, 2019). While further studies are required to investigate if proactive vs. reactive antipredator behaviours are directly related to predator abundance (Moll *et al.*, 2017), our study provides a steppingstone for the understanding predator-prey interactions in systems with reduced perception of predation risk.

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Chapter 7

General Discussion

This thesis offers a significant contribution to updating knowledge on south Angolan mammal wildlife after decades with near absent scientific surveys, assessing the current composition of the mammal communities from three different conservation areas, and comparing with the described historical records for these areas. Further it uses the war-driven depauperate mammal communities in southern Angola to investigate how community structure is regulated, the consequences of altered ecosystem on species space use, and behavioral adaptations to the lower predation pressure and/or increased human disturbance. Namely in understanding how top-down and bottom-up regulation forces act in disrupted systems. It represents a baseline to support conservation and restoration and guide research priorities for upcoming years. The general discussion is organized in two parts. In the first part, I discuss the achievements and implications of my findings about the current status of extant mammal diversity in southern Angola (Chapters 2 and 3). In the second part, the processes underlying the structure and functioning of mammal communities across southern Angola (Chapters 4, 5, and 6).

7.1 Extant Southern Angolan mammal communities, with a look to the past

7.1.1 Mammal community structure along the environmental gradient

The results from the different study areas support the existence of 21 meso and large mammal species in INP (Appendix 4: Table S.4.3), 32 in BNP, and 29 in CCA (Chapter 2). However, the different sampling methods used in the three study areas (i.e., direct observation counts in INP and camera trapping in BNP and CCA) precluded a direct comparison of the results and, consequently, the inclusion of INP in the analysis in Chapter 2. Recent camera trapping surveys in INP (Chicomo, 2021, Freixial, 2021, Nunes, 2021) provide evidence of the presence of seven additional mammal species, not detected in Chapter 4: Caracal (*Caracal caracal*), African wildcat (*Felis lybica*), large-spotted genet (*Genetta tigrina*), zorrilla (*Ictonyx striatus*), red-rocked rabbit (*Pronolagus randensis*), Cape porcupine (*Hystrix africaeaustralis*) and aardvark (*Orycteropus afer*).

Although the observed richness of extant species across the three areas is similar (INP: 28, BNP: 32, and CCA: 29 species), their relative community structure and composition have important differences. Fewer than 50% of the 28 species existing in INP are also found in the other study areas (13 species in BNP and 12 species in CCA). The INP community is mainly composed by arid-adapted species, such as springbok,

gemsbok, and brown-hyaena, which are not found in the other areas. Conversely, species less adapted to arid environments, such as the common duiker and roan antelope, are common in BNP and CCA but absent from INP.

The differences in the mammal community composition between the arid southwestern Angola and the south-central/eastern part of the country support the influence of the environmental gradient present in Angola. The Angolan escarpment may be one of the promoters of such gradient, due to its climatic and topographic peculiarities, may function as a physical barrier for many animal species (Heller, 1918, Hall, 1960, Cáceres *et al.*, 2016), promote the isolation of populations and thus create conditions for speciation and the occurrence of endemisms (Huntley, 1974, Baptista *et al.*, 2019, Dean *et al.*, 2019, Goyder and Gonçalves, 2019, Huntley, 2023). The differences in the communities' composition at the base of the escarpment and in the plateau have been proved for different taxa, for instance, birds (Hall, 1960, Mills, 2010) and reptiles (Baptista *et al.*, 2019). The results of this thesis support the notion that it may also occur with mammals, thus providing further evidence for the biogeographic regions of mammals, as suggested by Rodrigues *et al.* (2015). The influence of the escarpment as a barrier to the movement of fauna is further supported by a recent study that reported genetic differences between wild dog populations from the base of the escarpment and the plateau (Tensen *et al.*, 2022), which suggests limited gene flow between populations. Conversely, the absence of a physical barrier to the eastern part of the country, together with a more similar climate and habitat, creates conditions for more similar communities. In Chapter 2, I report that mammal communities from BNP and CCA share 69% (25 out of 36) of their mammal species and exhibit similar biodiversity levels. However, the structure of these communities differs, with CCA's mammal community being dominated by smaller mammals, whereas larger species are more common in BNP (Chapter 2).

Historical reports refute structural differences between the communities and document the existence of many large mammal species in southeast Angola (Chapter 2: Table 2.1). Additionally, surveys from adjacent areas in neighboring countries report the presence of elephant, rhino, giraffe, Cape buffalo, hippopotamus, blue wildebeest, Burchell's zebra, and African lion, species likely extirpated or reduced in southern Angola (e.g. Kamweneshe, Beilfesus and Simukonda, 2002, Ramberg *et al.*, 2006). The absence or reduction in the abundance of large mammal species at CCA may be the result of the absence of formal protection over extended periods of time, which facilitated human encroachment and poaching, especially since the civil-war (Breytenbach, 2001, 2015, Huntley, 2017, Huntley *et al.*, 2019a). Overhunting during the war is arguably

particularly intense in the Cuando-Cubango province (where CCA is located), fueling important illegal ivory and rhino horn trade to South Africa (Kumleben, 1996, Breytenbach, 2015).

7.1.2 A decline of Southern Angolan mammal communities

Although commonly accepted that two critical periods of overhunting – pre-establishment of protected areas (Huntley *et al.*, 2019a) and civil war – have been instrumental to the extirpation of many large mammal species (Chase and Griffin, 2011, Schlossberg *et al.*, 2018, Vaz Pinto, 2019, Braga-Pereira *et al.*, 2020b, Braga-Pereira *et al.*, 2021b), to my knowledge, no comprehensive study has ever formally compared wildlife communities in Angola between the pre- and the post-war period. I performed such analysis in Chapters 1 and 2 and report the likely local or regional extinction of 16 mammal species across the study areas [13 out of 28 (46 %) in CCA and 16 out of 41 (39 %) in BNP] since the last surveys done before the war. Although other studies report war-driven decrease in species richness (e.g. Gaynor *et al.*, 2021b) and reduction in species' abundance (Stalmans *et al.*, 2019, Braga-Pereira *et al.*, 2020b), I did not find any quantitative study for war-driven extinctions. Despite the absence of quantified examples to compare with my systems, the large ungulate species data from Gorongosa National Park (perhaps one of the best-studied disrupted areas in Africa) indicates that the first aerial surveys after the Mozambican civil war (Dunham, 2004) did not detect 36% (6 out of 17) of the species known to occur before the unrest (Tinley, 1977), i.e., similar values to the ones found for BNP.

The contribution of large mammal species to these numbers is disproportionately high. From 15 expected large herbivore and carnivore species occurring in BNP, I only reported seven, and out of the 12 species with known occurrence in CCA, only three were detected. These findings are supported by the described overhunting in southeast Angola, where militias established their headquarters. These militias may have had to resort to bushmeat and wildlife-based illegal trade to support and finance their warfare (Huntley, 2017). A similar scenario of large mammal decimation is also described for other parts of the country (e.g., in Quiçama National Park; Braga-Pereira *et al.* (2020b). Contrariwise, my results suggest that the extirpation of smaller species was less evident and refers primarily to smaller ungulates, such as oribi (*Ourebia ourebi*), black-faced impala (*Aepyceros melampus*) and lechwe (*Kobus leche*), that could have been targeted alongside larger antelopes. Consistently, several studies have demonstrated that antelopes may be particularly prone to declines under heavy poaching and may be the

preferred type of bushmeat (Carpaneto and Fusari, 2000, Hema *et al.*, 2019, Nieman *et al.*, 2019). This is coherent with studies elsewhere in Angola (Taylor *et al.*, 2018, Braga-Pereira *et al.*, 2020b) and other countries, such as Mozambique (Gaynor *et al.*, 2021) or Serra Leone (Lindsell, Klop and Siaka, 2011), recently recovering from civil unrests. These studies report a disproportionally high contribution of smaller-sized species in wildlife communities and the decline of larger species. The dominance of smaller-sized species in disrupted communities is a consequence of multiple factors working in conjunction. Firstly, larger species are typically the target of hunters (Lindsey *et al.*, 2013, Ripple *et al.*, 2016a) and, secondly, on average, large-bodied species live at lower densities than small-bodied ones (Cotgreave, 1993), which additionally leads to more likely local extinctions. Consequently, the extinction of larger species releases the competition over smaller-sized species, which may expand and hamper the posterior recovery of larger-bodied species. One example of this cascading effect happened in Gorongosa National Park (Mozambique), where the collapse of formerly dominant populations of larger mammals led to an asymmetric recovery in favour of intermediate-sized antelopes, which replaced and occupied the niche after the extinction of larger-bodied herbivores (Stalmans *et al.*, 2019).

We failed to detect several species (Chapter 2) that had been detected in other studies carried out in my study areas (Overton *et al.*, 2017), which were then detected in our surveys performed after those included in this thesis. These include the ground pangolin (*Manis temminckii*), spotted-hyaena and Cape buffalo in CCA, and the dwarf mongoose (*Helogale parvula*), black-backed jackal (*Canis mesomelas*) and aardwolf (*Proteles cristata*) in BNP. In Chapter 2, the Multi-Region Community Models (Tenan *et al.*, 2017) indicate a significant likelihood that a species is present in the study areas but has not been detected ($\Omega_{BNP} = 0.60$ and $\Omega_{CCA} = 0.54$), which acknowledge the possibility of the existence of undetected species. These species are thus suspected to have highly restricted distribution and abundance, supported by the low occupancy (ca. 0.2) derived from the community models. Despite the likely presence of species that were never detected, the same number of species observed and estimated by the model in both study areas (32 in BNP and 29 in CCA) suggest the sampling method is fairly reliable, yielding accurate and precise estimates (Guillera-Aroita, Kéry and Lahoz-Monfort, 2019).

The lack of reliable statistics on historical wildlife population abundances precludes the quantification of the consequences of the war for the extant populations. Nevertheless, low occupancy levels are reported for many existing species (Chapter 2:

Fig. 2.3). Since occupancy is reported to be closely proportional to abundance (e.g. Gaston *et al.*, 2000), the results presented in this thesis may be an indicator for the low abundance of most extant mammal species. For instance, only common duiker and elephant in BNP, and steenbok and side-striped jackal (*Canis adustus*) in CCA present occupancy probability above 0.5, indicative of the rarity of most other species. Nevertheless, future research should focus on a more in-depth characterization of remnant populations to assess and guide adequate rehabilitation measures.

7.1.3 Knowledge gaps and historical biases in Angolan wildlife records

The limited research on Angolan biodiversity has led to incomplete or biased records of its extant wildlife. Advances in technology, including the availability of remote sensing methods, have allowed the documentation of species that had slid unnoticed in traditional expeditions. Using these tools allowed me to report the presence of new species previously of unknown occurrence in the study areas. I documented the existence of scrub hare (*Lepus saxatilis*), southern galago (*Galago moholi*), spring hare (*Pedetes capensis*), cape porcupine (*Hystrix africaeaustralis*), slender (*Galerella sanguinea*) and white-tailed mongooses (*Ichneumia albicauda*) in BNP, where they had not been previously described. The number of previously non-documented species detected is even higher in CCA. It includes scrub hare, Malbrouck monkey (*Chlorocebus cynosuros*), spring hare, cape porcupine, bushpig, greater kudu, bat-eared fox (*Otocyon megalotis*), African wildcat, caracal, Selous' mongoose (*Paracynictis selousi*), common (*Genetta genetta*) and miombo (*Genetta angolensis*) genets, cheetah, and leopard.

Despite the absence of these species in historical records, the IUCN (2021) distribution maps of some of them include the study areas of this thesis. The exceptions are bushpig, bat-eared fox, and miombo genet, whose distribution maps do not include CCA. Additionally, the distribution map of scrub hare does not have any of the study areas (Table 7.1). Reporting these species brings further importance to this work since the existence of mammal species is confirmed in areas barely explored, contributing to the update of the distribution ranges.

Table 7.1 – Comparison between each species' IUCN Red List distribution and recent detections obtained in Iona and Bicular National Parks and Cuatir Conservation Area. ✓ refers to the detections in the current study, while numbers correspond to other study references (below the table). Species are organized by alphabetic order inside each taxonomic Order and Family.

Species	Iona National Park		Bicular National Park		Cuatir Conservation Area	
	IUCN range	Detection	IUCN range	Detection	IUCN range	Detection
ORDER CARNIVORA			FAMILY CANIDAE			
<i>Canis adustus</i>			✓	✓	✓	✓
<i>Canis mesomelas</i>	✓	✓	✓	✓		
<i>Lycaon pictus</i>				✓		✓
<i>Otocyon megalotis</i>	✓	✓	✓	✓		✓
<i>Vulpes chama</i>	✓	✓		1		
ORDER CARNIVORA			FAMILY FELIDAE			
<i>Acinonyx jubatus</i>	✓	✓			✓	✓
<i>Caracal caracal</i>	✓	2	✓	✓	✓	✓
<i>Felis lybica</i>	✓	2	✓	✓	✓	✓
<i>Leptailurus serval</i>				✓		✓
<i>Panthera pardus</i>	✓	✓	✓	✓	✓	✓
ORDER CARNIVORA			FAMILY HERPESTIDAE			
<i>Atilax paludinosus</i>						✓
<i>Cynictis penicillata</i>	✓					
<i>Helogale parvula</i>	✓		✓	✓	✓	
<i>Herpestes flavescens</i>	✓					
<i>Herpestes ichneumon</i>			✓		✓	
<i>Galerella sanguinea</i>	✓		✓	✓	✓	✓
<i>Ichneumia albicauda</i>			✓	✓	✓	✓
<i>Mungos mungo</i>	✓		✓		✓	
<i>Paracynictis selousi</i>			✓	✓	✓	✓
<i>Suricata suricatta</i>	✓	✓				
ORDER CARNIVORA			FAMILY HYAENIDAE			
<i>Crocuta crocuta</i>	✓		✓	✓	✓	✓
<i>Parahyaena brunnea</i>	✓	✓				
<i>Proteles cristata</i>	✓	✓	✓	✓	✓	
ORDER CARNIVORA			FAMILY MUSTELIDAE			
<i>Ictonyx striatus</i>	✓	3	✓	✓	✓	✓
<i>Mellivora capensis</i>	✓	✓	✓	✓	✓	✓
<i>Poecilogale albinucha</i>			✓	✓		
ORDER CARNIVORA			FAMILY VIVERRIDAE			
<i>Civettictis civetta</i>			✓	✓	✓	✓
<i>Genetta angolensis</i>			✓	✓		✓
<i>Genetta genetta</i>	✓		✓	✓	✓	✓
<i>Genetta maculata</i>	✓		✓		✓	
ORDER ARTIODACTYLA			FAMILY BOVIDAE			

<i>Aepyceros melampus</i>	✓	✓	✓		Reintroduced
<i>Antidorcas marsupialis</i>	✓	✓			
<i>Connochaetes taurinus</i>	✓		✓	✓	
<i>Damaliscus lunatus</i>				✓	
<i>Hippotragus equinus</i>			✓	✓	✓
<i>Kobus ellipsiprymnus</i>			✓		
<i>Madoqua kirkii</i>	✓	✓	✓		
<i>Oreotragus oreotragus</i>	✓	✓	✓		
<i>Oryx gazella</i>		✓			
<i>Ourebia ourebi</i>			✓	✓	
<i>Raphicerus campestris</i>	✓	✓	✓	✓	✓
<i>Redunca arundinum</i>			✓	✓	✓
<i>Sylvicapra grimmia</i>	✓		✓	✓	✓
<i>Syncerus caffer</i>					✓
<i>Taurotragus oryx</i>	✓		✓	✓	Reintroduced
<i>Tragelaphus scriptus</i>				✓	✓
<i>Tragelaphus strepsiceros</i>	✓	✓	✓	✓	✓
ORDER ARTIODACTYLA		FAMILY GIRAFFIDAE			
<i>Giraffa giraffa</i>					Reintroduced
ORDER ARTIODACTYLA		FAMILY SUIDAE			
<i>Phacochoerus africanus</i>	✓		✓	✓	✓
<i>Potamochoerus larvatus</i>			✓	✓	✓
ORDER HYRACOIDEA		FAMILY PROCAVIIDAE			
<i>Heterohyrax brucei</i>			✓		
<i>Procavia capensis</i>	✓	✓	✓		
ORDER LAGOMORPHA		FAMILY LEPORIDAE			
<i>Lepus saxatilis</i>			✓		✓
<i>Lepus victoriae</i>			✓	✓	
<i>Pronolagus randensis</i>	✓	2			
ORDER PERISSODACTYLA		FAMILY EQUIDAE			
<i>Equus quagga</i>	✓				Reintroduced
<i>Equus zebra</i>	✓	✓			
ORDER PERISSODACTYLA		FAMILY RHINOCEROTIDAE			
<i>Ceratotherium simum</i>	✓				
<i>Diceros bicornis</i>	✓		✓	✓	
ORDER PHOLIDOTA		FAMILY MANIDAE			
<i>Manis temminckii</i>			✓	✓	✓
ORDER PRIMATA		FAMILY CERCOPITHECIDAE			
<i>Chlorocebus cynosuros</i>	✓	✓	✓	✓	✓
<i>Papio ursinus</i>	✓	✓	✓	✓	
ORDER PRIMATA		FAMILY GALAGIDAE			
<i>Galago moholi</i>			✓	✓	✓

<i>Otolemur crassicaudatus</i>	✓		✓		
ORDER PROBOSCIDEA			FAMILY ELEPHANTIDAE		
<i>Loxodonta africana</i>			✓	✓	✓
ORDER RODENTIA			FAMILY HYSTRICIDAE		
<i>Hystrix africaeaustralis</i>	✓	2	✓	✓	✓
ORDER RODENTIA			FAMILY PEDETIDAE		
<i>Pedetes capensis</i>	✓		✓	✓	✓
ORDER RODENTIA			FAMILY SCIURIDAE		
<i>Funisciurus congicus</i>	✓		✓	✓	
<i>Paraxerus cepapi</i>			✓		
<i>Xerus princeps</i>	✓				
ORDER TUBULIDENTATA			FAMILY ORYCTEROPODIDAE		
<i>Orycteropus afer</i>	✓	3	✓	✓	✓

References: 1 - Overton *et al.* (2017); 2- Chicomo (2021); 3 - Nunes (2021) & Freixial (2021)

A closer look at the species reported to occur in INP, BNP, and CCA, according to IUCN (2021) distribution range assessments, shows important discrepancies with the species contemporarily reported as present (Table 7.1). For instance, the detection of cheetah, wild dog, gemsbok, and Cape buffalo in INP, BNP, and/or CCA, stresses the need to update IUCN distribution maps (Monterroso *et al.*, 2020b). Additionally, many species predicted as extant in the study areas by the IUCN (2021) are likely extirpated since they were not detected during five years of surveys (Table 7.1). For instance, among the 44, 50, and 39 intermediate and large mammals which IUCN (2021) distribution maps include INP, BNP, and CCA, respectively, recent surveys failed to detect 19 (43 %) in INP, 17 (37 %) in BNP and 13 (33%) at CCA. These discrepancies expose a persistent knowledge gap on the conservation status and distribution of Angolan wildlife and highlight the consequences of limited communication and knowledge sharing between organizations performing wildlife surveys in Angola and international conservation entities (such as the IUCN). To address this issue effectively, it is crucial to ensure that the results of surveys conducted in Angola, including the research presented in this thesis, are widely disseminated and accessible to the international scientific community and relevant entities. This can be achieved by publishing findings in reputable international scientific journals, presentation at conferences, inclusion in conservation reports, and availability of information in English. By making this information accessible, it will inform and update the international community about the current status of Angolan wildlife. To facilitate the flow of information, mechanisms for data and information sharing should be established

between local organizations, academia, and international conservation organizations. Such collaboration will enable the exchange of valuable insights and data, contributing to a more comprehensive understanding of the situation. While some progress has been made, such as the recent addition of mammal species records in Angola to databases like GBIF.org or iNaturalis.org, it is important to note that the contributors are currently limited and predominantly consist of tourists, photographers, and naturalists. Therefore, it is of utmost relevance that organizations involved in wildlife surveys commit to making their results publicly available. The cooperative efforts and knowledge sharing among stakeholders is crucial to accurately assess the conservation status of Angolan mammal communities and provide updated information to international organizations and databases. By taking these steps, a significant contribution can be made towards filling the knowledge gap and ensuring the availability of accurate and up-to-date information on Angolan wildlife to support conservation efforts.

7.1.4 A future for Angolan mammals

In the previous sections, I discussed the likely loss of many species in Angola. In Chapter 2, I have also raised concerns regarding the insufficient implementation of effective management strategies, rehabilitation measures, and law enforcement in Bicular National Park, that may apply to other Angolan protected areas. Furthermore, policies that reinforce the protection of non-protected areas and the importance of their preservation for wildlife conservation are required. These policies should prevent habitat destruction (von Staden *et al.*, 2022) and ensure the connectivity and recovery of wildlife in these areas (Thapa *et al.*, 2021). Different alternatives for landscape management may be considered, including (i) an integrative management with the engagement of landholders and local communities, with resulting benefits (e.g., financial) shared between them, i.e., conservancies (Barnard *et al.*, 1998), or (ii) public-private partnerships to manage the land with the commitment of promoting conservation (Saporiti, 2006). These private agencies allocate funding and/or expertise for conservation in countries that financial and/or technical the capacity to invest. This requires careful management of the areas and budgets, with investments in infrastructures, capacity development for various roles such as rangers, conservationists, and logistics personnel (Buckley, 2010, Massé and Lunstrum, 2016). Given the magnitude of the investments, public-private partnerships require long-term tourism time frames to be sustainable and allow goals to be achieved. The sustainability and integration of each alternative should be assessed considering each area's socio-

politic and environmental contexts. Nevertheless, measures should be implemented to prevent the continuous depletion of biodiversity outside protected areas and to foster the proliferation of species and ecosystem services.

Understanding wildlife communities' status is crucial to planning and implementing management and restoration projects. Additionally, an assessment for the potential natural recovery of wildlife populations, and consequently of the ecological processes, is also important to define conservation priorities and investments. For instance, the habitat in the surroundings of BNP is mostly degraded by human and livestock encroachment (Huntley, 2017, Godlee *et al.*, 2020), limiting the connectivity between populations (Overton *et al.*, 2020, Tensen *et al.*, 2022). In this context, priority should be given to reintroducing extirpated and depleted species in the Park to restore the ecological processes lost with the extirpation of species, alongside the restoration of historical ecologic corridors to re-establish connectivity with other conservation units. On the other hand, the almost pristine landscape and good river network in CCA facilitates connectivity with other areas inside the KAZA (Kavango Zambezi) Transfrontier Conservation Area that conserve stable wildlife populations. Studies inside KAZA have demonstrated that the prevalence of pristine habitats with reduced human perturbation is the main factor facilitating connectivity between areas and populations (Naidoo *et al.*, 2018, Brennan *et al.*, 2020). The proximity of CCA to KAZA and the similarity of its landscape characteristics that facilitate wildlife movements may create conditions for natural recolonizations. Future research should focus on the potential for restoration of natural areas that suffered severe declines in wildlife communities, namely in identifying extant wildlife hotspots and ecological corridors that can enhance the connectivity between populations.

CCA is an excellent example of private conservation management of non-protected land. The owners have invested in the area, creating conditions for extant wildlife to thrive and reintroducing species extirpated during the war (Ribeiro, 2021). The funding for these actions comes mostly from safari tourism and international donors. The country's protected area administrations could also apply this model, but the lack of investment and trained staff preclude the success of the actions. One alternative could be applying the knowledge and investment of international organizations and/or local people with experience managing and rehabilitating protected areas. Fortunately, the first signs for a prosperous future for Angolan protected areas has already started, with the concession of Iona National Park to African Parks (a South African non-governmental organization focused on conservation) and, more recently, Mavinga and Luengue-Luiana

National Parks. These organizations have been rehabilitating Parks' headquarters and training staff for conservation and patrolling. Plans are underway to re-introduce extirpated species in the near future.

7.2 Processes governing the structure and the functioning of mammal communities in southern Angola

7.2.1 Bottom-up processes prevail in reduced populations

Understanding the process that governs a community is intrinsically complex since various factors may be involved, such as resource availability or predation intensity. The regulation of a community frequently results from a miscellanea of processes, with seasonal shifts in the dominant process, according to changes in resource availability (Owen-Smith, 2015). The chapters of this thesis demonstrate that the simplification of communities likely leads to an increased prevalence of bottom-up processes. Chapter 4 presents evidence supporting how ungulate species from a desert environment have their distribution constrained by food and/or surface water availability. Nevertheless, the extension of the constraints differs between species. While Hartmann's mountain zebra and gemsbok have their distribution primarily limited by water availability, springbok are affected mainly by access to good quality vegetation, which allows them to suppress their water requirements. Likewise, Chapter 6 suggests that the spatiotemporal behavior of prey species is mainly governed by bottom-up processes, even when resources are not limited (Letnic and Ripple, 2017). I propose that the patterns found, especially in Chapter 6, are likely driven by a generalized low predator density rather than resource limitation (Laundré *et al.*, 2014). This is supported by consistent bottom-up regulation across seasons, regardless of resource availability, prey dietary type, and water dependency.

In Chapter 5, I report changes in herbivore occupancy patterns likely due to a reduction in forage availability after perturbations in the ecosystem, i.e., bushfires. The results of this chapter show that, despite a short-term increase in the occupancy levels by grazer species after bushfires [where they may use the area seeking green and nutritious short-grass (Van de Vijver *et al.*, 1999, Eby and Ritchie, 2016, Nieman *et al.*, 2022)], as the grass grows, herbivore occupancy decrease to below pre-fire values. The negative trend in herbivore occupancy patterns in burned areas after a fire may suggest that the herbivores need to move to unburned areas to find food (Burkepile *et al.*, 2016). Moreover, I hypothesize that the reduction or change in functional herbivory processes

caused by the decline of large herbivore populations (Chapter 2) and the occurrence of frequent fires (Chapter 5) induce the growth of less nutritious and palatable tall grass (Archibald *et al.*, 2005, Archibald and Hempson, 2016), producing undesirable habitat for herbivores. This pattern exacerbates the importance of resource-driven constraints for herbivore populations and may explain the changes in herbivore space use. Although not tested here, if top-down constraints dominated the systems, herbivores should seek burned areas as an antipredator strategy since the open burned areas offer good visibility (Green *et al.*, 2015). This would increase the detectability of predators and reduce the likelihood of an ambush (Burkepile *et al.*, 2013). Other authors have attributed deviations in herbivore space use after a fire from the expected bottom-up constraints (Eby *et al.*, 2014, Burkepile *et al.*, 2016, Eby and Ritchie, 2016). These authors justify that the search for nutrients and the type of food available override the risk of predation in herbivores' space use decisions.

The results presented in this thesis do not support the Exploitation Ecosystem Hypothesis (EEH). According to EEH, a predominance of bottom-up processes was expected in the Namibe desert ecosystem - INP - (Hopcraft *et al.*, 2010, Veldhuis *et al.*, 2019), while top-down processes should dominate in more productive areas (Hopcraft *et al.*, 2010) - BNP and CCA. Although the results meet the expectations for INP, the broadly bottom-up regulation seen in BNP and CCA contradicts the theory. The reduced herbivore populations from these study systems could have led to an increase in vegetation availability (Hambäck and Beckerman, 2003, Silfver *et al.*, 2020), which, presumably, would decrease bottom-up constraints. Moreover, as reported in Chapters 2 and 6, carnivore populations are also reduced. This decrease in carnivore abundance reduces predation pressure on prey species and lowers the need for pre-emptive antipredator behaviors (Atkins *et al.*, 2019). As a result, herbivore populations are released from top-down constraints. Therefore, it is reasonable to assume that resource availability combined with reduced predation pressure could have led to increased herbivore populations, as observed in other systems that suffered from war-induced wildlife collapses (e.g. Stalmans *et al.*, 2019). Here, although small antelopes present high occupancy levels, such as common duiker in BNP and CCA or steenbok at CCA (Chapter 2: Fig. 2.3), the population growth of these species is not comparable to, for example, the waterbuck (*Kobus ellipsiprymnus*) population growth in Gorongosa National Park (Stalmans *et al.*, 2019). This may indicate that the vegetation available does not fully meet the dietary preferences of the extant herbivore community. Supporting this premise, in Chapter 5, I propose that the depleted populations and the

altered fire regimes in Angola, with more frequent fires (Stellmes *et al.*, 2013), may have changed the plant community for less palatable and less nutritive species (Archibald and Hempson, 2016, Johnson *et al.*, 2018). Additionally, the persistence of human actions, namely poaching and encroachment, have also prevented wildlife populations from growing (Petracca *et al.*, 2019). This topic is further discussed in the upcoming section.

7.2.2 The role of top-down forces

Various theories suggest that body size plays a crucial role in determining the vulnerability of prey species to predation. It is widely recognized that smaller species experience a more significant impact from top-down forces, including predation and other regulatory interactions (Hopcraft *et al.*, 2010). Accordingly, it was expected that smaller and intermediate-sized herbivores, such as springbok and common duiker, would be more constrained by top-down processes. However, the results presented in this thesis reveal contrasting patterns. In support of the initial expectation, Chapter 4 demonstrates that the spatial distribution of springbok may be an adaptive response to avoid competition and predation. Springbok, being a subordinate competitor to larger, more water-dependent species like Hartmann's mountain zebra and gemsbok (Kihwele *et al.*, 2020), potentially utilizes physiological adaptations to reduce their reliance on surface water, thereby mitigating the risk of competition and predation. Conversely, Chapter 6 highlights the absence of proactive antipredator responses exhibited by prey species, regardless of body size, predator hunting mode, season, and resource availability. The outcome is particularly surprising for the common duiker since it constitutes the primary prey item for leopards (ca. 73% of the diet; Jesus, 2021, Kosmas, unpublished data) and spotted-hyaena (ca. 80% of the diet; Bacchiocchi, 2020, Kosmas, unpublished data) in BNP. As a result, this species was expected to exhibit strong behavioral constraints to avoid predation. Yet, our findings do not provide evidence of predator influence on the spatiotemporal distribution of duikers.

Predators' hunting mode frequently induces different types of responses by prey. Ambush predators rely on specific landscape features for concealment, creating high-risk areas that prey species tend to avoid. In contrast, cursorial predators, which do not depend on such features, make it harder for prey to perceive high-risk areas (Preisser *et al.*, 2007, van der Meer *et al.*, 2011). As a result, the spatial variation in ambush predators' hunting grounds has a greater impact on prey species' antipredator strategies than the occurrence of the predators themselves. Conversely, the employment of antipredator behavior towards cursorial predators is expected to be weaker and more

influenced by predator occurrence (Moll *et al.*, 2016). Coherently, in Chapter 6, I expected different antipredator responses by prey towards leopard, an ambush predator, and spotted-hyaena, a cursorial predator. However, I failed to detect spatiotemporal proactive antipredator behaviors by prey species (Chapter 6). I propose that the observed pattern may result from the low predator abundance in BNP (leopard density: 2-3 ind/100km²; spotted-hyaena density: 0.7 ind/100km²; Monterroso, unpublished data). In the following paragraph, I explain the reasoning behind my hypothesis. However, empirical confirmation is necessary to validate it.

The low number of predators decreases the likelihood of antagonistic encounters between predators and prey (Heithaus *et al.*, 2009), which reduces the perception of the spatiotemporal variation of predation risk. Consequently, prey species are not able to create the mental mapping of risk predicted by the “Landscape of Fear” (Gaynor *et al.*, 2019, Palmer *et al.*, 2022). Limited perception of predation risk precludes prey species from proactively avoiding predation. In these cases, they are expected to adopt reactive responses in the imminence of an attack (Wirsing *et al.*, 2021). Additionally, and according to the ‘Control of Risk Hypothesis’ (Creel, 2018), proactive antipredator responses presume prey species have to face food-security trade-offs due to energetic costs and constraints to their spatiotemporal routines, i.e., changes in space use (Valeix *et al.*, 2009, Thaker *et al.*, 2011, Makin *et al.*, 2017a) and activity patterns (Tambling *et al.*, 2015, Gaynor *et al.*, 2021c, Rocha *et al.*, 2022b). Conversely, the adoption of reactive responses should release prey from food security trade-offs (Creel, 2018) but require them to be constantly alert, which increases endocrine stress (Creel *et al.*, 2009). However, the low likelihood and the rarity of encounters between predators and prey in systems with low predator abundance (Heithaus *et al.*, 2009) may release prey from stress-mediated effects. In this context, the adoption of reactive responses in predator-depleted communities may be the most efficient strategy for prey since it does not entail an energetic cost, and the endocrine stress should be limited.

While this reasoning has not been widely explored in the scientific literature, the work developed in this thesis provides a steppingstone for understanding predator-prey interactions in systems with reduced perception of predation risk, recognizing the lack of spatiotemporal proactive antipredator responses. Nevertheless, further research is needed to investigate if other proactive behaviors, such as routine vigilance or grouping behavior, are also absent in predator-deprived systems. Additionally, a comparison with systems with higher predator density is required to understand if proactive vs. reactive antipredator behaviors are directly related to predator abundance.

Another factor that may be influencing the patterns observed along the chapters of this thesis is the continued poaching and human encroachment that may also have led to changes in species' behavior and habitat use. Coherently, human-induced top-down constraints are also present in the study systems. In Chapter 4, I report the use of suboptimal habitat by Hartmann's mountain zebra and gemsbok. These species' optimal habitat should be the rugged areas, with the more productive grasslands and most water springs. However, the results estimate higher abundance of Hartmann's mountain zebra and gemsbok in the plains of rock and gravel of Iona National Park, with less availability of nutritious vegetation and surface water. I argue that the intense human activities and livestock herding on the mountains of INP may be pushing herbivore species to suboptimal areas.

Human-induced top-down constraints significantly impact wildlife (e.g. Gaynor *et al.*, 2018, Yamashita *et al.*, 2018), eventually overriding natural predators' constraints (e.g. Ciuti *et al.*, 2012, Darimont *et al.*, 2015, Smith *et al.*, 2017, Gaynor *et al.*, 2021c). In contrast to natural predators whose dynamics are interconnected with those of their prey to maintain population balance, human activities, particularly overhunting, exert a disproportionate and detrimental impact on prey demography and effectiveness (Darimont *et al.*, 2015). Additionally, human hunters frequently target species, such as megafauna or apex predators, not usually preyed upon by natural predators. This selective hunting disrupts the natural ecological functions (Darimont *et al.*, 2015) and leads to changes in wildlife behavior (Wilson *et al.*, 2020). Human-induced top-down constraints elicit physiological responses in animals similar to non-consumptive effects and create an anthropogenic 'Landscape of Fear' (Støen *et al.*, 2015, Moleón and Sánchez-Zapata, 2023). Specifically, the fear of humans can induce heightened endocrine stress responses in animals (Støen *et al.*, 2015) and constraints in the diel activities, such as reduced feeding time for large carnivores (Smith *et al.*, 2017) and large herbivores (Ciuti *et al.*, 2012). In addition, prey species also exhibit a degree of tolerance towards natural predators to avoid human activities (Van Scoyoc *et al.*, 2023), as was evidenced by the increased temporal overlap between mountain lions (*Puma concolor*) and Columbian black-tailed deer (*Odocoileus hemionus columbianus*) to avoid the sport hunting periods (Gaynor *et al.*, 2021c). Possibly, the observed absence of spatiotemporal proactive antipredator responses reported in Chapter 6 may result from poorly enforced top-down constraints due to low natural predator abundance and a long period of human pressure and overhunting during the Angolan wars. Perhaps prey species created adaptations during the period of augmented persecution and tolerate

the threat posed by natural predators to avoid human activities. These adaptations may persist even with the release of human pressure in the center of BNP since the reactivation of the park. Coherently with this rationale, Muhly *et al.* (2011) suggest that human activity creates refugia for prey species through two distinct mechanisms. Firstly, human activity can directly impact predator abundance, leading to a reduction in predator numbers. Secondly, human presence can indirectly displace predators to a greater extent than prey, particularly in areas with high human activity. Further research is needed to understand the role of human-induced top-down constraints in systems with limited natural predation and investigate if the lack of proactive responses towards natural predators results from low predator abundance or if the predation risk is suppressed by the “human risk”.

7.3 Conclusions

This thesis conciliates two main topics: the first one, more conservation-related, includes a detailed description of the status of mammalian wildlife communities across South Angolan; the second focuses on investigating the relative importance of different forces in the structuring and functioning of mammal communities. I expect this thesis to contribute to understanding the processes governing mammal communities in simplified systems that have experienced significant losses in wildlife diversity and abundance. The different communities used in this research provided an opportunity to evaluate ecological theories (such as “Optimal Forage Theory” and “Landscape of Fear”) in communities with different states of conservation or complexity.

As a secondary objective, I anticipate that this work will contribute to acquiring and disseminating knowledge regarding the status of the Angolan wild mammal community, thereby filling a crucial knowledge gap. Additionally, this research has the potential to serve as a foundation for future research projects and for implementing practical conservation and rehabilitation measures in Angola.

The main conclusions achieved with the research developed in the scope of this thesis are:

1. Angolan wildlife suffered severe declines in species richness over the last 50 years, and most extant species currently present reduced occupancy levels. The declines are more pronounced in larger than smaller mammals, with a particular incidence in antelope species.

2. The information regarding Angolan mammals in international databases (such as the IUCN red list) is outdated. More studies, communication, and cooperation between organizations are required to collect and disseminate the information.
3. Bottom-up processes dominate mammal communities of simplified systems, regardless of resource availability. These results contradict the “Ecosystem Exploitation Hypothesis”, likely by poorly enforced top-down constraints due to low predator abundance.
4. Human and livestock encroachment in natural areas influences wildlife space use, displacing species from their preferred areas. The restrictions on access to resources by wildlife are particularly alarming in desert environments, where the availability of water and vegetation is reduced.
5. Although some herbivore species temporary increase occupancy patterns of burned areas, bush fires have long-term detrimental effects on herbivore space use.
6. Absence of spatiotemporal antipredator responses, regardless of predator’s hunting mode or predation pressure. These results might result from the low predator abundance in the study systems, which precludes the perception of predation risk required for employing proactive antipredator strategies. In such cases, it may be more profitable for prey to reactively respond to short-term predation risk, but further research is required to validate this premise.

7.4 Prospects for future research

Many questions remain to be explored and are relevant for understanding the community functioning in simplified systems and for the conservation and restoration of ecological processes lost with the extirpation of some species. I propose four areas of research that should be prioritized in the near future: (i) assess if the extant mammal populations are recovering in the communities in study, (ii) explore if frequent fires are inducing changes in vegetal structure and understand its consequences for herbivores, (iii) investigate whether that low predator density preclude the use of proactive antipredator responses (iv) test if human-induced top-down constraints contribute to the lack of spatiotemporal proactive antipredator responses.

- i. Assess if the extant mammal populations are recovering in the communities in study*

In this thesis, I have provided a comprehensive description of the current mammal communities in three specific areas of southern Angola, representing the first quantitative research to assess potential species losses over the past 50 years (Chapter 2). However, to better understand the status of Angolan wildlife communities and inform conservation efforts, it is crucial to employ inference metrics that enable the estimation of population densities and trends within these study areas. Furthermore, dynamic hierarchical models can be used to evaluate potential population recovery following the years of neglect and overhunting.

These assessments are essential as they help comprehend the consequences of community simplification and the ecological processes that may have been lost due to species extinction. This information is a cornerstone for understanding the global implications of wildlife declines, as evident in previous studies (e.g. Craigie *et al.*, 2010, Ripple *et al.*, 2014, Ripple *et al.*, 2015). Additionally, the current understanding of restoration processes emphasizes rehabilitating ecological processes rather than solely focusing on recovering flagship species populations (Ford, 2021). Therefore, incorporating demographic information alongside the existing knowledge of community composition and likely extirpated species within Angolan ecosystems enables investigation of the persisting ecological processes and those that have been lost. This information is crucial for guiding potential rehabilitation measures.

Furthermore, in conjunction with this thesis and other projects conducted by the WildECOL group from CIBIO-BIOPOLIS, we have generated five years of camera trapping data from INP, BNP, and CCA. This extensive dataset can help infer population trends, accurately assess whether the community is recovering, and more precisely estimate the restoration of ecological processes.

ii. Explore if frequent fires are inducing changes in vegetal structure and understand its consequences for herbivores

In Chapter 5 of this thesis, I hypothesize that the reduced herbivory, due to the decline of mammal communities and the altered fire regimes observed in Angola, for more frequent and intense fires (Stellmes *et al.*, 2013), promote the homogenization of the landscape dominated by less palatable and fast-growing plant species. This hypothesis is supported by findings from Archibald and Hempson (2016), and Donaldson *et al.* (2018) in the Kruger National Park (South Africa), but has not been much explored by the scientific community. Thus, empiric research should be performed to confirm the hypothesis I raised. Recent research has demonstrated that fire frequency and season

change plant communities (Meller *et al.*, 2022). Still, whether these changes are sufficient to create undesirable habitats for herbivores remains unexplored.

Understanding this dynamic is essential for the recovery of ecosystems since fire is a fundamental ecological process, and changes in fire regimes have profound ecological impacts on plant communities and, consequently, on animals (McLauchlan *et al.*, 2020). Fire is frequently used as a management measure to promote the growth of fresh and nutritious grass for herbivores (Fynn *et al.*, 2019). However, if my rationale is correct, managers may unintentionally achieve the opposite outcome and create undesirable habitats for herbivores. This understanding will advance the scientific knowledge about changes in fire regimes and is crucial for informing effective management strategies that promote desirable habitat conditions, ensuring the long-term viability of wild herbivore populations.

iii. Investigate whether that low predator density preclude the use of proactive antipredator responses

In Chapter 6, I postulated that the lack of proactive spatiotemporal antipredator behavior exhibited by prey species could be attributed to the diminished perception of variations in predation risk within the landscape, primarily resulting from low predator abundance. This postulation aligns with the "Control of Risk Hypothesis" (Creel, 2018), suggesting that implementing preemptive antipredator behaviors comes with inherent costs. Consequently, it may not be advantageous for prey to restrict their activities in response to a potentially reduced and challenging-to-accurately-perceive predation risk. In turn, it may be preferable for prey to respond reactively in case of an immediate attack.

The validation of this hypothesis requires further research, which should be conducted in two distinct parts. Firstly, in Chapter 6, my focus was solely on spatiotemporal patterns, disregarding other proactive antipredator behaviors such as non-induced vigilance or grouping behavior, which prey species may employ but were not evaluated in this study. Additionally, it would be valuable to explore reactive responses by testing the reaction of prey to artificial cues of predator presence, such as playbacks. The WildECOL group is collaborating on a project that is already implementing this method in Gorongosa National Park (Mozambique), and we intend to extend these surveys to the Bicular National Park shortly.

Secondly, the same empirical methodology employed in Chapter 6 should be replicated in comparable systems characterized by higher predator abundance and, hypothetically, an elevated predation risk. This would allow for a comparative analysis to

assess the potential influence of predator abundance on the manifestation of proactive antipredator behaviors.

iv. Test if human-induced top-down constraints contribute to the lack of spatiotemporal proactive antipredator responses

Another topic raised in this thesis that deserves further investigation is human-induced top-down constraints' potential role in the absence of proactive antipredator responses in systems with low predator abundance. Previous research has demonstrated that human-induced top-down constraints can surpass the limitations imposed by the risk of predation by natural predators (Ciuti *et al.*, 2012, Darimont *et al.*, 2015). Although human disturbance in the core area of Bicular National Park, where our data is collected, has decreased significantly in recent years, behavioral adaptations acquired during higher human persecution may have persisted. It is essential to recognize that no single factor operates in isolation within a system. If the fear of humans endures and continues to outweigh responses to natural predators, it is likely due to insufficient predation pressure from natural predators to reverse this situation. Understanding the influence of past human pressure on current animal behavioral decisions can provide valuable insights into disruptions in altered systems. Further investigation into this topic would contribute to a comprehensive understanding of the dynamics between human-induced constraints and natural predation effects on prey behavior in low-predator abundance systems.

Chapter 8

References

- Abraham, J. O., Hempson, G. P., Staver, A. C. (2019). Drought-response strategies of savanna herbivores. *Ecology and Evolution* 9, 7047. DOI: <https://doi.org/10.1002/ece3.5270>.
- Abu Baker, M. A., Brown, J. S. (2014). Foraging and habitat use of common duikers, *Sylvicapra grimmia*, in a heterogeneous environment within the Soutpansberg, South Africa. *African Journal of Ecology* 52, 318. DOI: <https://doi.org/10.1111/aje.12122>.
- Allee, W. C., Park, T. (1939). Concerning Ecological Principles. *Science* 89, 166. DOI: <https://doi.org/10.1126/science.89.2304.166>.
- Allison, Steven D. (2006). Brown Ground: A Soil Carbon Analogue for the Green World Hypothesis? *The American Naturalist* 167, 619. DOI: <https://doi.org/10.1086/503443>.
- Allred, B. W., Fuhlendorf, S. D., Engle, D. M., Elmore, R. D. (2011). Ungulate preference for burned patches reveals strength of fire–grazing interaction. *Ecology and Evolution* 1, 132. DOI: <https://doi.org/10.1002/ece3.12>.
- Anderson, T. M., Ritchie, Mark E., Mayemba, E., Eby, S., Grace, James B., McNaughton, Samuel J. (2007). Forage Nutritive Quality in the Serengeti Ecosystem: The Roles of Fire and Herbivory. *The American Naturalist* 170, 343. DOI: <https://doi.org/10.1086/520120>.
- Anderson, T. M., White, S., Davis, B., Erhardt, R., Palmer, M., Swanson, A., Kosmala, M., Packer, C. (2016). The spatial distribution of African savannah herbivores: species associations and habitat occupancy in a landscape context. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371. DOI: <https://doi.org/10.1098/rstb.2015.0314>.
- Anderwald, P., Herfindal, I., Haller, R. M., Risch, A. C., Schütz, M., Schweiger, A. K., Filli, F. (2015). Influence of migratory ungulate management on competitive interactions with resident species in a protected area. *Ecosphere* 6, art228. DOI: <https://doi.org/10.1890/ES15-00365.1>.
- Andrade, A. (1985). *O naturalista José de Anchieta*. Lisbon: Instituto de Investigação Científica Tropical.
- Archibald, S., Bond, W. J., Stock, W. D., Fairbanks, D. H. K. (2005). Shaping the landscape: fire-grazer interactions in an African savanna. *Ecological Applications* 15, 96. DOI: <https://doi.org/10.1890/03-5210>.
- Archibald, S., Hempson, G. P. (2016). Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371, 20150309. DOI: <https://doi.org/10.1098/rstb.2015.0309>.

- Archibald, S., Roy, D. P., Van Wilgen, B. W. , Scholes, R. J. (2009). What limits fire? An examination of drivers of burnt area in Southern Africa. *Global Change Biology* 15, 613. DOI: <https://doi.org/10.1111/j.1365-2486.2008.01754.x>.
- Armsworth, P. R., Jackson, H. B., Cho, S.-H., Clark, M., Fargione, J. E., Iacona, G. D., Kim, T., Larson, E. R., Minney, T. , Sutton, N. A. (2018). Is conservation right to go big? Protected area size and conservation return-on-investment. *Biological Conservation* 225, 229. DOI: <https://doi.org/10.1016/j.biocon.2018.07.005>.
- Atkins, J. L., Long, R. A., Pansu, J., Daskin, J. H., Potter, A. B., Stalmans, M. E., Tarnita, C. E. , Pringle, R. M. (2019). Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science* 364, 173. DOI: <https://doi.org/10.1126/science.aau3561>.
- Augustine, D. J. , Derner, J. D. (2014). Controls over the strength and timing of fire–grazer interactions in a semi-arid rangeland. *Journal of Applied Ecology* 51, 242. DOI: <https://doi.org/10.1111/1365-2664.12186>.
- Ayling, J. (2013). What Sustains Wildlife Crime? Rhino Horn Trading and the Resilience of Criminal Networks. *Journal of International Wildlife Law & Policy* 16, 57. DOI: <https://doi.org/10.1080/13880292.2013.764776>.
- Azevedo, F. C., Lemos, F. G., Freitas-Junior, M. C., Rocha, D. G. , Azevedo, F. C. C. (2018). Puma activity patterns and temporal overlap with prey in a human-modified landscape at Southeastern Brazil. *Journal of Zoology* 305, 246. DOI: <https://doi.org/10.1111/jzo.12558>.
- Bacchiocchi, I. (2020). *Diet assessment of spotted hyena in Bicular National Park, Angola*. University of Bologna.
- Baptista, N., Conradie, W., Vaz Pinto, P. , Branch, W. R. (2019). The Amphibians of Angola: Early Studies and the Current State of Knowledge. In *Biodiversity of Angola: Science & Conservation: A Modern Synthesis*: 243-281. Huntley, B. J., Russo, V., Lages, F. , Ferrand, N. (Eds.). Cham: Springer International Publishing.
- Barnard, P., Brown, C. J., Jarvis, A. M., Robertson, A. , Rooyen, L. V. (1998). Extending the Namibian protected area network to safeguard hotspots of endemism and diversity. *Biodiversity & Conservation* 7, 531. DOI: <https://doi.org/10.1023/A:1008831829574>.
- Barnier, F., Valeix, M., Duncan, P., Chamaillé-Jammes, S., Barre, P., Loveridge, A. J., Macdonald, D. W. , Fritz, H. (2014). Diet quality in a wild grazer declines under the threat of an ambush predator. *Proceedings of the Royal Society B: Biological Sciences* 281, 20140446. DOI: <https://doi.org/10.1098/rspb.2014.0446>.
- Beale, C. M., Courtney Mustaphi, C. J., Morrison, T. A., Archibald, S., Anderson, T. M., Dobson, A. P., Donaldson, J. E., Hempson, G. P., Probert, J. , Parr, C. L. (2018).

Pyrodiversity interacts with rainfall to increase bird and mammal richness in African savannas. *Ecology Letters* 21, 557. DOI: <https://doi.org/10.1111/ele.12921>.

Beck, H. E., Zimmermann, N. E., McVicar, T. R., Vergopolan, N., Berg, A. , Wood, E. F. (2018). Present and future Köppen-Geiger climate classification maps at 1-km resolution. *Scientific Data* 5, 180214. DOI: <https://doi.org/10.1038/sdata.2018.214>.

Becker, M. S., Durant, S. M., Watson, F. G. R., Parker, M., Gottelli, D., M'Soka, J., Droge, E., Nyirenda, M., Schuette, P., Dunkley, S. , Brummer, R. (2017). Using dogs to find cats: detection dogs as a survey method for wide-ranging cheetah. *Journal of Zoology* 302, 184. DOI: <https://doi.org/10.1111/jzo.12445>.

Beja, P., Vaz Pinto, P., Veríssimo, L., Bersacola, E., Fabiano, E., Palmeirim, J. M., Monadjem, A., Monterroso, P., Svensson, M. S. , Taylor, P. J. (2019). The Mammals of Angola. In *Biodiversity of Angola: Science & Conservation: A Modern Synthesis*: 357-443. Huntley, B. J., Russo, V., Lages, F. , Ferrand, N. (Eds.). Cham: Springer International Publishing.

Belda, M., Holtanová, E., Halenka, T. , Kalvová, J. (2014). Climate classification revisited: from Köppen to Trewartha. *Climate Research* 59, 1. DOI: <https://doi.org/10.3354/cr01204>.

Birch, L. C. , Ehrlich, P. R. (1967). Evolutionary History and Population Biology. *Nature* 214, 349. DOI: <https://doi.org/10.1038/214349a0>.

Bombo, A. B., Siebert, F. , Fidelis, A. (2022). Fire and herbivory shape belowground bud banks in a semi-arid African savanna. *African Journal of Range & Forage Science* 39, 16. DOI: <https://doi.org/10.2989/10220119.2021.1982004>.

Bond, W. J. (2005). Large parts of the world are brown or black: A different view on the 'Green World'hypothesis. *Journal of Vegetation Science* 16, 261. DOI: <https://doi.org/10.1111/j.1654-1103.2005.tb02364.x>.

Boonstra, R., Hik, D., Singleton, G. R. , Tinnikov, A. (1998). The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs* 68, 371. DOI: [https://doi.org/10.1890/0012-9615\(1998\)068\[0371:TIOPIS\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1998)068[0371:TIOPIS]2.0.CO;2).

Boyers, M., Parrini, F., Owen-Smith, N., Erasmus, B. F. N. , Hetem, R. S. (2019). How free-ranging ungulates with differing water dependencies cope with seasonal variation in temperature and aridity. *Conservation Physiology* 7. DOI: <https://doi.org/10.1093/conphys/coz064>.

Braga-Pereira, F., Bogoni, J. A. , Alves, R. R. N. (2020a). From spears to automatic rifles: The shift in hunting techniques as a mammal depletion driver during the Angolan civil war. *Biological Conservation* 249, 108744. DOI: <https://doi.org/10.1016/j.biocon.2020.108744>.

- Braga-Pereira, F., Peres, C. A., Campos-Silva, J. V., Santos, C. V.-D. , Alves, R. R. N. (2020b). Warfare-induced mammal population declines in Southwestern Africa are mediated by species life history, habitat type and hunter preferences. *Scientific Reports* 10, 15428. DOI: <https://doi.org/10.1038/s41598-020-71501-0>.
- Braga-Pereira, F., Peres, C. A., da Nóbrega Alves, R. R. , Van-Dúnem Santos, C. (2021a). Intrinsic and extrinsic motivations governing prey choice by hunters in a post-war African forest-savannah macromosaic. *PLOS ONE* 16, e0261198. DOI: <https://doi.org/10.1371/journal.pone.0261198>.
- Braga-Pereira, F., Van-Dúnem Santos, C., Alves, R. R. N. , Hunter, L. (2021b). Persistence of wild felids after a protracted civil war in Quiçama National Park and Quiçama Game Reserve, Angola. *African Journal of Ecology* n/a. DOI: <https://doi.org/10.1111/aje.12946>.
- Brennan, A., Beytell, P., Aschenborn, O., Du Preez, P., Funston, P. J., Hanssen, L., Kilian, J. W., Stuart-Hill, G., Taylor, R. D. , Naidoo, R. (2020). Characterizing multispecies connectivity across a transfrontier conservation landscape. *Journal of Applied Ecology* 57, 1700. DOI: <https://doi.org/10.1111/1365-2664.13716>.
- Breytenbach, J. (2001). *The Plunderers*: Covos-Day Books.
- Breytenbach, J. (2015). *Eden's Exiles*. Pretoria: Protea Boekhuis.
- Brito, J. C., Godinho, R., Martínez-Freiría, F., Pleguezuelos, J. M., Rebelo, H., Santos, X., Vale, C. G., Velo-Antón, G., Boratyński, Z., Carvalho, S. B., Ferreira, S., Gonçalves, D. V., Silva, T. L., Tarroso, P., Campos, J. C., Leite, J. V., Nogueira, J., Álvares, F., Sillero, N., Sow, A. S., Fahd, S., Crochet, P.-A. , Carranza, S. (2014). Unravelling biodiversity, evolution and threats to conservation in the Sahara-Sahel. *Biological Reviews* 89, 215. DOI: <https://doi.org/10.1111/brv.12049>.
- Brito, J. C. , Pleguezuelos, J. M. (2019). Desert Biodiversity—World's Hot Spots/Globally Outstanding Biodiverse Deserts. In *Reference Module in Earth Systems and Environmental Sciences*: Elsevier.
- Brodie, J. F., Helmy, O. E., Mohd-Azlan, J., Granados, A., Bernard, H., Giordano, A. J. , Zipkin, E. (2018). Models for assessing local-scale co-abundance of animal species while accounting for differential detectability and varied responses to the environment. *Biotropica* 50, 5. DOI: <https://doi.org/10.1111/btp.12500>.
- Brown, J. S., Laundré, J. W. , Gurung, M. (1999). The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. *Journal of Mammalogy* 80, 385. DOI: <https://doi.org/10.2307/1383287>.
- Brugière, D., Chardonnet, B. , Scholte, P. (2015). Large-Scale Extinction of Large Carnivores (Lion *Panthera Leo*, Cheetah *Acinonyx Jubatus* and Wild Dog *Lycaon Pictus*) in Protected Areas of West and Central Africa. *Tropical Conservation Science* 8, 513. DOI: <https://doi.org/10.1177/194008291500800215>.

- Brun, P., Zimmermann, N. E., Hari, C., Pellissier, L. , Karger, D. N. (2022a). CHELSA-BIOCLIM+ A novel set of global climate-related predictors at kilometre-resolution.): EnviDat.
- Brun, P., Zimmermann, N. E., Hari, C., Pellissier, L. , Karger, D. N. (2022b). Global climate-related predictors at kilometer resolution for the past and future. *Earth System Science Data* 14, 5573. DOI: <https://doi.org/10.5194/essd-14-5573-2022>.
- Buchhorn, M., Smets, B., Bertels, L., Roo, B. D., Lesiv, M., Tsendbazar, N.-E., Li, L. , Tarko, A. (2021). Copernicus Global Land Service: Land Cover 100m: version 3 Globe 2015-2019: Product User Manual (Dataset v3.0, doc issue 3.4.): Zenodo.
- Buckley, R. (2010). *Conservation tourism*: CABI.
- Bukombe, J., Kittle, A., Senzota, R., Mduma, S., Fryxell, J. , Sinclair, A. R. E. (2018). Resource selection, utilization and seasons influence spatial distribution of ungulates in the western Serengeti National Park. *African Journal of Ecology* 56, 3. DOI: <https://doi.org/10.1111/aje.12410>.
- Burger, J., Safina, C. , Gochfeld, M. (2000). Factors affecting vigilance in springbok: importance of vegetative cover, location in herd, and herd size. *Acta Ethologica* 2, 97. DOI: <https://doi.org/10.1007/s102119900013>.
- Burgess, N., Hales, J. A., Underwood, E., Dinerstein, E., Olson, D., Itoua, I., Schipper, J., Ricketts, T. , Newman, K. (2004). *Terrestrial ecoregions of Africa and Madagascar: a conservation assessment*: Island Press.
- Burkepile, D. E., Burns, C. E., Tambling, C. J., Amendola, E., Buis, G. M., Govender, N., Nelson, V., Thompson, D. I., Zinn, A. D. , Smith, M. D. (2013). Habitat selection by large herbivores in a southern African savanna: the relative roles of bottom-up and top-down forces. *Ecosphere* 4, 1. DOI: <https://doi.org/10.1890/ES13-00078.1>.
- Burkepile, D. E., Thompson, D. I., Fynn, R. W. S., Koerner, S. E., Eby, S., Govender, N., Hagenah, N., Lemoine, N. P., Matchett, K. J., Wilcox, K. R., Collins, S. L., Kirkman, K. P., Knapp, A. K. , Smith, M. D. (2016). Fire frequency drives habitat selection by a diverse herbivore guild impacting top-down control of plant communities in an African savanna. *Oikos* 125, 1636. DOI: <https://doi.org/10.1111/oik.02987>.
- Cáceres, A., Melo, M., Barlow, J. , Mills, M. S. L. (2016). Radiotelemetry reveals key data for the conservation of *Sheppardia gabela* (Rand, 1957) in the Angolan Escarpment forest. *African Journal of Ecology* 54, 317. DOI: <https://doi.org/10.1111/aje.12283>.
- Cain III, J. W., Gedir, J. V., Marshal, J. P., Krausman, P. R., Allen, J. D., Duff, G. C., Jansen, B. D. , Morgart†, J. R. (2017). Extreme precipitation variability, forage quality and large herbivore diet selection in arid environments. *Oikos* 126, 1459. DOI: <https://doi.org/10.1111/oik.04282>.

Cain III, J. W., Krausman, P. R., Rosenstock, S. S. , Turner, J. C. (2005). Literature Review and Annotated Bibliography: Water Requirements of Desert Ungulates.

Cain III, J. W., Krausman, P. R., Rosenstock, S. S. , Turner, J. C. (2006). Mechanisms of Thermoregulation and Water Balance in Desert Ungulates. *Wildlife Society Bulletin* 34, 570. DOI: [https://doi.org/10.2193/0091-7648\(2006\)34\[570:MOTAWB\]2.0.CO;2](https://doi.org/10.2193/0091-7648(2006)34[570:MOTAWB]2.0.CO;2).

Caro, T. (2015). Conservation in the African Anthropocene. In *Protecting the Wild: Parks and Wilderness, the Foundation for Conservation*: 164-169. Wuerthner, G., Crist, E. , Butler, T. (Eds.). Washington, DC: Island Press/Center for Resource Economics.

Carpaneto, G. M. , Fusari, A. (2000). Subsistence hunting and bushmeat exploitation in central-western Tanzania. *Biodiversity & Conservation* 9, 1571. DOI: <https://doi.org/10.1023/A:1008943003752>.

Carter, N. H., López-Bao, J. V., Bruskotter, J. T., Gore, M., Chapron, G., Johnson, A., Epstein, Y., Shrestha, M., Frank, J., Ohrens, O. , Treves, A. (2017). A conceptual framework for understanding illegal killing of large carnivores. *Ambio* 46, 251. DOI: <https://doi.org/10.1007/s13280-016-0852-z>.

Castro, A. J., Martín-López, B., López, E., Plieninger, T., Alcaraz-Segura, D., Vaughn, C. C. , Cabello, J. (2015). Do protected areas networks ensure the supply of ecosystem services? Spatial patterns of two nature reserve systems in semi-arid Spain. *Applied Geography* 60, 1. DOI: <https://doi.org/10.1016/j.apgeog.2015.02.012>.

Catarino, S., Romeiras, M. M., Figueira, R., Aubard, V., Silva, J. M. N. , Pereira, J. M. C. (2020). Spatial and Temporal Trends of Burnt Area in Angola: Implications for Natural Vegetation and Protected Area Management. *Diversity* 12, 307. DOI: <https://doi.org/10.3390/d12080307>.

Chase, M. J. , Griffin, C. R. (2011). Elephants of south-east Angola in war and peace: their decline, re-colonization and recent status. *African Journal of Ecology* 49, 353. DOI: <https://doi.org/10.1111/j.1365-2028.2011.01272.x>.

Cherry, M. J., Chandler, R. B., Garrison, E. P., Crawford, D. A., Kelly, B. D., Shindle, D. B., Godsea, K. G., Miller, K. V. , Conner, L. M. (2018). Wildfire affects space use and movement of white-tailed deer in a tropical pyric landscape. *Forest Ecology and Management* 409, 161. DOI: <https://doi.org/10.1016/j.foreco.2017.11.007>.

Chicomo, M. (2018). *Diversidade de Mamíferos do Parque Nacional do Bicular*. Instituto Superior de Ciências de Educação da Huíla - ISCED-Huíla.

Chicomo, M. (2021). *Assessment of the abundance and selected population characteristics of Hartmann's mountain zebra Equus zebra hartmannae in Iona National Park, Angola*. Namibia University of Science and Technology.

- Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., Boyce, M. S. (2012). Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. *PLOS ONE* 7, e50611. DOI: <https://doi.org/10.1371/journal.pone.0050611>.
- Clinchy, M., Sheriff, M. J., Zanette, L. Y. (2013). Predator-induced stress and the ecology of fear. *Functional Ecology* 27, 56. DOI: <https://doi.org/10.1111/1365-2435.12007>.
- Cohen, B. S., Prebyl, T. J., Collier, B. A., Chamberlain, M. J. (2019). Spatiotemporal variability of fire characteristics affect animal responses in pyric landscapes. *Fire Ecology* 15, 41. DOI: 10.1186/s42408-019-0058-4.
- Cotgreave, P. (1993). The relationship between body size and population abundance in animals. *Trends in Ecology & Evolution* 8, 244. DOI: [https://doi.org/10.1016/0169-5347\(93\)90199-Y](https://doi.org/10.1016/0169-5347(93)90199-Y).
- Courbin, N., Loveridge, A., Fritz, H., Macdonald, D., Patin, R., Valeix, M., Chamaillé-Jammes, S. (2017). Zebra diel migrations reduce encounter risk with lions over selection for safe habitats. *bioRxiv*, 165597. DOI: <https://doi.org/10.1101/165597>.
- Courbin, N., Loveridge, A. J., Fritz, H., Macdonald, D. W., Patin, R., Valeix, M., Chamaillé-Jammes, S. (2019). Zebra diel migrations reduce encounter risk with lions at night. *Journal of Animal Ecology* 88, 92. DOI: <https://doi.org/10.1111/1365-2656.12910>.
- Craigie, I. D., Baillie, J. E. M., Balmford, A., Carbone, C., Collen, B., Green, R. E., Hutton, J. M. (2010). Large mammal population declines in Africa's protected areas. *Biological Conservation* 143, 2221. DOI: <https://doi.org/10.1016/j.biocon.2010.06.007>.
- Crawford-Cabral, J., Simões, A. (1988a). Distributional data and notes on Angolan carnivores (Mammalia: Carnivora) I – Small and medium-sized species. *Garcia de Orta: Série de Zoologia* 14, 3. DOI:
- Crawford-Cabral, J., Simões, A. (1988b). Distributional data and notes on Angolan carnivores (Mammalia: Carnivora) II – Larger species. *Garcia de Orta: Série de Zoologia* 15, 9. DOI:
- Crawford-Cabral, J., Veríssimo, L. N. (2005). *The Ungulate Fauna of Angola: Systematic List, Distribution Maps, Database Report*: Ministério da Ciência, Tecnologia e Ensino Superior, Instituto de Investigação Científica Tropical.
- Creel, S. (2018). The control of risk hypothesis: reactive vs. proactive antipredator responses and stress-mediated vs. food-mediated costs of response. *Ecology Letters* 21, 947. DOI: <https://doi.org/10.1111/ele.12975>.

- Creel, S. , Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology & Evolution* 23, 194. DOI: <https://doi.org/10.1016/j.tree.2007.12.004>.
- Creel, S., Christianson, D., Liley, S. , Winnie, J. A. (2007). Predation risk affects reproductive physiology and demography of elk. *Science* 315, 960. DOI: <https://doi.org/10.1126/science.1135918>.
- Creel, S., Winnie, J. A. , Christianson, D. (2009). Glucocorticoid stress hormones and the effect of predation risk on elk reproduction. *Proceedings of the National Academy of Sciences* 106, 12388. DOI: <https://doi.org/10.1073/pnas.0902235106>.
- Crête, M. (1999). The distribution of deer biomass in North America support the hypothesis of exploitation ecosystems. *Ecology Letters* 2, 223. DOI: <https://doi.org/10.1046/j.1461-0248.1999.00076.x>.
- Crosmar, W. G., Valeix, M., Fritz, H., Madzikanda, H. , Côté, S. D. (2012). African ungulates and their drinking problems: hunting and predation risks constrain access to water. *Animal Behaviour* 83, 145. DOI: <https://doi.org/10.1016/j.anbehav.2011.10.019>.
- Darimont, C. T., Fox, C. H., Bryan, H. M. , Reimchen, T. E. (2015). The unique ecology of human predators. *Science* 349, 858. DOI: <https://doi.org/10.1126/science.aac4249>.
- Darwin, C. (1859). *On the origin of species by means of natural selection, or preservation of favoured races in the struggle for life*: London : John Murray, 1859.
- Daskin, J. H. , Pringle, R. M. (2018). Warfare and wildlife declines in Africa's protected areas. *Nature* 553, 328. DOI: <https://doi.org/10.1038/nature25194>.
- Daskin, J. H., Stalmans, M. , Pringle, R. M. (2016). Ecological legacies of civil war: 35-year increase in savanna tree cover following wholesale large-mammal declines. *Journal of Ecology* 104, 79. DOI: <https://doi.org/10.1111/1365-2745.12483>.
- Davidson, Z., Valeix, M., Van Kesteren, F., Loveridge, A. J., Hunt, J. E., Murindagomo, F. , Macdonald, D. W. (2013). Seasonal Diet and Prey Preference of the African Lion in a Waterhole-Driven Semi-Arid Savanna. *PLoS ONE* 8, e55182. DOI: <https://doi.org/10.1371/journal.pone.0055182>.
- Davies, A. B., Crooms, J. P. G. M., Tambling, C. J., le Roux, E., Vaughn, N., Druce, D. J., Marneweck, D. G. , Asner, G. P. (2021). Environmental controls on African herbivore responses to landscapes of fear. *Oikos* 130, 171. DOI: <https://doi.org/10.1111/oik.07559>.

- Davis, M. A. , Pelsor, M. (2001). Experimental support for a resource-based mechanistic model of invasibility. *Ecology Letters* 4, 421. DOI: <https://doi.org/10.1046/j.1461-0248.2001.00246.x>.
- Davis, R. S., Stone, E. L., Gentle, L. K., Mgoola, W. O., Uzal, A. , Yarnell, R. W. (2021). Spatial partial identity model reveals low densities of leopard and spotted hyaena in a miombo woodland. *Journal of Zoology* 313, 43. DOI: <https://doi.org/10.1111/jzo.12838>.
- De Cauwer, V. , Lages, F. (2018). SCIONA: Angola kick-off trip report. Namibian University of Science and Technology.
- de Merode, E., Smith, K. H., Homewood, K., Pettifor, R., Rowcliffe, M. , Cowlshaw, G. (2007). The impact of armed conflict on protected-area efficacy in Central Africa. *Biology letters* 3, 299. DOI: <https://doi.org/10.1098/rsbl.2007.0010>.
- Dean, W. R. J., Melo, M. , Mills, M. S. L. (2019). The Avifauna of Angola: Richness, Endemism and Rarity. In *Biodiversity of Angola: Science & Conservation: A Modern Synthesis*: 335-356. Huntley, B. J., Russo, V., Lages, F. , Ferrand, N. (Eds.). Cham: Springer International Publishing.
- Dlamini, T. B., Reilly, B. K., Thompson, D. I., Burkepile, D. E., Botha, J. M. , Rebelo, A. G. (2020). Differential herbivore occupancy of fire-manipulated savannas in the Satara region of the Kruger National Park, South Africa. *Koedoe : African Protected Area Conservation and Science* 62, 1. DOI: <https://doi.org/10.4102/koedoe.v62i1.1603>.
- Donadio, E. , Buskirk, S. W. (2016). Linking predation risk, ungulate antipredator responses, and patterns of vegetation in the high Andes. *Journal of Mammalogy* 97, 966. DOI: <https://doi.org/10.1093/jmammal/gyw020>.
- Donaldson, J. E., Archibald, S., Govender, N., Pollard, D., Luhdo, Z. , Parr, C. L. (2018). Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns. *Journal of Applied Ecology* 55, 225. DOI: <https://doi.org/10.1111/1365-2664.12956>.
- Dorazio, R. M. , Royle, J. A. (2005). Estimating Size and Composition of Biological Communities by Modeling the Occurrence of Species. *Journal of the American Statistical Association* 100, 389. DOI: <https://doi.org/10.1198/016214505000000015>.
- Dudley, J. P., Ginsberg, J. R., Plumptre, A. J., Hart, J. A. , Campos, L. C. (2002). Effects of War and Civil Strife on Wildlife and Wildlife Habitats. *Conservation Biology* 16, 319. DOI: <https://doi.org/10.1046/j.1523-1739.2002.00306.x>.
- Dudley, N. (2008). *Guidelines for applying protected area management categories*: IUCN.

Dudley, N., MacKinnon, K. , Stolton, S. (2014). The role of protected areas in supplying ten critical ecosystem services in drylands: a review. *Biodiversity* 15, 178. DOI: <https://doi.org/10.1080/14888386.2014.928790>.

Dunham, K. M. (2004). Aerial Survey of Large Herbivores in Gorongosa National Park, Mozambique: 2004. Gorongosa National Park.

Durant, S., Mitchell, N., Ipavec, A. , Groom, R. (2015). *Acinonyx jubatus*.

Easter, T., Bouley, P. , Carter, N. (2019). Opportunities for biodiversity conservation outside of Gorongosa National Park, Mozambique: A multispecies approach. *Biological Conservation* 232, 217. DOI: <https://doi.org/10.1016/j.biocon.2019.02.007>.

Eby, S. , Ritchie, M. E. (2016). Alternative hypotheses for mammalian herbivore preference of burned areas in a savannah ecosystem. *African Journal of Ecology*, n/a. DOI: <https://doi.org/10.1111/aje.12306>.

Eby, S. L., Anderson, T. M., Mayemba, E. P. , Ritchie, M. E. (2014). The effect of fire on habitat selection of mammalian herbivores: the role of body size and vegetation characteristics. *Journal of Animal Ecology* 83, 1196. DOI: <https://doi.org/10.1111/1365-2656.12221>.

Elizalde, S., Elizalde, D., Lutondo, E., Groom, R., Kesch, K. , Durant, S. (2019). Reserva Natural Integral do Luando, Angola - Levantamento de Mamíferos de Grande e Médio Porte. Instituto Nacional da Biodiversidade e Áreas de Conservação (INBAC)/ The Range Wide Conservation Programme for Cheetah and African Wild Dog (RWCP).

Elmhagen, B., Ludwig, G., Rushton, S. P., Helle, P. , Lindén, H. (2010). Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. *Journal of Animal Ecology* 79, 785. DOI: <https://doi.org/10.1111/j.1365-2656.2010.01678.x>.

Elton, C. S. (1927). The Nature and Origin of Soil-Polygons in Spitsbergen. *Quarterly Journal of the Geological Society* 83, 163. DOI: <https://doi.org/10.1144/GSL.JGS.1927.083.01-05.07>.

Eriksen, C. (2007). Why do they burn the 'bush'? Fire, rural livelihoods, and conservation in Zambia. *The Geographical Journal* 173, 242. DOI: <https://doi.org/10.1111/j.1475-4959.2007.00239.x>.

Estes, R. D. (2012). *The behavior guide to African mammals: including hoofed mammals, carnivores, primates*: The University of California Press.

- Fabiano, E. C., Alvares, F., Kosmas, S., Godinho, R., Castro, I. (2017). The conservation status of the endangered African Wild Dogs in Angola: An historical and contemporary perspective. University of Namibia, Katima-Mulilo.
- Facility), G. G. B. I. (2019). *gbif.org* [accessed 20 June 2019]
- Farr, T. G., Rosen, P. A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., Alsdorf, D. (2007). The Shuttle Radar Topography Mission. *Reviews of Geophysics* 45. DOI: <https://doi.org/10.1029/2005rg000183>.
- Finke, D. L., Denno, R. F. (2004). Predator diversity dampens trophic cascades. *Nature* 429, 407. DOI: <https://doi.org/10.1038/nature02554>.
- Ford, A. T. (2021). Operationalizing process-based restoration for terrestrial communities. *Restoration Ecology* 29, e13457. DOI: <https://doi.org/10.1111/rec.13457>.
- Foster, W. A., Treherne, J. E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* 293, 466. DOI: <https://doi.org/10.1038/293466a0>.
- Freixial, C. (2021). *The Mammals of Iona National Park and surrounding areas, Namibe Province, southwestern Angola: a preliminary checklist*. University of Évora.
- Fretwell, S. D., Barach, A. L. (1977). The regulation of plant communities by the food chains exploiting them. *Perspectives in biology and medicine* 20, 169. DOI: <https://doi.org/10.1353/pbm.1977.0087>.
- Fuller, A., Mitchell, D., Maloney, S. K., Hetem, R. S. (2016). Towards a mechanistic understanding of the responses of large terrestrial mammals to heat and aridity associated with climate change. *Climate Change Responses* 3, 10. DOI: <https://doi.org/10.1186/s40665-016-0024-1>.
- Funston, P., Henschel, P., Petracca, L. S., MacLennan, S. D., Whitesell, C., Fabiano, E., Castro, I. (2017). The Distribution and Status of Lions and Other Large Carnivores in Luengue-Luiana and Mavinga National Parks, Angola. Kasane, Botswana.
- Fynn, R. W. S., Augustine, D. J., Fuhlendorf, S. D. (2019). Managing browsing and grazing ungulates. In *The Ecology of Browsing and Grazing II*: 321-338. Gordon, I. J., Prins, H. H. T. (Eds.). Cham: Springer International Publishing.
- García, Y., Castellanos, M. C., Pausas, J. G. (2016). Fires can benefit plants by disrupting antagonistic interactions. *Oecologia* 182, 1165. DOI: 10.1007/s00442-016-3733-z.

- Gaston, K. J., Blackburn, T. M., Greenwood, J. J. D., Gregory, R. D., Quinn, R. M. , Lawton, J. H. (2000). Abundance–occupancy relationships. *Journal of Applied Ecology* 37, 39. DOI: <https://doi.org/10.1046/j.1365-2664.2000.00485.x>.
- Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E. , Brashares, J. S. (2019). Landscapes of Fear: spatial patterns of risk perception and response. *Trends in Ecology & Evolution* 34, 355. DOI: <https://doi.org/10.1016/j.tree.2019.01.004>.
- Gaynor, K. M., Cherry, M. J., Gilbert, S. L., Kohl, M. T., Larson, C. L., Newsome, T. M., Prugh, L. R., Suraci, J. P., Young, J. K. , Smith, J. A. (2021a). An applied ecology of fear framework: linking theory to conservation practice. *Animal Conservation* 24, 308. DOI: <https://doi.org/10.1111/acv.12629>.
- Gaynor, K. M., Daskin, J. H., Rich, L. N. , Brashares, J. S. (2021b). Postwar wildlife recovery in an African savanna: evaluating patterns and drivers of species occupancy and richness. *Animal Conservation* 24, 510. DOI: <https://doi.org/10.1111/acv.12661>.
- Gaynor, K. M., Fiorella, K. J., Gregory, G. H., Kurz, D. J., Seto, K. L., Withey, L. S. , Brashares, J. S. (2016). War and wildlife: linking armed conflict to conservation. *Frontiers in Ecology and the Environment* 14, 533. DOI: <https://doi.org/10.1002/fee.1433>.
- Gaynor, K. M., Hojnowski, C. E., Carter, N. H. , Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science* 360, 1232. DOI: <https://doi.org/10.1126/science.aar7121>.
- Gaynor, K. M., McInturff, A. , Brashares, J. S. (2021c). Contrasting patterns of risk from human and non-human predators shape temporal activity of prey. *Journal of Animal Ecology* 91, 46. DOI: <https://doi.org/10.1111/1365-2656.13621>.
- GBIF.org (17 September 2021). GBIF Occurrence Download <https://doi.org/10.15468/dl.6hmda5>.
- Geary, W. L., Doherty, T. S., Nimmo, D. G., Tulloch, A. I. T. , Ritchie, E. G. (2020). Predator responses to fire: A global systematic review and meta-analysis. *Journal of Animal Ecology* 89, 955. DOI: <https://doi.org/10.1111/1365-2656.13153>.
- Geldmann, J., Barnes, M., Coad, L., Craigie, I. D., Hockings, M. , Burgess, N. D. (2013). Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. *Biological Conservation* 161, 230. DOI: <https://doi.org/10.1016/j.biocon.2013.02.018>.
- Gelman, A., Meng, X.-L. , Stern, H. (1996). Posterior Predictive Assessment of Model Fitness Via Realized Discrepancies. *Statistica Sinica* 6, 733. DOI: <https://www.jstor.org/stable/24306036>.

- Gelman, A. , Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science* 7, 457. DOI: <https://doi.org/10.1214/ss/1177011136>.
- Gigliotti, L. C., Curveira-Santos, G., Slotow, R., Sholto-Douglas, C., Swanepoel, L. H. , Jachowski, D. S. (2022). Community-level responses of African carnivores to prescribed burning. *Journal of Applied Ecology* 59, 251. DOI: <https://doi.org/10.1111/1365-2664.14050>.
- Gill, J. L., Williams, J. W., Jackson, S. T., Lininger, K. B. , Robinson, G. S. (2009). Pleistocene Megafaunal Collapse, Novel Plant Communities, and Enhanced Fire Regimes in North America. *Science* 326, 1100. DOI: <https://doi.org/10.1126/science.1179504>.
- Godlee, J. L., Gonçalves, F. M., Tchamba, J. J., Chisingui, A. V., Muledi, J. I., Shutcha, M. N., Ryan, C. M., Brade, T. K. , Dexter, K. G. (2020). Diversity and structure of an arid woodland in Southwest Angola, with comparison to the wider miombo ecoregion. *Diversity* 12, 140. DOI: <https://doi.org/10.3390/d12040140>.
- Gonçalves, F. M. P., Luís, J. C., Tchamba, J. J., Cachissapa, M. J. , Chisingui, A. V. (2019). A rapid assessment of hunting and bushmeat trade along the roadside between five Angolan major towns. *Nature Conservation* 37. DOI: <https://doi.org/10.3897/natureconservation.37.37590>.
- González, C. C., Medellín, D., Urios, V., Zarza, H. , Ceballos, G. (2021). Movement ecology of jaguars and predator-prey interactions. *Authorea Preprints*. DOI: <https://doi.org/10.22541/au.163253797.76061040/v1>.
- Gosling, L. M., Muntifering, J., Kolberg, H., Uiseb, K. , King, S. R. B. (2019). *Equus zebra* (amended version of 2019 assessment).
- Goyder, D. J. , Gonçalves, F. M. P. (2019). The Flora of Angola: Collectors, Richness and Endemism. In *Biodiversity of Angola: Science & Conservation: A Modern Synthesis*: 79-96. Huntley, B. J., Russo, V., Lages, F. , Ferrand, N. (Eds.). Cham: Springer International Publishing.
- Gray, C. L., Hill, S. L. L., Newbold, T., Hudson, L. N., Börger, L., Contu, S., Hoskins, A. J., Ferrier, S., Purvis, A. , Scharlemann, J. P. W. (2016). Local biodiversity is higher inside than outside terrestrial protected areas worldwide. *Nature Communications* 7, 12306. DOI: <https://doi.org/10.1038/ncomms12306>.
- Green, D. S., Roloff, G. J., Heath, B. R. , Holekamp, K. E. (2015). Temporal dynamics of the reponses by African mammals to prescribed fire. *The Journal of Wildlife Management* 79, 235. DOI: <https://doi.org/10.1002/jwmq.827>.
- Gruner, D. S. (2004). Attenuation of top-down and bottom-up forces in a complex terrestrial community. *Ecology* 85, 3010. DOI: <https://doi.org/10.1890/04-0020>.

- Guillera-Aroita, G., Kéry, M., Lahoz-Monfort, J. J. (2019). Inferring species richness using multispecies occupancy modeling: Estimation performance and interpretation. *Ecology and Evolution* 9, 780. DOI: <https://doi.org/10.1002/ece3.4821>.
- Gurera, D., Bhushan, B. (2020). Passive water harvesting by desert plants and animals: lessons from nature. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 378, 20190444. DOI: <https://doi.org/10.1098/rsta.2019.0444>.
- Hairston, N. G., Smith, F. E., Slobodkin, L. B. (1960). Community structure, population control, and competition. *The American Naturalist* 94, 421. DOI: <https://doi.org/10.1086/282146>.
- Hall, B. (1960). The faunistic importance of the scarp of Angola. *The Ibis* 102, 420. DOI: <https://doi.org/10.1111/j.1474-919X.1960.tb08418.x>.
- Hambäck, P. A., Beckerman, A. P. (2003). Herbivory and plant resource competition: a review of two interacting interactions. *Oikos* 101, 26. DOI: <https://doi.org/10.1034/j.1600-0706.2003.12568.x>.
- Hanson, T. (2018). Biodiversity conservation and armed conflict: a warfare ecology perspective. *Annals of the New York Academy of Sciences* 1429, 50. DOI: <https://doi.org/10.1111/nyas.13689>.
- Havemann, C. P., Retief, T. A., Collins, K., Fynn, R. W. S., Tosh, C. A., de Bruyn, P. J. N. (2022). Home range and habitat use of roan antelope *Hippotragus equinus* in Northern Botswana. *Journal of Arid Environments* 196, 104648. DOI: <https://doi.org/10.1016/j.jaridenv.2021.104648>.
- Havmøller, R. W., Jacobsen, N. S., Scharff, N., Rovero, F., Zimmermann, F. (2020). Assessing the activity pattern overlap among leopards (*Panthera pardus*), potential prey and competitors in a complex landscape in Tanzania. *Journal of Zoology* 311, 175. DOI: <https://doi.org/10.1111/jzo.12774>.
- Havmøller, R. W., Tenan, S., Scharff, N., Rovero, F. (2019). Reserve size and anthropogenic disturbance affect the density of an African leopard (*Panthera pardus*) meta-population. *PLOS ONE* 14, e0209541. DOI: <https://doi.org/10.1371/journal.pone.0209541>.
- Hayward, M. W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., Kerley, G. I. H. (2006a). Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* 270, 298. DOI: <https://doi.org/10.1111/j.1469-7998.2006.00139.x>.
- Hayward, M. W., Hofmeyr, M., O'Brien, J., Kerley, G. I. H. (2006b). Prey preferences of the cheetah (*Acinonyx jubatus*) (Felidae: Carnivora): morphological limitations or the need to capture rapidly consumable prey before kleptoparasites arrive? *Journal of Zoology* 270, 615. DOI: <https://doi.org/10.1111/j.1469-7998.2006.00184.x>.

- Hayward, M. W. , Slotow, R. (2009). Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. *South African Journal of Wildlife Research* 39, 109. DOI: <https://doi.org/10.10520/EJC117325>.
- Heithaus, M. R., Wirsing, A. J., Burkholder, D., Thomson, J. , Dill, L. M. (2009). Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *Journal of Animal Ecology* 78, 556. DOI: <https://doi.org/10.1111/j.1365-2656.2008.01512.x>.
- Heller, E. (1918). The Geographical Barriers to the Distribution of Big Game Animals in Africa. *Geographical Review* 6, 297. DOI: <https://doi.org/10.2307/207845>.
- Hema, E. M., Ouattara, V., Parfait, G., Di Vittorio, M., Sirima, D., Dendi, D., Guenda, W., Petrozzi, F. , Luiselli, L. (2019). Bushmeat consumption in the West African Sahel of Burkina Faso, and the decline of some consumed species. *Oryx* 53, 145. DOI: <https://doi.org/10.1017/S0030605316001721>.
- Hempson, G. P., Archibald, S. , Bond, W. J. (2015). A continent-wide assessment of the form and intensity of large mammal herbivory in Africa. *Science* 350, 1056. DOI: <https://doi.org/10.1126/science.aac7978>.
- Hempson, G. P., Archibald, S. , Staver, C. (2019). Fire and Browsers in Savannas. In *Savanna Woody Plants and Large Herbivores*: 439-468).
- Hempson, G. P., Parr, C. L., Archibald, S., Anderson, T. M., Mustaphi, C. J. C., Dobson, A. P., Donaldson, J. E., Morrison, T. A., Probert, J. , Beale, C. M. (2018). Continent-level drivers of African pyrodiversity. *Ecography* 41, 889. DOI: <https://doi.org/10.1111/ecog.03109>.
- Hengl, T., Mendes de Jesus, J., Heuvelink, G. B. M., Ruiperez Gonzalez, M., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M. N., Geng, X., Bauer-Marschallinger, B., Guevara, M. A., Vargas, R., MacMillan, R. A., Batjes, N. H., Leenaars, J. G. B., Ribeiro, E., Wheeler, I., Mantel, S. , Kempen, B. (2017). SoilGrids250m: Global gridded soil information based on machine learning. *PLOS ONE* 12, e0169748. DOI: <https://doi.org/10.1371/journal.pone.0169748>.
- Hetem, R. S., Fuller, A., Maloney, S. K. , Mitchell, D. (2014). Responses of large mammals to climate change. *Temperature* 1, 115. DOI: <https://doi.org/10.4161/temp.29651>.
- Hill, J. E. , Carter, T. D. (1941). *The mammals of Angola, Africa*: American Museum of Natural History.
- Hofmann, R. R., Knight, M. H. , Skinner, J. D. (1995). On structural characteristics and morphophysiological adaptation of the springbok (*Antidorcas marsupialis*) digestive system. *Transactions of the Royal Society of South Africa* 50, 125. DOI: <https://doi.org/10.1080/00359199509520344>.

Hopcraft, J. G. C., Anderson, T. M., Pérez-Vila, S., Mayemba, E. , Olf, H. (2012). Body size and the division of niche space: food and predation differentially shape the distribution of Serengeti grazers. *Journal of Animal Ecology* 81, 201. DOI: <https://doi.org/10.1111/j.1365-2656.2011.01885.x>.

Hopcraft, J. G. C., Morales, J. M., Beyer, H. L., Borner, M., Mwangomo, E., Sinclair, A. R. E., Olf, H. , Haydon, D. T. (2014). Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecological Monographs* 84, 355. DOI: <https://doi.org/10.1890/13-1446.1>.

Hopcraft, J. G. C., Olf, H. , Sinclair, A. R. E. (2010). Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution* 25, 119. DOI: <https://doi.org/10.1016/j.tree.2009.08.001>.

Hunter, L. T. B. , Skinner, J. D. (1998). Vigilance Behaviour in African Ungulates: The Role of Predation Pressure. *Behaviour* 135, 195. DOI: <https://doi.org/10.1163/156853998793066320>.

Huntley, B. J. (1973). Distribuição e Situação da Grande Fauna Selvagem de Angola com referência especial às espécies raras e em perigo de extinção - Primeiro Relatório sobre o estado atual. Direcção Provincial dos Serviços de Veterinária. Luanda, Angola.

Huntley, B. J. (1974). Outlines of wildlife conservation in Angola. *South African Journal of Wildlife Research* 4, 157. DOI: https://hdl.handle.net/10520/AJA03794369_2870.

Huntley, B. J. (2017). *Wildlife at war in Angola: The Rise and Fall of an African Eden*. 1 edn. Pretoria (South Africa): Protea Book House.

Huntley, B. J. (2023). The Angolan Escarpment Zone. In *Ecology of Angola: Terrestrial Biomes and Ecoregions*: 393-404). Cham: Springer International Publishing.

Huntley, B. J., Beja, P., Vaz Pinto, P., Russo, V., Veríssimo, L. , Morais, M. (2019a). Biodiversity Conservation: History, Protected Areas and Hotspots. In *Biodiversity of Angola: Science & Conservation: A Modern Synthesis*: 495-512. Huntley, B. J., Russo, V., Lages, F. , Ferrand, N. (Eds.). Cham: Springer International Publishing.

Huntley, B. J., Russo, V., Lages, F. , Ferrand, N. (2019b). *Biodiversity of Angola*: Springer, Cham.

Hurlbert, S. H., Zedler, J. , Fairbanks, D. (1972). Ecosystem Alteration by Mosquitofish (*Gambusia affinis*) Predation. *Science* 175, 639. DOI: <https://doi.org/10.1126/science.175.4022.639>.

Hutchinson, G. E. (1959). Homage to Santa Rosalia or Why Are There So Many Kinds of Animals? *The American Naturalist* 93, 145. DOI: <https://doi.org/10.1086/282070>.

- IUCN (2021). *IUCN Red List of Threatened Species. Version 2021-3* www.iucnredlist.org.
- IUCN SSC Antelope Specialist Group (2016a). *Antidorcas marsupialis* (errata version published in 2017).
- IUCN SSC Antelope Specialist Group (2016b). *Oryx gazella*.
- IUCN/SSC (2015). Review of the Regional Conservation Strategy for the Cheetah and African Wild Dogs in Southern Africa.): IUCN Species Survival Commission Gland, Switzerland.
- Jackson, T. P., Skinner, J. D. , Richardson, P. R. K. (1993). Some costs of maintaining a perennial territory in the springbok, *Antidorcas marsupialis*. *African Journal of Ecology* 31, 242. DOI: <https://doi.org/10.1111/j.1365-2028.1993.tb00537.x>.
- Jannasch, H. W. , Wirsén, C. O. (1979). Chemosynthetic Primary Production at East Pacific Sea Floor Spreading Centers. *BioScience* 29, 592. DOI: <https://doi.org/10.2307/1307765>.
- Jesus, D. (2021). *Spatial co-occurrence and predation in southern Angolan terrestrial mammals*. University of Porto.
- Johnson, C. N., Prior, L. D., Archibald, S., Poulos, H. M., Barton, A. M., Williamson, G. J. , Bowman, D. M. J. S. (2018). Can trophic rewilding reduce the impact of fire in a more flammable world? *Philosophical Transactions of the Royal Society B: Biological Sciences* 373, 20170443. DOI: <https://doi.org/10.1098/rstb.2017.0443>.
- Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., Safi, K., Sechrest, W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R., Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A., Rist, J., Teacher, A., Bininda-Emonds, O. R. P., Gittleman, J. L., Mace, G. M. , Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90, 2648. DOI: <https://doi.org/10.1890/08-1494.1>.
- Joppa, L. N., Loarie, S. R. , Pimm, S. L. (2008). On the protection of "protected areas". *Proceedings of the National Academy of Sciences* 105, 6673. DOI: <https://doi.org/10.1073/pnas.0802471105>.
- Kamweneshe, B., Beilfesus, R. , Simukonda, C. (2002). Population and distribution of the Kafue lechwe and other large mammals on the Kafue flats, Zambia. *Lusaka: WWF partners for Wetlands* 23. DOI:
- Kar, D. , Spanjers, J. (2017). Transnational crime and the developing world. *Global Financial Integrity*, 53. DOI:

Kaseke, K. F., Tian, C., Wang, L., Seely, M., Vogt, R., Wassenaar, T. , Mushi, R. (2018). Fog Spatial Distributions over the Central Namib Desert - An Isotope Approach. *Aerosol and Air Quality Research* 18, 49. DOI: <https://doi.org/10.4209/aagr.2017.01.0062>.

Keeley, J. E. (2009). Fire intensity, fire severity and burn severity: A brief review and suggested usage. *International Journal of Wildland Fire* 18, 116. DOI: <https://doi.org/10.1071/WF07049>.

Keeping, D. , Pelletier, R. (2014). Animal Density and Track Counts: Understanding the Nature of Observations Based on Animal Movements. *PLOS ONE* 9, e96598. DOI: <https://doi.org/10.1371/journal.pone.0096598>.

Kellner, K. , Meredith, M. (2019). Package 'jagsUI'.

Kéry, M. , Royle, J. A. (Eds.) (2015) *Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1: Prelude and Static Models*, Academic Press.

Kéry, M. , Royle, J. A. (2021). Chapter 4 - Modeling Species Distribution and Range Dynamics, and Population Dynamics Using Dynamic Occupancy Models. In *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS*: 207-297. Kéry, M. , Royle, J. A. (Eds.): Academic Press.

Kihwele, E. S., McHomvu, V., Owen-Smith, N., Hetem, R. S., Hutchinson, M. C., Potter, A. B., Olf, H. , Veldhuis, M. P. (2020). Quantifying water requirements of African ungulates through a combination of functional traits. *Ecological Monographs* 90. DOI: <https://doi.org/10.1002/ecm.1404>.

Kingdon, J. (2015). *The Kingdon field guide to African mammals*. Second Edition edn. London: Bloomsbury Publishing Plc.

Klop, E., van Goethem, J. , de Jongh, H. H. (2007). Resource selection by grazing herbivores on post-fire regrowth in a West African woodland savanna. *Wildlife Research* 34, 77. DOI: <https://doi.org/10.1071/WR06052>.

Knight, M. (2013). Gemsbok (*Oryx gazella*). In *Mammals of Africa : Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids*: 572-576. Kingdon, J. , Hoffmann, M. (Eds.). London: Bloomsbury Publishing.

Koutroulis, A. G. (2019). Dryland changes under different levels of global warming. *Science of The Total Environment* 655, 482. DOI: <https://doi.org/10.1016/j.scitotenv.2018.11.215>.

Kumleben, M. E. (1996). Commission of inquiry into the alleged smuggling of and illegal trade in ivory and rhinoceros horn in South Africa: Report. Pretoria, South Africa.

- Latombe, G., Fortin, D. , Parrott, L. (2014). Spatio-temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. *Journal of Animal Ecology* 83, 185. DOI: <https://doi.org/10.1111/1365-2656.12108>.
- Laundré, J. W., Hernández, L. , Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* 79, 1401. DOI: <https://doi.org/10.1139/z01-094>.
- Laundré, J. W., Hernández, L., Medina, P. L., Campanella, A., López-Portillo, J., González-Romero, A., Grajales-Tam, K. M., Burke, A. M., Gronemeyer, P. , Browning, D. M. (2014). The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology* 95, 1141. DOI: <https://doi.org/10.1890/13-1083.1>.
- le Roux, E., Kerley, G. I. H. , Cromsigt, J. P. G. M. (2018). Megaherbivores Modify Trophic Cascades Triggered by Fear of Predation in an African Savanna Ecosystem. *Current Biology* 28, 2493. DOI: <https://doi.org/10.1016/j.cub.2018.05.088>.
- Lehtonen, J. , Jaatinen, K. (2016). Safety in numbers: the dilution effect and other drivers of group life in the face of danger. *Behavioral Ecology and Sociobiology* 70, 449. DOI: <https://doi.org/10.1007/s00265-016-2075-5>.
- Letnic, M., Feit, A. , Forsyth, D. M. (2018). Strength of a Trophic Cascade Between an Apex Predator, Mammalian Herbivore and Grasses in a Desert Ecosystem Does Not Vary with Temporal Fluctuations in Primary Productivity. *Ecosystems* 21, 153. DOI: <https://doi.org/10.1007/s10021-017-0141-0>.
- Letnic, M. , Ripple, W. J. (2017). Large-scale responses of herbivore prey to canid predators and primary productivity. *Global Ecology and Biogeography* 26, 860. DOI: <https://doi.org/10.1111/geb.12593>.
- Lewis, J. S., LeSueur, L., Oakleaf, J. , Rubin, E. S. (2022). Mixed-severity wildfire shapes habitat use of large herbivores and carnivores. *Forest Ecology and Management* 506, 119933. DOI: <https://doi.org/10.1016/j.foreco.2021.119933>.
- Li, B., Wang, L., Kaseke, K. F., Li, L. , Seely, M. K. (2016). The Impact of Rainfall on Soil Moisture Dynamics in a Foggy Desert. *PLOS ONE* 11, e0164982. DOI: <https://doi.org/10.1371/journal.pone.0164982>.
- Lima, S. L. , Bednekoff, P. A. (1999). Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis. *The American Naturalist* 153, 649. DOI: <https://doi.org/10.1086/303202>.
- Lima, S. L. , Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68, 619. DOI: <https://doi.org/10.1139/z90-092>.

Lindeman, R. L. (1942). The trophic-dynamic aspect of ecology. *Ecology* 23, 399. DOI: <https://doi.org/10.2307/1930126>.

Lindenmayer, D. B., Blanchard, W., MacGregor, C., Barton, P., Banks, Sam C., Crane, M., Michael, D., Okada, S., Berry, L., Florance, D., Gill, M. (2016). Temporal trends in mammal responses to fire reveals the complex effects of fire regime attributes. *Ecological Applications* 26, 557. DOI: <https://doi.org/10.1890/15-0575>.

Lindsell, J. A., Klop, E., Siaka, A. M. (2011). The impact of civil war on forest wildlife in West Africa: mammals in Gola Forest, Sierra Leone. *Oryx* 45, 69. DOI: <https://doi.org/10.1017/S0030605310000347>.

Lindsey, P. A., Balme, G., Becker, M., Begg, C., Bento, C., Bocchino, C., Dickman, A., Diggle, R. W., Eves, H., Henschel, P., Lewis, D., Marnewick, K., Mattheus, J., Weldon McNutt, J., McRobb, R., Midlane, N., Milanzi, J., Morley, R., Murphree, M., Opyene, V., Phadima, J., Purchase, G., Rentsch, D., Roche, C., Shaw, J., Westhuizen, H. v. d., Vliet, N. V., Zisadza-Gandiwa, P. (2013). The bushmeat trade in African savannas: Impacts, drivers, and possible solutions. *Biological Conservation* 160, 80. DOI: <https://doi.org/10.1016/j.biocon.2012.12.020>.

Lindsey, P. A., Petracca, L. S., Funston, P. J., Bauer, H., Dickman, A., Everatt, K., Flyman, M., Henschel, P., Hinks, A. E., Kasiki, S., Loveridge, A., Macdonald, D. W., Mandisodza, R., Mgoola, W., Miller, S. M., Nazerali, S., Siegel, L., Uiseb, K., Hunter, L. T. B. (2017). The performance of African protected areas for lions and their prey. *Biological Conservation* 209, 137. DOI: <https://doi.org/10.1016/j.biocon.2017.01.011>.

Linkie, M., Ridout, M. S. (2011). Assessing tiger–prey interactions in Sumatran rainforests. *Journal of Zoology* 284, 224. DOI: <https://doi.org/10.1111/j.1469-7998.2011.00801.x>.

Lone, K., Loe, L. E., Gobakken, T., Linnell, J. D. C., Odden, J., Remmen, J., Mysterud, A. (2014). Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. *Oikos* 123, 641. DOI: <https://doi.org/10.1111/j.1600-0706.2013.00938.x>.

MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., Franklin, A. B. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84, 2200. DOI: <https://doi.org/10.1890/02-3090>.

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L., Hines, J. E. (2017). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*: Elsevier.

Mahood, A. L., Lindrooth, E. J., Cook, M. C., Balch, J. K. (2022). Country-level fire perimeter datasets (2001–2021). *Scientific Data* 9, 458. DOI: 10.1038/s41597-022-01572-3.

- Makin, D. F., Chamaillé-Jammes, S. , Shrader, A. M. (2017a). Changes in feeding behavior and patch use by herbivores in response to the introduction of a new predator. *Journal of Mammalogy* 99, 341. DOI: <https://doi.org/10.1093/jmammal/gyx177>.
- Makin, D. F., Chamaillé-Jammes, S. , Shrader, A. M. (2017b). Herbivores employ a suite of antipredator behaviours to minimize risk from ambush and cursorial predators. *Animal Behaviour* 127, 225. DOI: <https://doi.org/10.1016/j.anbehav.2017.03.024>.
- Marker, L. L., Fabiano, E. , Nghikembua, M. (2010). A rapid ecological survey in the Iona National Park, Namibe, Angola. Cheetah Conservation Fund. Otjiwarongo, Namibia.
- Martin, R. , Sapsis, D. (1992). Fires as agents of biodiversity: pyrodiversity promotes biodiversity. In *Proceedings: symposium on biodiversity of northwestern California. Center of. Wildland Resources Report*. Kerner, H. (Ed.).
- Massé, F. , Lunstrum, E. (2016). Accumulation by securitization: Commercial poaching, neoliberal conservation, and the creation of new wildlife frontiers. *Geoforum* 69, 227. DOI: <https://doi.org/10.1016/j.geoforum.2015.03.005>.
- McLauchlan, K. K., Higuera, P. E., Miesel, J., Rogers, B. M., Schweitzer, J., Shuman, J. K., Tepley, A. J., Varner, J. M., Veblen, T. T., Adalsteinsson, S. A., Balch, J. K., Baker, P., Batllori, E., Bigio, E., Brando, P., Cattau, M., Chipman, M. L., Coen, J., Crandall, R., Daniels, L., Enright, N., Gross, W. S., Harvey, B. J., Hatten, J. A., Hermann, S., Hewitt, R. E., Kobziar, L. N., Landesmann, J. B., Loranty, M. M., Maezumí, S. Y., Mearns, L., Moritz, M., Myers, J. A., Pausas, J. G., Pellegrini, A. F. A., Platt, W. J., Roozeboom, J., Safford, H., Santos, F., Scheller, R. M., Sherriff, R. L., Smith, K. G., Smith, M. D. , Watts, A. C. (2020). Fire as a fundamental ecological process: Research advances and frontiers. *Journal of Ecology* 108, 2047. DOI: <https://doi.org/10.1111/1365-2745.13403>.
- Meek, P. D., Ballard, G., Claridge, A., Kays, R., Moseby, K., O'Brien, T., O'Connell, A., Sanderson, J., Swann, D. E., Tobler, M. , Townsend, S. (2014). Recommended guiding principles for reporting on camera trapping research. *Biodiversity and Conservation* 23, 2321. DOI: <https://doi.org/10.1007/s10531-014-0712-8>.
- Meise, K., Franks, D. W. , Bro-Jørgensen, J. (2020). Alarm communication networks as a driver of community structure in African savannah herbivores. *Ecology Letters* 23, 293. DOI: <https://doi.org/10.1111/ele.13432>.
- Meller, P., Frazão, R., Lages, F., Jürgens, N. , Finckh, M. (2022). Tipping the scales: how fire controls the balance among functional groups in Angolan grasslands. *African Journal of Range & Forage Science* 39, 56. DOI: <https://doi.org/10.2989/10220119.2021.2012822>.
- Mendelsohn, J. , Mendelsohn, S. (2018). *South West Angola A protrait of land and life*. Porto (Portugal): Arte e Ciência.

- Mendelsohn, J. M. (2019). Landscape Changes in Angola. In *Biodiversity of Angola: Science & Conservation: A Modern Synthesis*: 123-137. Huntley, B. J., Russo, V., Lages, F. , Ferrand, N. (Eds.). Cham: Springer International Publishing.
- Mendoza, M. , Araújo, M. B. (2019). Climate shapes mammal community trophic structures and humans simplify them. *Nature Communications* 10, 5197. DOI: <https://doi.org/10.1038/s41467-019-12995-9>.
- Meserve, P. L., Kelt, D. A., Milstead, W. B. , Gutiérrez, J. R. (2003). Thirteen Years of Shifting Top-Down and Bottom-Up Control. *BioScience* 53, 633. DOI: 10.1641/0006-3568(2003)053[0633:tyosta]2.0.co;2
- Middleton, A. D., Kauffman, M. J., McWhirter, D. E., Jimenez, M. D., Cook, R. C., Cook, J. G., Albeke, S. E., Sawyer, H. , White, P. J. (2013). Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecology Letters* 16, 1023. DOI: <https://doi.org/10.1111/ele.12133>.
- Mills, K. L. , Harris, N. C. (2020). Humans disrupt access to prey for large African carnivores. *eLife* 9, e60690. DOI: <https://doi.org/10.7554/eLife.60690>.
- Mills, M. S. L. (2010). Angola's central scarp forests: patterns of bird diversity and conservation threats. *Biodiversity and Conservation* 19, 1883. DOI: <https://doi.org/10.1007/s10531-010-9810-4>.
- Mittelbach, G. G. , McGill, B. J. (2019). *Community ecology*: Oxford University Press.
- Moleón, M. , Sánchez-Zapata, J. A. (2023). Extending the dynamic landscape of fear in a human-dominated world. *Trends in Ecology & Evolution*. DOI: <https://doi.org/10.1016/j.tree.2022.10.001>.
- Moll, R. J., Killion, A. K., Montgomery, R. A., Tambling, C. J. , Hayward, Matt W. (2016). Spatial patterns of African ungulate aggregation reveal complex but limited risk effects from reintroduced carnivores. *Ecology* 97, 1123. DOI: <https://doi.org/10.1890/15-0707.1>.
- Moll, R. J., Redilla, K. M., Mudumba, T., Muneza, A. B., Gray, S. M., Abade, L., Hayward, M. W., Millspaugh, J. J. , Montgomery, R. A. (2017). The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. *Journal of Animal Ecology* 86, 749. DOI: <https://doi.org/10.1111/1365-2656.12680>.
- Monk, J. D. , Schmitz, O. J. (2022). Landscapes shaped from the top down: predicting cascading predator effects on spatial biogeochemistry. *Oikos* 2022, e08554. DOI: <https://doi.org/10.1111/oik.08554>.
- Monterroso, P., Alves, P. C. , Ferreras, P. (2013). Catch me if you can: diel activity patterns of mammalian prey and predators. *Ethology* 119, 1044. DOI: <https://doi.org/10.1111/eth.12156>.

- Monterroso, P., Díaz-Ruiz, F., Lukacs, P. M., Alves, P. C. , Ferreras, P. (2020a). Ecological traits and the spatial structure of competitive coexistence among carnivores. *Ecology* 101, e03059. DOI: <https://doi.org/10.1002/ecy.3059>.
- Monterroso, P., Rocha, F., van Wyk, S., António, T., Chicomo, M., Kosmas, S., Lages, F., Fabiano, E. , Godinho, R. (2020b). Updated ranges of the Vulnerable cheetah and Endangered African wild dog in Angola. *Oryx*, 1. DOI: <https://doi.org/10.1017/S0030605319000966>.
- Morris, T. , Letnic, M. (2017). Removal of an apex predator initiates a trophic cascade that extends from herbivores to vegetation and the soil nutrient pool. *Proceedings of the Royal Society B: Biological Sciences* 284, 20170111. DOI: <https://doi.org/10.1098/rspb.2017.0111>.
- Muhly, T. B., Semeniuk, C., Massolo, A., Hickman, L. , Musiani, M. (2011). Human Activity Helps Prey Win the Predator-Prey Space Race. *PLOS ONE* 6, e17050. DOI: <https://doi.org/10.1371/journal.pone.0017050>.
- Muntifering, J. R., Ditmer, M. A., Stapleton, S., Naidoo, R. , Harris, T. H. (2019). Hartmann's mountain zebra resource selection and movement behavior within a large unprotected landscape in northwest Namibia. *Endangered Species Research* 38, 159. DOI: <https://doi.org/10.3354/esr00941>.
- Murdoch, W. W. (1966). "Community Structure, Population Control, and Competition"-A Critique. *The American Naturalist* 100, 219. DOI: <https://doi.org/10.1086/282415>.
- Nagy, K. A. , Knight, M. H. (1994). Energy, Water, and Food Use by Springbok Antelope (*Antidorcas marsupialis*) in the Kalahari Desert. *Journal of Mammalogy* 75, 860. DOI: <https://doi.org/10.2307/1382468>.
- Naidoo, R., Kilian, J. W., Du Preez, P., Beytell, P., Aschenborn, O., Taylor, R. D. , Stuart-Hill, G. (2018). Evaluating the effectiveness of local- and regional-scale wildlife corridors using quantitative metrics of functional connectivity. *Biological Conservation* 217, 96. DOI: <https://doi.org/10.1016/j.biocon.2017.10.037>.
- Neutel, A.-M., Heesterbeek, J. A. P. , de Ruiter, P. C. (2002). Stability in Real Food Webs: Weak Links in Long Loops. *Science* 296, 1120. DOI: <https://doi.org/10.1126/science.1068326>.
- Niedballa, J., Sollmann, R., Courtiol, A. , Wilting, A. (2016). camtrapR: an R package for efficient camera trap data management. *Methods in Ecology and Evolution* 7, 1457. DOI: <https://doi.org/10.1111/2041-210x.12600>.
- Nieman, W. A., Leslie, A. J., Wilkinson, A. , Wossler, T. C. (2019). Socioeconomic and biophysical determinants of wire-snare poaching incidence and behaviour in the Boland Region of South Africa. *Journal for Nature Conservation* 52, 125738. DOI: <https://doi.org/10.1016/j.jnc.2019.125738>.

- Nieman, W. A., van Wilgen, B. W., Radloff, F. G. T., Tambling, C. J. , Leslie, A. J. (2022). The effects of fire frequency on vegetation structure and mammal assemblages in a savannah-woodland system. *African Journal of Ecology* 60, 407. DOI: <https://doi.org/10.1111/aje.12971>.
- Nimmo, D. G., Avitabile, S., Banks, S. C., Bliege Bird, R., Callister, K., Clarke, M. F., Dickman, C. R., Doherty, T. S., Driscoll, D. A., Greenville, A. C., Haslem, A., Kelly, L. T., Kenny, S. A., Lahoz-Monfort, J. J., Lee, C., Leonard, S., Moore, H., Newsome, T. M., Parr, C. L., Ritchie, E. G., Schneider, K., Turner, J. M., Watson, S., Westbrooke, M., Wouters, M., White, M. , Bennett, A. F. (2019). Animal movements in fire-prone landscapes. *Biological Reviews* 94, 981. DOI: <https://doi.org/10.1111/brv.12486>.
- Novellie, P., Lindeque, M., Lindeque, P., Lloyd, P. , Koen, J. (2002). Status and action plan for the mountain zebra (*Equus zebra*). *Equids: Zebras, Asses, and Horses: Status, Survey and Conservation Action Plan*, 28. DOI:
- Nunes, S. (2021). *Preliminary assessment on the distribution and density of the carnivores and ungulates of the Iona National Park*. University of Évora (Portugal).
- Ogutu, J. O., Reid, R. S., Piepho, H.-P., Hobbs, N. T., Rainy, M. E., Kruska, R. L., Worden, J. S. , Nyabenge, M. (2014). Large herbivore responses to surface water and land use in an East African savanna: implications for conservation and human-wildlife conflicts. *Biodiversity and Conservation* 23, 573. DOI: <https://doi.org/10.1007/s10531-013-0617-y>.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R., Simpson, G. L., Solymos, P., Stevens, M. H. H. , Wagner, H. (2019). Package 'vegan': Community ecology package. *R package version 2.5-6*, 1. DOI:
- Oksanen, L. (1990). Exploitation Ecosystems in Seasonal Environments. *Oikos* 57, 14. DOI: <https://doi.org/10.2307/3565732>.
- Oksanen, L., Fretwell, S. D., Arruda, J. , Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *The American Naturalist* 118, 240. DOI: <https://doi.org/10.1086/283817>.
- Oksanen, L. , Oksanen, T. (2000). The Logic and Realism of the Hypothesis of Exploitation Ecosystems. *The American Naturalist* 155, 703. DOI: <https://doi.org/10.1086/303354>.
- Oksanen, T., Oksanen, L., Vuorinen, K. E. M., Wolf, C., Mäkynen, A., Olofsson, J., Ripple, W. J., Virtanen, R. , Utsi, T. A. (2020). The impact of thermal seasonality on terrestrial endotherm food web dynamics: a revision of the Exploitation Ecosystem Hypothesis. *Ecography* 43, 1859. DOI: <https://doi.org/10.1111/ecog.05076>.

- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., Kassem, K. R. (2001). Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* 51, 933. DOI: [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:Teotwa\]2.0.Co;2](https://doi.org/10.1641/0006-3568(2001)051[0933:Teotwa]2.0.Co;2).
- Orians, G. H., Pfeiffer, E. W. (1970). Ecological Effects of the War in Vietnam. *Science* 168, 544. DOI: <https://doi.org/10.1126/science.168.3931.544>.
- Overton, J., Fernandes, S., Elizalde, D., Groom, R., Funston, P. (2017). A Large Mammal Survey of Bicular and Mupa National Parks, Angola With Special Emphasis on the Presence and Status of Cheetah and African Wild Dogs. Instituto Nacional da Biodiversidade e Áreas de Conservação.
- Overton, J. M., Elizalde Castells, D., Figueira Fernandes Elizalde, S. R., Valério, H. M., Alexandre Zumbo, M. N., Groom, R. J., Durant, S. M. (2020). Endangered African wild dogs (*Lycaon pictus* Temm.) in Angola: Filling a 50-year gap of knowledge with findings from two National Parks. *African Journal of Ecology* 58, 582. DOI: <https://doi.org/10.1111/aje.12715>.
- Owen-Smith, N. (2015). Mechanisms of coexistence in diverse herbivore–carnivore assemblages: demographic, temporal and spatial heterogeneities affecting prey vulnerability. *Oikos* 124, 1417. DOI: <https://doi.org/10.1111/oik.02218>.
- Owen-Smith, N., Cooper, S., Novellie, P. (1983). Aspects of the feeding ecology of a browsing ruminant: the kudu. *South African Journal of Animal Science* 13, 35. DOI:
- Owen-Smith, N., Mills, M. G. L. (2008). Predator–prey size relationships in an African large-mammal food web. *Journal of Animal Ecology* 77, 173. DOI: <https://doi.org/10.1111/j.1365-2656.2007.01314.x>.
- Owen-Smith, N., Traill, L. W. (2017). Space use patterns of a large mammalian herbivore distinguished by activity state: fear versus food? *Journal of Zoology* 303, 10. DOI: <https://doi.org/10.1111/jzo.12490>.
- Owens, M. J., Owens, D. D. (1978). Feeding ecology and its influence on social organization in Brown hyenas (*Hyaena brunnea*, Thunberg) of the Central Kalahari Desert. *African Journal of Ecology* 16, 113. DOI: <https://doi.org/10.1111/j.1365-2028.1978.tb00433.x>.
- Pacifici, M., Di Marco, M., Watson, J. E. M. (2020). Protected areas are now the last strongholds for many imperiled mammal species. *Conservation Letters* 13, e12748. DOI: <https://doi.org/10.1111/conl.12748>.
- Palmer, M. S., Fieberg, J., Swanson, A., Kosmala, M., Packer, C. (2017). A 'dynamic' landscape of fear: prey responses to spatiotemporal variations in predation risk

across the lunar cycle. *Ecology Letters* 20, 1364. DOI: <https://doi.org/10.1111/ele.12832>.

Palmer, M. S., Gaynor, K. M., Abraham, J. O. , Pringle, R. M. (2023). The role of humans in dynamic landscapes of fear. *Trends in Ecology & Evolution*. DOI: <https://doi.org/10.1016/j.tree.2022.12.007>.

Palmer, M. S., Gaynor, K. M., Becker, J. A., Abraham, J. O., Mumma, M. A. , Pringle, R. M. (2022). Dynamic landscapes of fear: understanding spatiotemporal risk. *Trends in Ecology & Evolution*. DOI: <https://doi.org/10.1016/j.tree.2022.06.007>.

Palmer, M. S. , Packer, C. (2021). Reactive anti-predator behavioral strategy shaped by predator characteristics. *PLOS ONE* 16, e0256147. DOI: <https://doi.org/10.1371/journal.pone.0256147>.

Palmer, M. S., Portales-Reyes, C., Potter, C., Mech, L. D. , Isbell, F. (2021). Behaviorally-mediated trophic cascade attenuated by prey use of risky places at safe times. *Oecologia* 195, 235. DOI: <https://doi.org/10.1007/s00442-020-04816-4>.

Parris, R. , Child, G. (1979). The importance of pans to wildlife in the Kalahari and the effect of human settlement on these areas. *South African Journal of Wildlife Research* 3, 1. DOI: https://hdl.handle.net/10520/AJA03794369_3442.

Pastore, M. , Calcagni, A. (2019). Measuring Distribution Similarities Between Samples: A Distribution-Free Overlapping Index. *Frontiers in Psychology* 10. DOI: <https://doi.org/10.3389/fpsyg.2019.01089>.

Pearson, K. (1900). X. On the criterion that a given system of deviations from the probable in the case of a correlated system of variables is such that it can be reasonably supposed to have arisen from random sampling. *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science* 50, 157. DOI: <https://doi.org/10.1080/14786440009463897>.

Pengelly, I. , Hamer, D. (2006). Grizzly Bear Use of Pink Hedysarum Roots following Shrubland Fire in Banff National Park, Alberta. *Ursus* 17, 124. DOI: [https://doi.org/10.2192/1537-6176\(2006\)17\[124:GBUOPH\]2.0.CO;2](https://doi.org/10.2192/1537-6176(2006)17[124:GBUOPH]2.0.CO;2).

Penzhorn, B. (2013). *Equus zebra* Mountain Zebra. In *Mammals of Africa : Carnivores, Pangolins, Equids and Rhinoceroses*: 438-443. Kingdon, J. , Hoffmann, M. (Eds.). London: Bloomsbury Publishing.

Périquet, S., Todd-Jones, L., Valeix, M., Stapelkamp, B., Elliot, N., Wijers, M., Pays, O., Fortin, D., Madzikanda, H., Fritz, H., Macdonald, D. W. , Loveridge, A. J. (2012). Influence of immediate predation risk by lions on the vigilance of prey of different body size. *Behavioral Ecology* 23, 970. DOI: <https://doi.org/10.1093/beheco/ars060>.

- Périquet, S., Valeix, M., Loveridge, A. J., Madzikanda, H., Macdonald, D. W. , Fritz, H. (2010). Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. *Animal Behaviour* 79, 665. DOI: <https://doi.org/10.1016/j.anbehav.2009.12.016>.
- Petracca, L. S., Funston, P. J., Henschel, P., Cohen, J. B., MacLennan, S. , Frair, J. L. (2019). Modeling community occupancy from line transect data: a case study with large mammals in post-war Angola. *Animal Conservation* n/a. DOI: <https://doi.org/10.1111/acv.12555>.
- Phillips, J. (1931). The Biotic Community. *Journal of Ecology* 19, 1. DOI: <https://doi.org/10.2307/2255934>.
- Plummer, M. (2016). rjags: Bayesian graphical models using MCMC.
- Polis, G. A. (1999). Why Are Parts of the World Green? Multiple Factors Control Productivity and the Distribution of Biomass. *Oikos* 86, 3. DOI: <https://doi.org/10.2307/3546565>.
- Polis, G. A. , Strong, D. R. (1996). Food Web Complexity and Community Dynamics. *The American Naturalist* 147, 813. DOI: <https://doi.org/10.1086/285880>.
- Preisser, E. L., Bolnick, D. I. , Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86, 501. DOI: <https://doi.org/10.1890/04-0719>.
- Preisser, E. L., Orrock, J. L. , Schmitz, O. J. (2007). Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. *Ecology* 88, 2744. DOI: <https://doi.org/10.1890/07-0260.1>.
- Pringle, R. M. (2017). Upgrading protected areas to conserve wild biodiversity. *Nature* 546, 91. DOI: <https://doi.org/10.1038/nature22902>.
- Pringle, R. M. (2018). Ecology: Megaherbivores Homogenize the Landscape of Fear. *Current Biology* 28, R835. DOI: <https://doi.org/10.1016/j.cub.2018.06.050>.
- Prins, H. H. T. (2000). Competition Between Wildlife and Livestock in Africa. In *Wildlife Conservation by Sustainable Use*: 51-80. Prins, H. H. T., Grootenhuys, J. G. , Dolan, T. T. (Eds.). Dordrecht: Springer Netherlands.
- Pudyatmoko, S. (2019). Spatiotemporal inter-predator and predator–prey interactions of mammalian species in a tropical savanna and deciduous forest in Indonesia. *Mammal Research* 64, 191. DOI: <https://doi.org/10.1007/s13364-018-0391-z>.
- Purcell, A. (2018). *Basic Biology: An Introduction*: New Zealand ISBN Agency, National Library of New Zealand.

Purchase, G., Marker, L., Marnewick, K., Klein, R. , Williams, S. (2007). Regional assessment of the status, distribution and conservation needs of cheetahs in southern Africa. *Cat News* 3, 44. DOI:

Pyke, G. H., Pulliam, H. R. , Charnov, E. L. (1977). Optimal Foraging: a selective review of theory and tests. *The Quarterly Review of Biology* 52, 137. DOI: <https://doi.org/10.1086/409852>.

R Core Team (2021). R: A language and environment for statistical computing.

Ramberg, L., Hancock, P., Lindholm, M., Meyer, T., Ringrose, S., Sliva, J., Van As, J. , Vander Post, C. (2006). Species diversity of the Okavango Delta, Botswana. *Aquatic Sciences* 68, 310. DOI: 10.1007/s00027-006-0857-y.

Rao, M., Terborgh, J. , Nuñez, P. (2001). Increased Herbivory in Forest Isolates: Implications for Plant Community Structure and Composition. *Conservation Biology* 15, 624. DOI: <https://doi.org/10.1046/j.1523-1739.2001.015003624.x>.

Redford, K. H. (1992). The Empty Forest. *BioScience* 42, 412. DOI: <https://doi.org/10.2307/1311860>.

Reily, S. J., DeGloria, S. D. , Elliot, R. A. (1999). Terrain Ruggedness Index That Quantifies Topographic Heterogeneity. Intermountain. *Journal of Science* 5, 23. DOI:

Relton, C. E. (2015). *Movement ecology of gemsbok in the central Kalahari in response to vegetation greenness as assessed by satellite imagery*. University of the Witwatersrand.

Revelle, W. (2020). psych: Procedures for Psychological, Psychometric, and Personality Research. R package version 2.0.12. Northwestern University. Evanston, Illinois.

Ribeiro, C. (2021). *Assessing colonization trends of translocated ungulates using camera trapping data*. Universidade do Porto.

Rich, L. N., Davis, C. L., Farris, Z. J., Miller, D. A. W., Tucker, J. M., Hamel, S., Farhadinia, M. S., Steenweg, R., Di Bitetti, M. S., Thapa, K., Kane, M. D., Sunarto, S., Robinson, N. P., Paviolo, A., Cruz, P., Martins, Q., Gholikhani, N., Taktehrani, A., Whittington, J., Widodo, F. A., Yoccoz, N. G., Wulsch, C., Harmsen, B. J. , Kelly, M. J. (2017a). Assessing global patterns in mammalian carnivore occupancy and richness by integrating local camera trap surveys. *Global Ecology and Biogeography* 26, 918. DOI: <https://doi.org/10.1111/geb.12600>.

Rich, L. N., Miller, D. A. W., Robinson, H. S., McNutt, J. W. , Kelly, M. J. (2016). Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. *Journal of Applied Ecology* 53, 1225. DOI: <https://doi.org/10.1111/1365-2664.12650>.

- Rich, L. N., Miller, D. A. W., Robinson, H. S., McNutt, J. W. , Kelly, M. J. (2017b). Carnivore distributions in Botswana are shaped by resource availability and intraguild species. *Journal of Zoology*. DOI: <https://doi.org/10.1111/jzo.12470>.
- Ricklefs, R. E. (2001). *The economy of nature*. fifth edn. New York: W. H. Freeman and Company.
- Ridout, M. S. , Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics* 14, 322. DOI: <https://doi.org/10.1198/jabes.2009.08038>.
- Riggio, J., Jacobson, A. P., Hijmans, R. J. , Caro, T. (2019). How effective are the protected areas of East Africa? *Global Ecology and Conservation* 17, e00573. DOI: <https://doi.org/10.1016/j.gecco.2019.e00573>.
- Riginos, C. (2015). Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology* 84, 124. DOI: <https://doi.org/10.1111/1365-2656.12262>.
- Ripple, W. J., Abernethy, K., Betts, M. G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P. A., Macdonald, D. W., Machovina, B., Newsome, T. M., Peres, C. A., Wallach, A. D., Wolf, C. , Young, H. (2016a). Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science* 3, 160498. DOI: <https://doi.org/10.1098/rsos.160498>.
- Ripple, W. J. , Beschta, R. L. (2004). Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? *BioScience* 54, 755. DOI: [https://doi.org/10.1641/0006-3568\(2004\)054\[0755:wateof\]2.0.co;2](https://doi.org/10.1641/0006-3568(2004)054[0755:wateof]2.0.co;2).
- Ripple, W. J. , Beschta, R. L. (2007a). Hardwood tree decline following large carnivore loss on the Great Plains, USA. *Frontiers in Ecology and the Environment* 5, 241. DOI: [https://doi.org/10.1890/1540-9295\(2007\)5\[241:HTDFLC\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[241:HTDFLC]2.0.CO;2).
- Ripple, W. J. , Beschta, R. L. (2007b). Restoring Yellowstone's aspen with wolves. *Biological Conservation* 138, 514. DOI: <https://doi.org/10.1016/j.biocon.2007.05.006>.
- Ripple, W. J. , Beschta, R. L. (2012). Large predators limit herbivore densities in northern forest ecosystems. *European Journal of Wildlife Research* 58, 733. DOI: <https://doi.org/10.1007/s10344-012-0623-5>.
- Ripple, W. J., Chapron, G., López-Bao, J. V., Durant, S. M., Macdonald, D. W., Lindsey, P. A., Bennett, E. L., Beschta, R. L., Bruskotter, J. T., Campos-Arceiz, A., Corlett, R. T., Darimont, C. T., Dickman, A. J., Dirzo, R., Dublin, H. T., Estes, J. A., Everatt, K. T., Galetti, M., Goswami, V. R., Hayward, M. W., Hedges, S., Hoffmann, M., Hunter, L. T. B., Kerley, G. I. H., Letnic, M., Levi, T., Maisels, F., Morrison, J. C., Nelson, M. P., Newsome, T. M., Painter, L., Pringle, R. M., Sandom, C. J., Terborgh, J., Treves, A., Van Valkenburgh, B., Vucetich, J. A., Wirsing, A. J., Wallach, A. D., Wolf, C., Woodroffe, R., Young, H. , Zhang, L. (2016b). Saving the

World's Terrestrial Megafauna. *BioScience*. DOI: <https://doi.org/10.1093/biosci/biw092>.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., Wirsing, A. J. (2014). Status and Ecological Effects of the World's Largest Carnivores. *Science* 343, 1241484. DOI: <https://doi.org/10.1126/science.1241484>.

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M. W., Kerley, G. I. H., Levi, T., Lindsey, P. A., Macdonald, D. W., Malhi, Y., Painter, L. E., Sandom, C. J., Terborgh, J., Van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Science Advances* 1. DOI: <https://doi.org/10.1126/sciadv.1400103>.

Ripple, W. J., Wolf, C., Newsome, T. M., Betts, M. G., Ceballos, G., Courchamp, F., Hayward, M. W., Van Valkenburgh, B., Wallach, A. D., Worm, B. (2019). Are we eating the world's megafauna to extinction? *Conservation Letters* 12, e12627. DOI: <https://doi.org/10.1111/conl.12627>.

Ritter, R. C., Bednekoff, P. A. (1995). Dry season water, female movements and male territoriality in springbok: preliminary evidence of waterhole-directed sexual selection. *African Journal of Ecology* 33, 395. DOI: <https://doi.org/10.1111/j.1365-2028.1995.tb01048.x>.

Rocha, F., Bennett, B., Monterroso, P. (2022a). Understanding top-down and bottom-up processes in an ungulate community to define conservation priorities in a desert environment. *Biodiversity and Conservation* 31, 2179. DOI: <https://doi.org/10.1007/s10531-022-02438-1>.

Rocha, M., Serronha, A., Rodrigues, M., Alves, P. C., Monterroso, P. (2022b). Comfort over safety: thermoregulation overshadows predation risk effects in the activity of a keystone prey. *Journal of Zoology* n/a, 209. DOI: <https://doi.org/10.1111/jzo.12947>.

Rodrigues, P., Figueira, R., Beja, P. (2018). *Bibliographic records of Angola mammals. Version 2.2* <https://doi.org/10.15468/0v4b7o>.

Rodrigues, P., Figueira, R., Vaz Pinto, P., Araújo, M. B., Beja, P. (2015). A biogeographical regionalization of Angolan mammals. *Mammal Review* 45, 103. DOI: <https://doi.org/10.1111/mam.12036>.

Roerick, T. M., Cain, J. W., Gedir, J. V. (2019). Forest restoration, wildfire, and habitat selection by female mule deer. *Forest Ecology and Management* 447, 169. DOI: <https://doi.org/10.1016/j.foreco.2019.05.067>.

Rosenzweig, M. L. (1973). Exploitation in Three Trophic Levels. *The American Naturalist* 107, 275. DOI: <https://doi.org/10.1086/282830>.

- Ross, J., Hearn, A. J., Johnson, P. J., Macdonald, D. W. (2013). Activity patterns and temporal avoidance by prey in response to Sunda clouded leopard predation risk. *Journal of Zoology* 290, 96. DOI: <https://doi.org/10.1111/jzo.12018>.
- Rouet-Leduc, J., Pe'er, G., Moreira, F., Bonn, A., Helmer, W., Shahsavan Zadeh, S. A. A., Zizka, A., van der Plas, F. (2021). Effects of large herbivores on fire regimes and wildfire mitigation. *Journal of Applied Ecology* 58, 2690. DOI: <https://doi.org/10.1111/1365-2664.13972>.
- Royle, J. A., Dorazio, R. M., Link, W. A. (2007). Analysis of Multinomial Models With Unknown Index Using Data Augmentation. *Journal of Computational and Graphical Statistics* 16, 67. DOI: <https://doi.org/10.1198/106186007X181425>.
- Royle, J. A., Nichols, J. D. (2003). Estimating abundance from repeated presence-absence or point counts. *Ecology* 84, 777. DOI: [https://doi.org/10.1890/0012-9658\(2003\)084\[0777:EAFRPA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0777:EAFRPA]2.0.CO;2).
- Saporiti, N. (2006). Managing national parks: how public-private partnerships can aid conservation. In *Viewpoint: Public Policy for the Private Sector*. Washington, DC: © World Bank.
- Savo, V., Lepofsky, D., Benner, J. P., Kohfeld, K. E., Bailey, J., Lertzman, K. (2016). Observations of climate change among subsistence-oriented communities around the world. *Nature Climate Change* 6, 462. DOI: <https://doi.org/10.1038/nclimate2958>.
- Say-Sallaz, E., Chamaillé-Jammes, S., Fritz, H., Valeix, M. (2019). Non-consumptive effects of predation in large terrestrial mammals: Mapping our knowledge and revealing the tip of the iceberg. *Biological Conservation* 235, 36. DOI: <https://doi.org/10.1016/j.biocon.2019.03.044>.
- Schlossberg, S., Chase, M. J., Griffin, C. R. (2018). Poaching and human encroachment reverse recovery of African savannah elephants in south-east Angola despite 14 years of peace. *PLOS ONE* 13, e0193469. DOI: <https://doi.org/10.1371/journal.pone.0193469>.
- Schmidt, K., Kuijper, D. P. J. (2015). A “death trap” in the landscape of fear. *Mammal Research* 60, 275. DOI: <https://doi.org/10.1007/s13364-015-0229-x>.
- Schmitz, O. J. (2006). Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. *Ecology* 87, 1432. DOI: [https://doi.org/10.1890/0012-9658\(2006\)87\[1432:PHLEOE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1432:PHLEOE]2.0.CO;2).
- Schneibel, A., Stellmes, M., Röder, A., Finckh, M., Revermann, R., Frantz, D., Hill, J. (2016). Evaluating the trade-off between food and timber resulting from the conversion of Miombo forests to agricultural land in Angola using multi-temporal Landsat data. *Science of The Total Environment* 548-549, 390. DOI: <https://doi.org/10.1016/j.scitotenv.2015.12.137>.

- Schoener, T. W. , Spiller, D. A. (1999). Indirect Effects in an Experimentally Staged Invasion by a Major Predator. *The American Naturalist* 153, 347. DOI: <https://doi.org/10.1086/303177>.
- Scholte, P. (2011). Towards Understanding Large Mammal Population Declines in Africa's Protected Areas: A West-Central African Perspective. *Tropical Conservation Science* 4, 1. DOI: <https://doi.org/10.1177/194008291100400102>.
- Schuette, P., Creel, S. , Christianson, D. (2016). Ungulate distributions in a rangeland with competitors, predators and pastoralists. *Journal of Applied Ecology* 53, 1066. DOI: <https://doi.org/10.1111/1365-2664.12610>.
- Shannon, C. E. (1948). A mathematical theory of communication. *The Bell System Technical Journal* 27, 379. DOI: <https://doi.org/10.1002/j.1538-7305.1948.tb01338.x>.
- Sharma, P., Chettri, N. , Wangchuk, K. (2021). Human–wildlife conflict in the roof of the world: Understanding multidimensional perspectives through a systematic review. *Ecology and Evolution* 11, 11569. DOI: <https://doi.org/10.1002/ece3.7980>.
- Shea, K. , Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* 17, 170. DOI: [https://doi.org/10.1016/S0169-5347\(02\)02495-3](https://doi.org/10.1016/S0169-5347(02)02495-3).
- Shelford, V. E. (1931). Some Concepts of Bioecology. *Ecology* 12, 455. DOI: <https://doi.org/10.2307/1928991>.
- Sheriff, M. J., Peacor, S. D., Hawlena, D. , Thaker, M. (2020). Non-consumptive predator effects on prey population size: A dearth of evidence. *Journal of Animal Ecology* 89, 1302. DOI: <https://doi.org/10.1111/1365-2656.13213>.
- Shiffler, R. E. (1988). Maximum Z Scores and Outliers. *The American Statistician* 42, 79. DOI: <https://doi.org/10.1080/00031305.1988.10475530>.
- Silfver, T., Heiskanen, L., Aurela, M., Myller, K., Karhu, K., Meyer, N., Tuovinen, J.-P., Oksanen, E., Rousi, M. , Mikola, J. (2020). Insect herbivory dampens Subarctic birch forest C sink response to warming. *Nature Communications* 11, 2529. DOI: <https://doi.org/10.1038/s41467-020-16404-4>.
- Simões-Paias, A. (1971). Considerações Acerca de Algumas Zonas de Protecção da Fauna, Flora e Solo de Angola. Instituto de Investigação Científica de Angola. Luanda.
- Sinclair, A. R. E. , Arcese, P. (1995). Population Consequences of Predation-Sensitive Foraging: The Serengeti Wildebeest. *Ecology* 76, 882. DOI: <https://doi.org/10.2307/1939353>.

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- Sinclair, A. R. E., Mduma, S., Brashares, J. S. (2003). Patterns of predation in a diverse predator–prey system. *Nature* 425, 288. DOI: <https://doi.org/10.1038/nature01934>.
- Sinervo, B. (1997). Optimal Foraging Theory: constraints and cognitive processes. In *Behavioral Ecology*: 105–130). University of California, Santa Cruz.
- Sirot, E. (2019). Adjustments in compound defensive strategies in response to variation in predation risk. *Animal Behaviour* 147, 53. DOI: <https://doi.org/10.1016/j.anbehav.2018.10.023>.
- Sirot, E., Renaud, P. C., Pays, O. (2016). How competition and predation shape patterns of waterhole use by herbivores in arid ecosystems. *Animal Behaviour* 118, 19. DOI: <https://doi.org/10.1016/j.anbehav.2016.05.021>.
- Smit, I. P. J., Asner, G. P., Govender, N., Vaughn, N. R., van Wilgen, B. W. (2016). An examination of the potential efficacy of high-intensity fires for reversing woody encroachment in savannas. *Journal of Applied Ecology* 53, 1623. DOI: <https://doi.org/10.1111/1365-2664.12738>.
- Smith-Patten, B. D., Bridge, E. S., Crawford, P. H., Hough, D. J., Kelly, J. F., Patten, M. A. (2015). Is extinction forever? *Public Understanding of Science* 24, 481. DOI: <https://doi.org/10.1177/0963662515571489>.
- Smith, J. A., Donadio, E., Pauli, J. N., Sheriff, M. J., Middleton, A. D. (2019). Integrating temporal refugia into landscapes of fear: prey exploit predator downtimes to forage in risky places. *Oecologia* 189, 883. DOI: <https://doi.org/10.1007/s00442-019-04381-5>.
- Smith, J. A., Suraci, J. P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L. Y., Wilmers, C. C. (2017). Fear of the human "super predator" reduces feeding time in large carnivores. *Proceedings of the Royal Society B: Biological Sciences* 284, 20170433. DOI: <https://doi.org/10.1098/rspb.2017.0433>.
- Souza, C. V., Lourenço, Á., Vieira, E. M. (2023). Species-Specific Responses of Medium and Large Mammals to Fire Regime Attributes in a Fire-Prone Neotropical Savanna. *Fire* 6, 110. DOI:
- Stalmans, M. E., Massad, T. J., Peel, M. J. S., Tarnita, C. E., Pringle, R. M. (2019). War-induced collapse and asymmetric recovery of large-mammal populations in Gorongosa National Park, Mozambique. *PLOS ONE* 14, e0212864. DOI: <https://doi.org/10.1371/journal.pone.0212864>.
- Stassen, N. (2010). *William Chapman: Reminiscences Including an Account of the Entry of the Trek Boers Into Angola and of Their Sojourn During the Forty-eight Years They Struggled in that Country Under Portuguese Rule*: Protea Book House.

- Statham, J. C. B. (1924). From Mossamedes to the Victoria Falls. *The Geographical Journal* 63, 1. DOI: <https://doi.org/10.2307/1781781>.
- Stein, A. B., Athreya, V., Gerngross, P., Balme, G., Henschel, P., Karanth, U., Miquelle, D., Rostro-Garcia, S., Kamler, J. F., Laguardia, A., Khorozyan, I., Ghoddousi, A. (2016). *Panthera pardus* (errata version published in 2016). In *The IUCN Red List of Threatened Species 2016*: e.T15954A102421779).
- Stellmes, M., Frantz, D., Finckh, M., Revermann, R. (2013). Fire frequency, fire seasonality and fire intensity within the Okavango region derived from MODIS fire products. *Biodiversity and Ecology* 5, 351. DOI: <https://doi.org/10.7809/b-e.00288>.
- Støen, O.-G., Ordiz, A., Evans, A. L., Laske, T. G., Kindberg, J., Frøbert, O., Swenson, J. E., Arnemo, J. M. (2015). Physiological evidence for a human-induced landscape of fear in brown bears (*Ursus arctos*). *Physiology & Behavior* 152, 244. DOI: <https://doi.org/10.1016/j.physbeh.2015.09.030>.
- Su, Y.-S., Yajima, M. (2015). R2jags: Using R to run 'JAGS'.
- Suraci, J. P., Smith, J. A., Chamaillé-Jammes, S., Gaynor, K. M., Jones, M., Luttbeg, B., Ritchie, E. G., Sheriff, M. J., Sih, A. (2022). Beyond spatial overlap: harnessing new technologies to resolve the complexities of predator–prey interactions. *Oikos* n/a, e09004. DOI: <https://doi.org/10.1111/oik.09004>.
- Tablado, Z., Jenni, L. (2017). Determinants of uncertainty in wildlife responses to human disturbance. *Biological Reviews* 92, 216. DOI: <https://doi.org/10.1111/brv.12224>.
- Tambling, C. J., Druce, D. J., Hayward, M. W., Castley, J. G., Adendorff, J., Kerley, G. I. H. (2012). Spatial and temporal changes in group dynamics and range use enable anti-predator responses in African buffalo. *Ecology* 93, 1297. DOI: <https://doi.org/10.1890/11-1770.1>.
- Tambling, C. J., Minnie, L., Meyer, J., Freeman, E. W., Santymire, R. M., Adendorff, J., Kerley, G. I. H. (2015). Temporal shifts in activity of prey following large predator reintroductions. *Behavioral Ecology and Sociobiology* 69, 1153. DOI: <https://doi.org/10.1007/s00265-015-1929-6>.
- Taylor, P. J., Neef, G., Keith, M., Weier, S., Monadjem, A., Parker, D. M. (2018). Tapping into technology and the biodiversity informatics revolution: updated terrestrial mammal list of Angola, with new records from the Okavango Basin. *ZooKeys* 779. DOI: <https://doi.org/10.3897/zookeys.778.25964>.
- Tenan, S., Brambilla, M., Pedrini, P., Sutherland, C. (2017). Quantifying spatial variation in the size and structure of ecologically stratified communities. *Methods in Ecology and Evolution* 8, 976. DOI: <https://doi.org/10.1111/2041-210X.12719>.

- Tensen, L., Jansen van Vuuren, B., Groom, R., Bertola, L. D., de Iongh, H., Rasmussen, G., Du Plessis, C., Davies-Mostert, H., van der Merwe, D., Fabiano, E., Lages, F., Rocha, F., Monterroso, P., Godinho, R. (2022). Spatial genetic patterns in African wild dogs reveal signs of effective dispersal across southern Africa. *Frontiers in Ecology and Evolution* 10. DOI: <https://doi.org/10.3389/fevo.2022.992389>.
- Terborgh, J., Estes, J. A. (2010). *Trophic cascades: predators, prey, and the changing dynamics of nature*: Island press.
- Teutloff, N., Meller, P., Finckh, M., Cabalo, A. S., Ramiro, G. J., Neinhuis, C., Lautenschläger, T. (2021). Hunting techniques and their harvest as indicators of mammal diversity and threat in Northern Angola. *European Journal of Wildlife Research* 67, 101. DOI: <https://doi.org/10.1007/s10344-021-01541-y>.
- Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., Niemann, S. M., Slotow, R. (2011). Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology* 92, 398. DOI: <https://doi.org/10.1890/10-0126.1>.
- Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., Slotow, R. (2010). Group Dynamics of Zebra and Wildebeest in a Woodland Savanna: Effects of Predation Risk and Habitat Density. *PLOS ONE* 5, e12758. DOI: <https://doi.org/10.1371/journal.pone.0012758>.
- Thapa, A., Pradhan, P. K., Joshi, B. D., Mukherjee, T., Thakur, M., Chandra, K., Sharma, L. K. (2021). Non-protected areas demanding equitable conservation strategies as of protected areas in the Central Himalayan region. *PLOS ONE* 16, e0255082. DOI: <https://doi.org/10.1371/journal.pone.0255082>.
- Thomas, N., Nigam, S. (2018). Twentieth-Century Climate Change over Africa: Seasonal Hydroclimate Trends and Sahara Desert Expansion. *Journal of Climate* 31, 3349. DOI: <https://doi.org/10.1175/jcli-d-17-0187.1>.
- Thornton, P. K., Jones, P. G., Owiyo, T., Kruska, R. L., Herrero, M., Orindi, V., Bhadwal, S., Kristjanson, P., Notenbaert, A., Bekele, N., Omolo, A. (2008). Climate change and poverty in Africa: Mapping hotspots of vulnerability. *African Journal of Agricultural and Resource Economics* 02, 24. DOI: <https://doi.org/10.22004/ag.econ.56966>.
- Tinley, K. L. (1977). *A Framework of the Gorongosa Ecosystem, Mozambique*. University of Pretoria, South Africa.
- Titman, D. (1976). Ecological Competition Between Algae: Experimental Confirmation of Resource-Based Competition Theory. *Science* 192, 463. DOI: <https://doi.org/10.1126/science.192.4238.463>.

- Trites, A. W. , Joy, R. (2005). Dietary Analysis from Fecal Samples: How Many Scats are Enough? *Journal of Mammalogy* 86, 704. DOI: [https://doi.org/10.1644/1545-1542\(2005\)086\[0704:Daffsh\]2.0.Co;2](https://doi.org/10.1644/1545-1542(2005)086[0704:Daffsh]2.0.Co;2).
- Turner, G. F. , Pitcher, T. J. (1986). Attack Abatement: A Model for Group Protection by Combined Avoidance and Dilution. *The American Naturalist* 128, 228. DOI: <https://doi.org/10.1086/284556>.
- U. N. Environment (2019). *Global Environment Outlook – GEO-6: Healthy Planet, Healthy People*. Cambridge: Cambridge University Press.
- Vale, C. G. , Brito, J. C. (2015). Desert-adapted species are vulnerable to climate change: Insights from the warmest region on Earth. *Global Ecology and Conservation* 4, 369. DOI: <https://doi.org/10.1016/j.gecco.2015.07.012>.
- Valeix, M. (2011). Temporal dynamics of dry-season water-hole use by large African herbivores in two years of contrasting rainfall in Hwange National Park, Zimbabwe. *Journal of Tropical Ecology* 27, 163. DOI: <https://doi.org/10.1017/S0266467410000647>.
- Valeix, M., Fritz, H., Matsika, R., Matsvimbo, F. , Madzikanda, H. (2008). The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores. *African Journal of Ecology* 46, 402. DOI: <https://doi.org/10.1111/j.1365-2028.2007.00874.x>.
- Valeix, M., Loveridge, A. J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. , Macdonald, D. W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology* 90, 23. DOI: <https://doi.org/10.1890/08-0606.1>.
- Valério, H., Elizalde, S. , Elizalde, D. (2021). 1st National Meeting on Angolan Large Terrestrial Carnivores, their habitat and prey. INBAC and RWCP. Angola.
- Van Bael, S. A. , Brawn, J. D. (2005). The direct and indirect effects of insectivory by birds in two contrasting Neotropical forests. *Oecologia* 145, 658. DOI: <https://doi.org/10.1007/s00442-005-0134-0>.
- Van de Vijver, C. A. D. M., Poot, P. , Prins, H. H. T. (1999). Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. *Plant and Soil* 214, 173. DOI: <https://doi.org/10.1023/A:1004753406424>.
- van der Meer, E., Moyo, M., Rasmussen, G. S. A. , Fritz, H. (2011). An empirical and experimental test of risk and costs of kleptoparasitism for African wild dogs (*Lycaon pictus*) inside and outside a protected area. *Behavioral Ecology* 22, 985. DOI: <https://doi.org/10.1093/beheco/arr079>.

- van Dyke, F. , Darragh, J. A. (2007). Response of Elk to Changes in Plant Production and Nutrition Following Prescribed Burning. *The Journal of Wildlife Management* 71, 23. DOI: <https://doi.org/10.2193/2005-464>.
- van Wilgen, B. W. (2009). The evolution of fire management practices in savanna protected areas in South Africa. *South African Journal of Science* 105, 343. DOI: <https://hdl.handle.net/10520/EJC96965>.
- Van Scoyoc, A., Smith, J. A., Gaynor, K. M., Barker, K. , Brashares, J. S. (2023). The influence of human activity on predator–prey spatiotemporal overlap. *Journal of Animal Ecology* 92, 1124. DOI: <https://doi.org/10.1111/1365-2656.13892>.
- Vaz Pinto, P. (2019). The Giant Sable Antelope: Angola's National Icon. In *Biodiversity of Angola: Science & Conservation: A Modern Synthesis*: 471-491. Huntley, B. J., Russo, V., Lages, F. , Ferrand, N. (Eds.). Cham: Springer International Publishing.
- Vaz Pinto, P., Beja, P., Ferrand, N. , Godinho, R. (2016). Hybridization following population collapse in a critically endangered antelope. *Scientific Reports* 6, 18788. DOI: <https://doi.org/10.1038/srep18788>.
- Veen, G. F., Blair, J. M., Smith, M. D. , Collins, S. L. (2008). Influence of grazing and fire frequency on small-scale plant community structure and resource variability in native tallgrass prairie. *Oikos* 117, 859. DOI: <https://doi.org/10.1111/j.0030-1299.2008.16515.x>.
- Veldhuis, M. P., Hofmeester, T. R., Balme, G., Druce, D. J., Pitman, R. T. , Cromsigt, J. P. G. M. (2020). Predation risk constrains herbivores' adaptive capacity to warming. *Nature Ecology & Evolution* 4, 1069. DOI: <https://doi.org/10.1038/s41559-020-1218-2>.
- Veldhuis, M. P., Howison, R. A., Fokkema, R. W., Tielens, E. , Olf, H. (2014). A novel mechanism for grazing lawn formation: large herbivore-induced modification of the plant–soil water balance. *Journal of Ecology* 102, 1506. DOI: <https://doi.org/10.1111/1365-2745.12322>.
- Veldhuis, M. P., Kihwele, E. S., Cromsigt, J. P. G. M., Ogutu, J. O., Hopcraft, J. G. C., Owen-Smith, N. , Olf, H. (2019). Large herbivore assemblages in a changing climate: incorporating water dependence and thermoregulation. *Ecology Letters* 22, 1536. DOI: <https://doi.org/10.1111/ele.13350>.
- Veríssimo, L. N. (2008). Mucusso reserve. Larger mammals assessment. Preliminary report. Unpublished report. United States Agency International Development. Washington, DC, USA.
- Verlinden, A. (1997). Human settlements and wildlife distribution in the southern Kalahari of Botswana. *Biological Conservation* 82, 129. DOI: [https://doi.org/10.1016/S0006-3207\(96\)00156-5](https://doi.org/10.1016/S0006-3207(96)00156-5).

Vinks, M. A., Creel, S., Schuette, P., Rosenblatt, E., Matandiko, W., Sanguinetti, C., Banda, K., Goodheart, B., Becker, M., Chifunte, C., Simukonda, C. (2020). Testing the effects of anthropogenic pressures on a diverse African herbivore community. *Ecosphere* 11, e03067. DOI: <https://doi.org/10.1002/ecs2.3067>.

Vissia, S., Wadhwa, R., van Langevelde, F. (2021). Co-occurrence of high densities of brown hyena and spotted hyena in central Tuli, Botswana. *Journal of Zoology* 314, 143. DOI: <https://doi.org/10.1111/jzo.12873>.

von Staden, L., Lötter, M. C., Holness, S., Lombard, A. T. (2022). An evaluation of the effectiveness of Critical Biodiversity Areas, identified through a systematic conservation planning process, to reduce biodiversity loss outside protected areas in South Africa. *Land Use Policy* 115, 106044. DOI: <https://doi.org/10.1016/j.landusepol.2022.106044>.

Wallace, A. R. (1871). *Contributions to the theory of natural selection*: Macmillan and Company.

Wan, H. Y., Rhodes, A. C., St. Clair, S. B. (2014). Fire severity alters plant regeneration patterns and defense against herbivores in mixed aspen forests. *Oikos* 123, 1479. DOI: <https://doi.org/10.1111/oik.01521>.

Wang, L., Kaseke, K. F., Ravi, S., Jiao, W., Mushi, R., Shuuya, T., Maggs-Köling, G. (2019). Convergent vegetation fog and dew water use in the Namib Desert. *Ecohydrology* 12. DOI: <https://doi.org/10.1002/eco.2130>.

Ward, D. (2016). *The Biology of Deserts*. 2 edn. Oxford, United Kingdom: Oxford University Press.

Watson, J. E. M., Dudley, N., Segan, D. B., Hockings, M. (2014). The performance and potential of protected areas. *Nature* 515, 67. DOI: <https://doi.org/10.1038/nature13947>.

Weaver, J. E., Clements, F. E. (1929). *Plant Ecology*. New York: Illus.

Weeber, J., Hempson, G. P., February, E. C. (2020). Large herbivore conservation in a changing world: surface water provision and adaptability allow wildebeest to persist after collapse of long-range movements. *Global Change Biology* 26, 2841. DOI: <https://doi.org/10.1111/gcb.15044>.

Wegmann, M., Santini, L., Leutner, B., Safi, K., Rocchini, D., Bevanda, M., Latifi, H., Dech, S., Rondinini, C. (2014). Role of African protected areas in maintaining connectivity for large mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences* 369, 20130193. DOI: <https://doi.org/10.1098/rstb.2013.0193>.

- Werger, M. J. A. , Coetzee, B. J. (1978). The Sudano-Zambezian Region. In *Biogeography and Ecology of Southern Africa*: 301-462. Werger, M. J. A. (Ed.). Dordrecht: Springer Netherlands.
- Werner, P. A. , Prior, L. D. (2013). Demography and growth of subadult savanna trees: interactions of life history, size, fire season, and grassy understory. *Ecological Monographs* 83, 67. DOI: <https://doi.org/10.1890/12-1153.1>.
- Western, D., Russell, S. , Cuthill, I. (2009). The Status of Wildlife in Protected Areas Compared to Non-Protected Areas of Kenya. *PLOS ONE* 4, e6140. DOI: <https://doi.org/10.1371/journal.pone.0006140>.
- Wiesel, I. (2015). *Parahyaena brunnea*.
- Wilmshurst, J. F., Fryxell, J. M., Farm, B. P., Sinclair, A. R. E. , Henschel, C. P. (1999). Spatial distribution of Serengeti wildebeest in relation to resources. *Canadian Journal of Zoology* 77, 1223. DOI: <https://doi.org/10.1139/z99-088>.
- Wilson, D. E. , Mittermeier, R. A. (2011). *Handbook of the mammals of the world: Volume 2. Hoofed Mammals*. Barcelona: Lynx Ediciones.
- Wilson, J. Z. (2004). Paradoxes and Dilemmas of Institutional Change: Human Rights and Livelihoods in Rural War-Torn Angola. *Journal of Peacebuilding & Development* 2, 37. DOI: <https://doi.org/10.1080/15423166.2004.844905296755>.
- Wilson, M. W., Ridlon, A. D., Gaynor, K. M., Gaines, S. D., Stier, A. C. , Halpern, B. S. (2020). Ecological impacts of human-induced animal behaviour change. *Ecology Letters* 23, 1522. DOI: <https://doi.org/10.1111/ele.13571>.
- Wirsing, A. J., Heithaus, M. R., Brown, J. S., Kotler, B. P. , Schmitz, O. J. (2021). The context dependence of non-consumptive predator effects. *Ecology Letters* 24, 113. DOI: <https://doi.org/10.1111/ele.13614>.
- Wolf, C. , Ripple, W. J. (2016). Prey depletion as a threat to the world's large carnivores. *Royal Society Open Science* 3, 160252. DOI: <https://doi.org/10.1098/rsos.160252>.
- Woodroffe, R. , Sillero-Zubiri, C. (2012). *Lycaon pictus*. In *The IUCN Red List of Threatened Species 2012*: e.T12436A16711116.).
- Wrona, F. J. , Dixon, R. W. J. (1991). Group Size and Predation Risk: A Field Analysis of Encounter and Dilution Effects. *The American Naturalist* 137, 186. DOI: <https://doi.org/10.1086/285153>.
- Yamashita, T., Gaynor, K. M., Kioko, J., Brashares, J. , Kiffner, C. (2018). Antipredator behaviour of African ungulates around human settlements. *African Journal of Ecology* 56, 528. DOI: <https://doi.org/10.1111/aje.12489>.

Yang, H., Xie, B., Zhao, G., Gong, Y., Mou, P., Ge, J. , Feng, L. (2021). Elusive cats in our backyards: persistence of the North Chinese leopard (*Panthera pardus japonensis*) in a human-dominated landscape in central China. *Integrative Zoology* 16, 67. DOI: <https://doi.org/10.1111/1749-4877.12482>.

Zhang, Q., Ding, X. , Xu, K. (2015). Terrain Adaptability Mechanism of Large Ruminants' Feet on the Kinematics View. *Applied Bionics and Biomechanics* 2015, 9. DOI: <https://doi.org/10.1155/2015/151686>.

Zheng, Z., Zeng, Y., Li, S. , Huang, W. (2016). A new burn severity index based on land surface temperature and enhanced vegetation index. *International Journal of Applied Earth Observation and Geoinformation* 45, 84. DOI: <https://doi.org/10.1016/j.jag.2015.11.002>.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. , Smith, G. M. (2009a). *Mixed effects models and extensions in ecology with R*: Springer Science & Business Media.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. , Smith, G. M. (2009b). *Mixed effects models and extensions in ecology with R*: Springer Science & Business Media.

Supplementary Material

Appendix 1 – Paper Proofs

Biodiversity and Conservation
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ORIGINAL PAPER



Understanding top-down and bottom-up processes in an ungulate community to define conservation priorities in a desert environment

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Abstract

Deserts are typically governed by bottom-up forces and are predicted to be further depleted of their resources, exacerbating extinction risk for local wildlife populations. Additionally, human populations living in these ecosystems are predicted to increase, exposing wildlife to additional human-induced top-down constraints and intensifying human-wildlife conflicts. We aim to investigate how surface water availability, forage availability and other landscape factors shape the spatial arrangement of large herbivore populations in a desert region, and to explore wildlife-livestock co-occurrence patterns to inform coexistence strategies that maximize conservation outputs. We fitted Bayesian zero-inflated binomial N-mixture models (Kéry and Royle 2015) to group count data collected over a 4 year period in the northern Namib desert (Iona National Park, Angola), and found that Hartmann's mountain zebra and gemsbok preferentially forage in suboptimal low productivity flat areas, away from human activities. Conversely, springbok preferentially occurred in more productive and relatively rugged terrain. We also found a reliance of Hartmann's mountain zebra on natural water sources ($\beta_{DistWater} = -1.04 \pm 0.26$ and $\beta_{DistWater} = -0.77 \pm 0.20$, for dry and wet seasons, respectively), and a weaker reliance by gemsbok ($\beta_{DistWater} = 0.20 \pm 0.10$ and $\beta_{DistWater} = -0.15 \pm 0.10$, respectively for dry and wet seasons). Conversely, we found springbok to forage further from available water ($\beta_{DistWater} = 0.43 \pm 0.05$ and $\beta_{DistWater} = 0.26 \pm 0.06$, for dry and wet seasons, respectively), suggesting this species may be able to balance hydric requirements from dietary water. Our results support that human activities (inc. livestock herding) induce broad scale top-down regulation in landscape use by our target species, which are then susceptible to resource-driven bottom-up forces at a finer scale. These constraints reflect differences between the realized and expected conservation value of Iona National Park, because human-occupied areas force wildlife to suboptimal habitats. Additionally, we found significant stretches of the landscape to be co-occupied by wildlife and livestock, increasing competition for already limited resources. Our results are useful for informing conservation actions, namely through protected area zonation. Securing exclusive access to key resources by wildlife could be of utmost importance to ensure the long-term survival of these species, and to foster sustained human-wildlife coexistence.

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Updated ranges of the Vulnerable cheetah and Endangered African wild dog in Angola

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Abstract The civil unrest that ravaged Angola for nearly 30 years took a heavy toll on the country's wildlife, and led to a lengthy absence of reliable information for many threatened species, including the cheetah *Acinonyx jubatus* and African wild dog *Lycaon pictus*. Using camera trapping we assessed the status of these two species in two areas of southern Angola, and complemented our findings by reviewing recent survey reports and observations to provide an update on the species' status. We found unequivocal evidence that African wild dogs are resident and reproducing in Bicular National Park, where cheetahs appear to be absent. Conversely, cheetahs may be resident in western Cuando Cubango province, where African wild dogs may only be transient. Based on these and other recent records in Angola, we recommend a revision of these species' distribution ranges and note the need for monitoring of these remnant populations and for appropriate attention to any threats.

Keywords *Acinonyx jubatus*, Angola, cheetah, conservation status, distribution, *Lycaon pictus*, African wild dog, southern Africa

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Despite Angola's high biodiversity, the political unrest during 1975–2002 took a heavy toll on its wildlife, which suffered from widespread poaching and bushmeat hunting (Huntley, 2017). Although little is currently known about the status and trend of most Angolan wildlife populations, iconic and threatened species such as the cheetah *Acinonyx jubatus* and African wild dog *Lycaon pictus* are presumed to have suffered drastic declines and range contractions (Woodroffe & Sillero-Zubiri, 2012; Durant et al., 2015). However, the Angolan government has recently shown signs of political will to improve knowledge of the country's biodiversity, including for the large carnivore species.

Globally, the African wild dog and cheetah are categorized as Endangered and Vulnerable, respectively, on the IUCN Red List because of population declines, range loss and the fragmentation of populations (Woodroffe & Sillero-Zubiri, 2012; Durant et al., 2015). Although historical records indicate that both species formerly occurred widely in Angola (Beja et al., 2019), the majority of the country is currently classified as unknown range for both species (Fig. 1; IUCN/SSC, 2015). Updated knowledge about the distribution, abundance and population dynamics of both species, and any threats, is required for conservation planning.

Under the scope of ongoing institutional research and advanced training programmes, we surveyed c. 360 km² in Bicular National Park, which lies in the transition between the Angolan Miombo Woodlands and Zambebian baikiaea woodlands ecoregions (Olson et al., 2001) in the province of Huila, and c. 300 km² in Cuatir Private Reserve in western Cuando Cubango province, along the Cuatir river, one of the main tributaries of the Cubango (Okavango) river on its Angolan side, also in the Zambebian baikiaea woodlands ecoregion (Olson et al., 2001).

We deployed camera-trapping stations uniformly spaced at c. 2 km in the core of each study area using three camera-trap models: Hyperfire HC600 and HF2X Hyperfire 2 (Reconyx, Holmen, USA), and Cuddeback Model 1231 (Cuddeback, De Pere, USA). Fifty-one camera traps were deployed in Bicular National Park during July 2017–June 2018 (Supplementary Fig. 1), and 43 traps in Cuatir Private Reserve during June–December 2018 (Supplementary Fig. 2). Cameras were inspected every 2 months. Additional records were obtained in Cuatir Private Reserve from unstructured

Appendix 2 - Supporting information for Chapter 2

Table S.2.1 – Guilds defined for each community, ecological traits considered to assign guild membership to each species, species included in each guild and its' respective IUCN conservation status. Number of independent records of each species collected May and November 2019 in BNP and CCA. For each guild, species are presented in taxonomic order and adult body mass (Jones et al., 2009).

Guild	Traits	Species	Common name	IUCN status	Detections in Bicular National Park	Detection in Cuatir Conservation Area
Small-intermediate mammals	Herbivores, omnivores, or insectivores Body mass between 1kg and 10 kg	<i>Lepus saxatilis</i>	Scrub Hare	LC	168	123
		<i>Galago moholi</i>	Southern Galago	LC	1	0
		<i>Chlorocebus cynosuros</i>	Malbrouck Monkey	LC	83	118
		<i>Pedetes capensis</i>	Spring Hare	LC	7	201
		<i>Funisciurus congicus</i>	Congo Rope Squirrel	LC	0	0
Intermediate-large mammals	Herbivores, omnivores, or insectivores Body mass between 10 kg and 100 kg	<i>Madoqua kirkii</i>	Kirk's Dik-dik	LC	0	0
		<i>Raphicerus campestris</i>	Steenbok	LC	4	350
		<i>Oreotragus oreotragus</i>	Klipspringer	LC	0	0
		<i>Sylvicapra grimmia</i>	Common Duiker	LC	2125	2024
		<i>Ourebia ourebi</i>	Oribi	LC	0	0
		<i>Aepyceros melampus petersi</i>	Blacked-Faced Impala	VU	0	0
		<i>Aepyceros melampus melampus</i>	Impala	LC	0	0
		<i>Redunca arundinum</i>	Southern Reedbuck	LC	0	53
		<i>Tragelaphus spekii</i>	Sitatunga	LC	0	1
		<i>Kobus leche</i>	Lechwe	NT	0	0
		<i>Potamochoerus larvatus</i>	Bushpig	LC	123	27
		<i>Phacochoerus africanus</i>	Common Warthog	LC	53	83
		<i>Manis temminckii</i>	Ground Pangolin	VU	2	0
		<i>Hystrix africaeaustralis</i>	Cape porcupine	LC	51	82

Rediscovering Angolan Biodiversity: Patterns and regulation processes underlying large mammal community structure across South Angola

Large ungulates	Herbivores Body mass between 100 kg and 1000 kg	<i>Orycteropus afer</i>	Aardvark	LC	50	25
		<i>Damaliscus lunatus</i>	Common Tsessebe	LC	0	0
		<i>Alcelaphus buselaphus</i>	Hartebeest	LC	0	0
		<i>Connochaetes taurinus</i>	Blue Wildebeest	LC	0	0
		<i>Kobus ellipsiprymnus</i>	Waterbuck	LC	0	0
		<i>Kobus ellipsiprymnus defassa</i>	Defassa Waterbuck	NT	0	0
		<i>Tragelaphus strepsiceros</i>	Greater Kudu	LC	63	18
		<i>Hippotragus equinus</i>	Roan Antelope	LC	255	54
		<i>Equus quagga</i>	Plains Zebra	NT	0	0
		<i>Taurotragus oryx</i>	Common Eland	LC	54	0
Megafauna	Herbivores Body mass > 1000 kg Gregarious species	<i>Giraffa giraffa angolensis</i>	Angolan Giraffe	VU	0	0
		<i>Diceros bicornis</i>	Black Rhinoceros	VU	0	0
		<i>Loxodonta africana</i>	African Savannah Elephant	EN	233	0
Small and Meso-carnivores	Carnivores Body mass < 20 kg	<i>Otocyon megalotis</i>	Bat-Eared Fox	LC	6	35
		<i>Canis mesomelas</i>	Black-Backed Jackal	LC	1	0
		<i>Canis adustus</i>	Side-Striped Jackal	LC	2	148
		<i>Felis silvestris</i>	Wild Cat	LC	25	35
		<i>Caracal caracal</i>	Caracal	LC	68	13
		<i>Leptailurus serval</i>	Serval	LC	12	28
		<i>Helogale parvula</i>	Common Dwarf Mongoose	LC	1	0
		<i>Galerella sanguinea</i>	Slender Mongoose	LC	14	2
		<i>Paracynictis selousi</i>	Selous' Mongoose	LC	6	1
		<i>Atilax paludinosus</i>	Marsh Mongoose	LC	0	6
		<i>Ichneumia albicauda</i>	White-Tailed Mongoose	LC	6	2

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		<i>Proteles cristata</i>	Aardwolf	LC	0	0
		<i>Poecilogale albinucha</i>	African Striped Weasel	LC	0	0
		<i>Ictonyx striatus</i>	Zorilla	LC	9	16
		<i>Genetta genetta</i>	Common Genet	LC	37	9
		<i>Genetta angolensis</i>	Miombo Genet	LC	16	9
		<i>Genetta maculata</i>	Large-Spotted Genet	LC	0	0
		<i>Genetta tigrina</i>	Cape Genet	LC	0	0
		<i>Mellivora capensis</i>	Honey Badger	LC	23	10
Large Carnivores	Carnivores Body mass > 20 kg	<i>Lycaon pictus</i>	African Wild Dog	EN	44	1
		<i>Acinonyx jubatus</i>	Cheetah	VU	0	12
		<i>Panthera pardus</i>	Leopard	VU	93	17
		<i>Panthera leo</i>	African Lion	VU	0	0
		<i>Crocuta crocuta</i>	Spotted Hyaena	LC	229	0

References: Jones *et al.* (2009); Estes (2012); Kingdon (2015); Hempson *et al.* (2015); IUCN (2021)

Table S.2.2 – Mean proportion of grassland, shrubland and tree cover in the surveyed areas of BNP and CCA.

Proportion of	Bicuar National Park	Cuatir Conservation Area
Grassland cover	45.40 ± 11.08	18.58 ± 7.95
Shrubland cover	30.02 ± 5.14	33.46 ± 11.35
Tree cover	23.87 ± 8.68	42.46 ± 17.66

Table S.2.3 – Shannon's diversity index calculated considering the proportions of estimated area occupied by each species. Diversity index was calculated for the entire community and for each guild independently, for the BNP's and CCA's mammal community. One-way ANOVA was used to confirm if the estimated Shannon's diversity indices estimated from BNP and CCA were statistically different.

Guild	Bicuar National Park	Cuatir Conservation Area	Overlap Index
Entire community	3.55 [3.45; 3.64]	3.58 [3.48; 3.67]	0.86
Small-intermediate mammals	1.24 [1.01; 1.40]	1.45 [1.22; 1.59]	0.26
Intermediate-large mammals	2.12 [1.93; 2.28]	2.21 [2.04; 2.35]	0.63
Large ungulates	1.94 [1.71; 2.11]	1.89 [1.63; 2.09]	0.85
Small and meso-carnivores	2.56 [2.33; 2.75]	2.59 [2.42; 2.73]	0.80
Large carnivores	1.46 [1.24; 1.59]	1.30 [0.97; 1.52]	0.53

Table S.2.4 - Hyper parameter for the occupancy probability of detected species by guild and study areas. The results are presented as mean [95% posterior credible intervals]

Guild	Bicuar National Park	Cuatir Conservation Area
Small-intermediate Mammals	-2.34 [-4.90; -0.60]	-0.39 [-1.20; 0.27]
Intermediate-large Mammals	-1.34 [-4.41; 2.71]	-0.68 [-4.33; 3.02]
Large ungulates	-1.07 [-1.82; -0.25]	-1.19 [-2.18; -0.32]
Megafauna	0.32 [-0.12; 0.75]	NA
Small and Meso-carnivores	-2.66 [-4.70; -0.94]	-2.20 [-4.44; 0.20]
Large carnivores	-0.82 [-1.64; -0.14]	-2.44 [-4.84; -1.05]

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Table S.2. 5 – Occupancy probability of detected species in both study areas. The results are presented as mean [95% posterior credible intervals]

Guild	Common Name	Scientific Name	Bicuar National Park	Cuatir Conservation Area
Small-intermediate Mammals	Scrub Hare	<i>Lepus saxatilis</i>	0.29 [0.20; 0.40]	0.44 [0.32; 0.56]
	Malbrouck Monkey	<i>Chlorocebus cynosuros</i>	0.23 [0.15; 0.32]	0.46 [0.34; 0.59]
	Southern Galago	<i>Galago moholi</i>	0.02 [0.00; 0.06]	Not detected
	Spring Hare	<i>Pedetes capensis</i>	0.04 [0.01; 0.09]	0.32 [0.21; 0.44]
Intermediate-large Mammals	Steenbok	<i>Raphicerus campestris</i>	0.03 [0.01; 0.07]	0.77 [0.67; 0.86]
	Common Duiker	<i>Sylvicapra grimmia</i>	0.91 [0.85; 0.96]	0.93 [0.85; 0.98]
	Southern Reedbuck	<i>Redunca arundinum</i>	Not detected	0.21 [0.12; 0.32]
	Sitatunga	<i>Tragelaphus spekii</i>	Not detected	0.03 [0.00; 0.08]
	Bushpig	<i>Potamochoerus larvatus</i>	0.43 [0.33; 0.53]	0.22 [0.13; 0.33]
	Common Warthog	<i>Phacochoerus africanus</i>	0.18 [0.11; 0.27]	0.39 [0.27; 0.51]
	Ground Pangolin	<i>Manis temminckii</i>	0.03 [0.01; 0.07]	Not detected
	Cape Porcupine	<i>Hystrix africaeaustralis</i>	0.21 [0.13; 0.30]	0.26 [0.16; 0.37]
	Aardvark	<i>Orycteropus afer</i>	0.20 [0.12; 0.28]	0.21 [0.12; 0.31]
Large Mammals	Greater Kudu	<i>Tragelaphus strepsiceros</i>	0.20 [0.13; 0.29]	0.17 [0.09; 0.27]
	Roan Antelope	<i>Hippotragus equinus</i>	0.36 [0.27; 0.46]	0.31 [0.21; 0.44]
	Common Eland	<i>Taurotragus oryx</i>	0.23 [0.15; 0.32]	Not detected
Megafauna	African Savannah Elephant	<i>Loxodonta africana</i>	0.58 [0.48; 0.67]	Not detected
Small and meso-carnivores	Bat-Eared Fox	<i>Otocyon megalotis</i>	0.05 [0.02; 0.11]	0.28 [0.18; 0.40]
	Black-Backed Jackal	<i>Canis mesomelas</i>	0.02 [0.00; 0.06]	Not detected
	Side-Striped Jackal	<i>Canis adustus</i>	0.03 [0.01; 0.08]	0.52 [0.40; 0.64]
	Wild Cat	<i>Felis silvestris</i>	0.15 [0.09; 0.23]	0.24 [0.15; 0.35]
	Caracal	<i>Caracal caracal</i>	0.26 [0.17; 0.35]	0.15 [0.08; 0.24]
	Serval	<i>Leptailurus serval</i>	0.08 [0.03; 0.14]	0.13 [0.06; 0.22]
	Common Dwarf Mongoose	<i>Helogale parvula</i>	0.02 [0.00; 0.06]	Not detected
	Slender Mongoose	<i>Galerella sanguinea</i>	0.08 [0.03; 0.13]	0.04 [0.01; 0.10]
	Selous' Mongoose	<i>Paracynictis selousi</i>	0.04 [0.01; 0.08]	0.03 [0.00; 0.08]
	Marsh Mongoose	<i>Atilax paludinosus</i>	Not detected	0.07 [0.03; 0.14]
	White-Tailed Mongoose	<i>Ichneumia albicauda</i>	0.05 [0.01; 0.09]	0.03 [0.01; 0.08]
	Zorilla	<i>Ictonyx striatus</i>	0.08 [0.04; 0.15]	0.11 [0.05; 0.20]
	Honey Badger	<i>Mellivora capensis</i>	0.15 [0.09; 0.23]	0.12 [0.06; 0.21]
	Common Genet	<i>Genetta genetta</i>	0.20 [0.13; 0.29]	0.10 [0.04; 0.18]
	Miombo Genet	<i>Genetta angolensis</i>	0.07 [0.03; 0.13]	0.05 [0.01; 0.11]
Large carnivores	African Wild Dog	<i>Lycaon pictus</i>	0.22 [0.14; 0.31]	0.03 [0.01; 0.08]
	Cheetah	<i>Acinonyx jubatus</i>	Not detected	0.12 [0.05; 0.20]
	Leopard	<i>Panthera pardus</i>	0.33 [0.23; 0.43]	0.19 [0.10; 0.29]
	Spotted Hyaena	<i>Crocuta crocuta</i>	0.39 [0.28; 0.49]	Not detected

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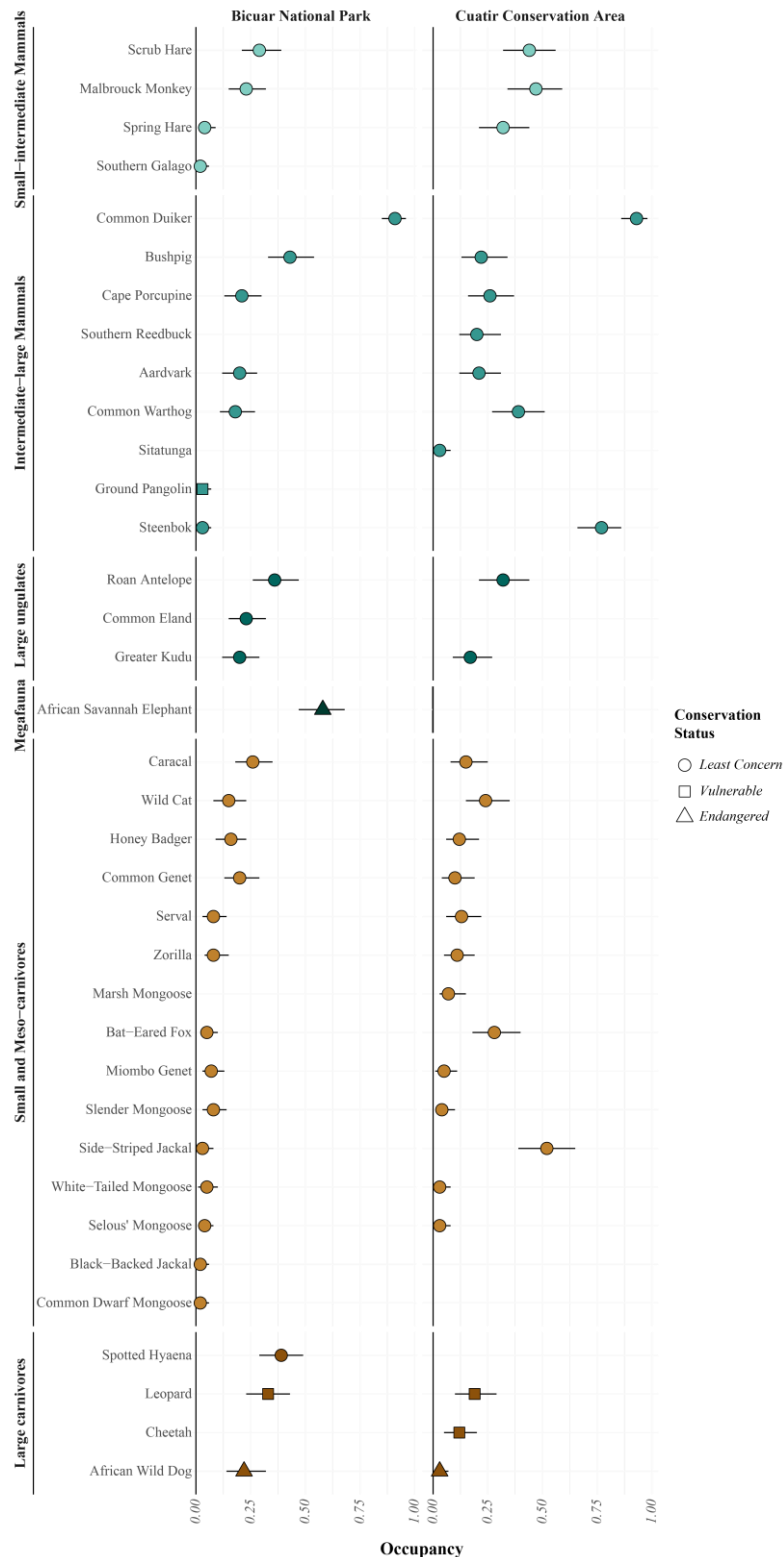


Figure S.2. 1 - Species' median occupancy probability and respective 95% Posterior Credible Intervals in BNP and CCA. Species are distributed by guild: (1) small mammal, non-carnivore mammals with <10 kg body mass; (2) intermediate mammals, solitary or small-group living non-carnivore mammals with >10 and <100 kg body mass; (3) large mammals, gregarious herbivores with >100 and <1000 kg body mass; (4) Megafauna, herbivores with >1000 kg body mass; (5) small carnivores, mammals from the order carnivora with <20 kg body mass; and (6) large carnivores, mammals from the order carnivora with >20 kg body mass; and by the conservation status from IUCN (IUCN, 2021)

Appendix 3 - Supporting information for Chapter 3

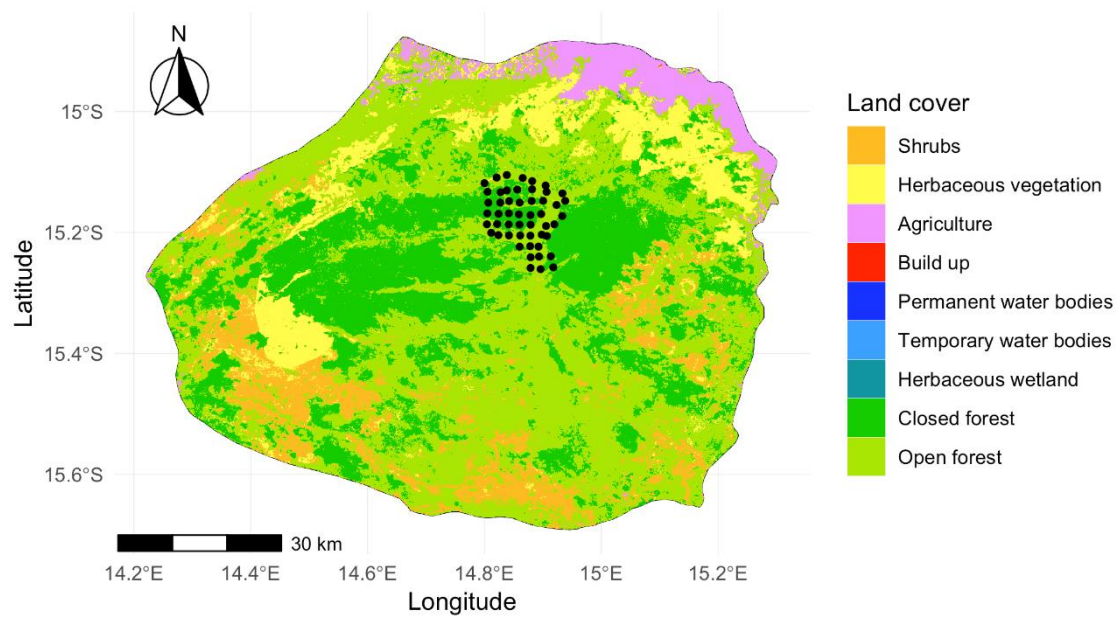


Figure S.3.1 - Locations of camera traps (black dots) at Bicular National Park (BNP), Angola, with respective 2015 land cover at 100m resolution (Copernicus Global Land Services, <http://land.copernicus.eu/global/products/lc>)

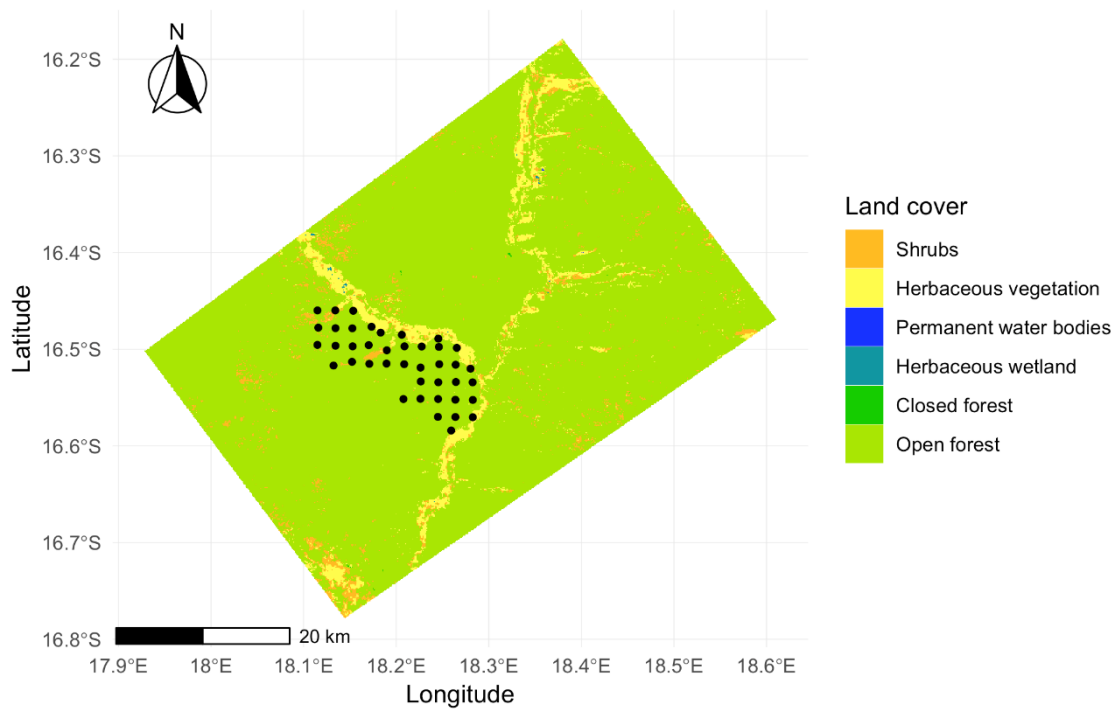


Figure S.3.2 - Locations of camera traps (black dots) at Cuatir Conservation Area (CPR), Angola, with respective 2015 land cover at 100m resolution (Copernicus Global Land Services, <http://land.copernicus.eu/global/products/lc>)

Appendix 4 - Supporting information for Chapter 4

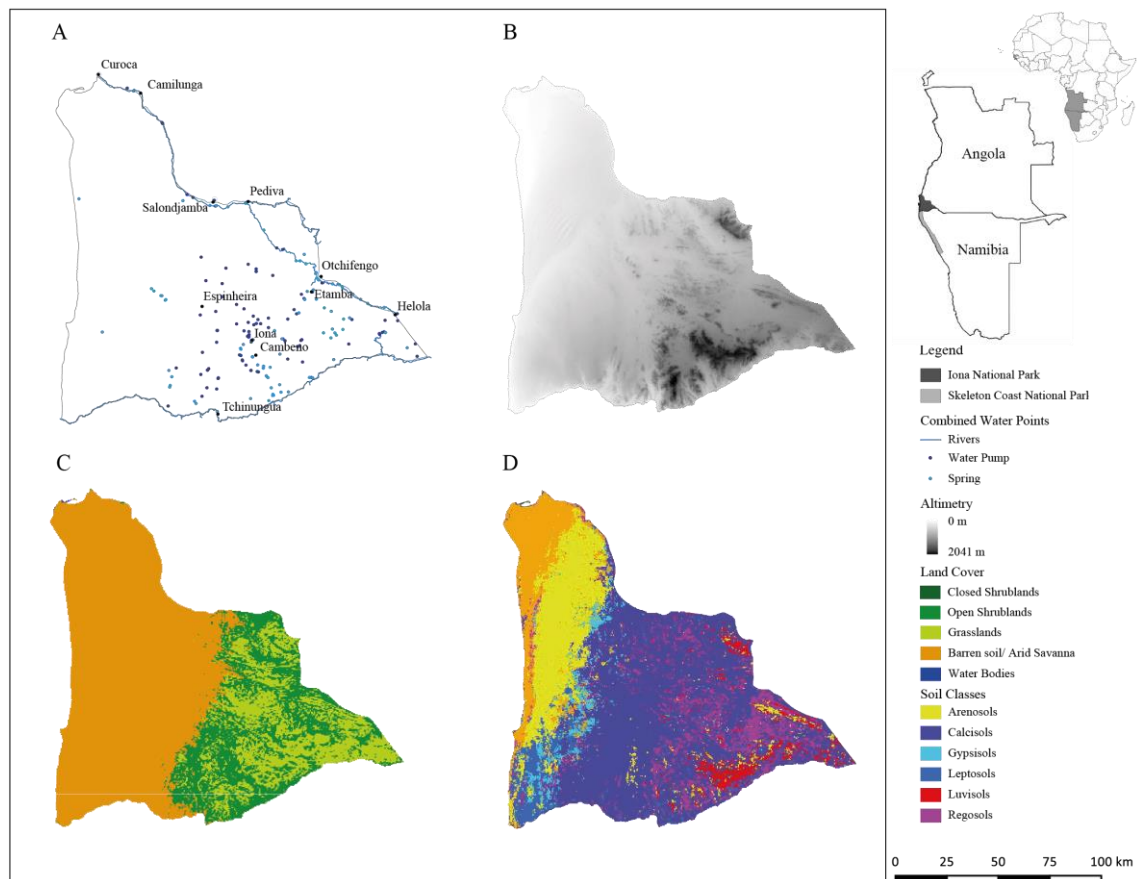


Figure S.4.1– Geographic location of the Iona National Park (Angola), within the Iona-Skeleton Coast Transfrontier Conservation area: A – Human settlements and water sources; B – Altimetry, according to Shuttle Radar Topography Mission Grid version 2 (SRTM) ; C – Land cover according to the Collection 6 MODIS Land Cover (MCD12Q1) class 1; D – Soil classes according to SoilGrids classifications updated in June 2016.

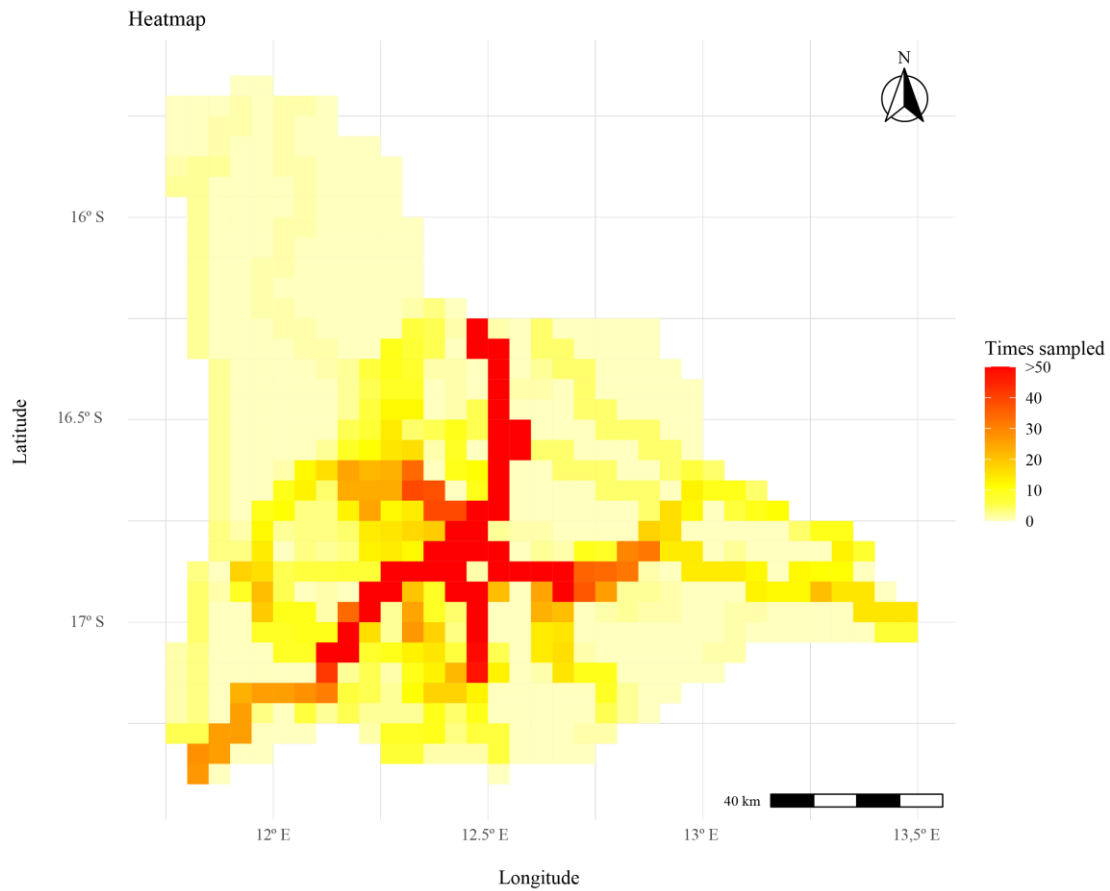


Figure S.4.2 – Heatmap with the intensity of the sampling at each cell, over the study period.

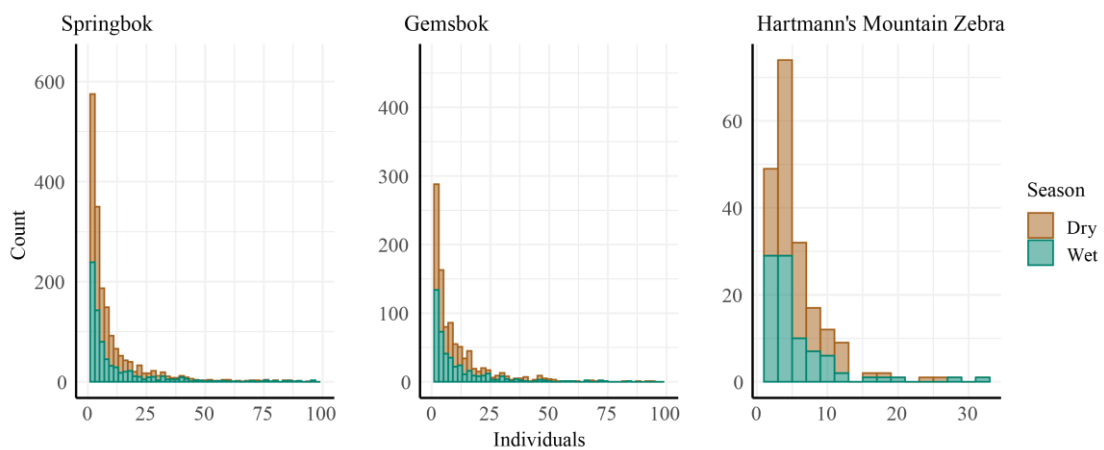


Figure S.4.3 – Histogram with the distribution of observed group size of each target wild species in INP, during dry and wet season.

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Table S.4.1 – Priors used for each parameter in the modelling. The priors were selected considering previous knowledge summarised in the Table 4.1.

Parameter	Prior
EVI	$\text{dnorm}(0, 0.001)T(-7, 0)$
EVI^2	$\text{dnorm}(0, 0.001)T(-10, 10)$
Distance to water	$\text{dnorm}(0, 0.001)T(-3, 1)$
TRI	$\text{dnorm}(0, 0.001)T(-10, 0)$
Proportion of sand	$\text{dnorm}(0, 0.001)T(-5, 1)$
α_0	$\text{dnorm}(0, 0.001)T(-10, 10)$
β_{0_k}	$\text{dnorm}(0, 0.001)T(-10, 10)$

Appendix 4.1 – General results and multicollinearity analysis

The exploratory analysis showed that some of the suggested covariates are collinear, especially among DEM covariates, TRI is strongly correlated with slope (0.99) and altitude (0.70); while the latter 2 covariates also have a big correlation factor (0.69). We decided to include the TRI in the models because it is a composite measure that gathers the information of the other two DEM covariates, moreover it has better relationship with the response variable than the altitude and slope. We selected the EVI over the proportion of grassland cover (correlation factor: 0.64), because EVI data changes periodically and allow to better inform the models about the differences in primary productivity between dry and wet seasons; moreover, the correlation coefficient between EVI and TRI is smaller (0.51), than proportion grassland cover (0.68). We also decided to discard the distance to human settlements because it has a strong negative correlation with the EVI (-0.60), and probably does not inform for the real human perturbation since Ovahimba people are semi-nomads. Distance to natural water sources and proportion of sand are not correlated to any of the considered covariates (Table S.4.2).

Table S.4.2 - Correlation matrix between the covariates in test. In red we show the correlation coefficient of correlated covariates (i.e. ≥ 0.5). TRI - topographic ruggedness index, DNW – distance to natural water sources, DW – distance to all water sources (natural and artificial); DH – distance to human settlements.

	Altitude	Slope	TRI	DNW	DW	DH	Sand	Grass	EVI
Altitude	1	0.69	0.70	-0.39	-0.69	-0.54	-0.23	0.81	0.75
Slope	0.69	1	0.99	-0.47	-0.47	-0.41	-0.17	0.66	0.49
TRI	0.70	0.99	1	-0.46	-0.50	-0.44	-0.17	0.68	0.51
DNW	-0.39	-0.47	-0.46	1	0.38	0.49	0.17	-0.44	-0.42
DW	-0.69	-0.47	-0.05	0.38	1	0.77	0.39	-0.7	-0.59
DH	-0.54	-0.41	-0.44	0.49	0.77	1	0.32	-0.64	-0.60
Sand	-0.23	-0.17	-0.17	0.17	0.39	0.32	1	-0.41	-0.05
Grass	0.81	0.66	0.68	-0.44	-0.70	-0.64	-0.41	1	0.68
EVI	0.75	0.49	0.51	-0.42	-0.59	-0.60	-0.05	0.68	1

Table S.4.3 – Summary table of the data collected between October 2013 and October 2017, divided into dry and wet season.

Order	Family	Species	Scientific Name	Dry Season		Wet Season	
				Number of Groups	Number of Animals	Number of Groups	Number of Animals
Artiodactyla	Bovidae	Cattle	<i>Bos taurus</i>	650	14837	354	8251
		Sheep and Goats	-	351	31014	184	15149
		Springbok	<i>Antidorcas marsupialis</i>	1498	25862	1009	16210
		Gemsbok	<i>Oryx gazella</i>	733	7692	714	4874
		Steenbok	<i>Raphicerus campestris</i>	56	66	34	40
		Greater Kudu	<i>Tragelaphus strepsiceros</i>	8	18	3	10
		Kirk's Dik-dik	<i>Madoqua kirkii</i>	38	67	15	28
		Impala	<i>Aepyceros melampus</i>	3	28	1	1
Carnivora	Canidae	Klipspringer	<i>Oreotragus oreotragus</i>	1	3	0	0
		Bat-Eared-Fox	<i>Otocyon megalotis</i>	13	25	7	17
		Black-Backed Jackal	<i>Canis mesomelas</i>	41	53	26	40
	Felidae	Cape Fox	<i>Vulpes chama</i>	3	3	2	4
		Cheetah	<i>Acinonyx jubatus</i>	6	17	2	2
		Leopard	<i>Panthera pardus</i>	4	4	0	0
	Herpestidae	Meerkat	<i>Suricata suricatta</i>	5	34	2	10
		Mongoose	-	1	1	1	1
	Hyaenidae	Brown Hyena	<i>Hyaena brunnea</i>	5	7	7	7
		Aardwolf	<i>Proteles cristata</i>	1	2	1	1
	Mustelidae	Honey Badger	<i>Mellivora capensis</i>	2	3	1	1
Crocodylia	Crocodylidae	Nile Crocodile	<i>Crocodylus niloticus</i>	1	1	0	0
Hyracoidea	Procaviidae	Rock Hyrax	<i>Procavia capensis</i>	9	44	3	44
Perissodactyla	Equidae	Donkey	<i>Equus asinus</i>	175	564	185	835
		Hartmann's Mountain Zebra	<i>Equus zebra hartmannae</i>	114	800	88	494
Primates	Cercopithecidae	Malbrouck Monkey	<i>Chlorocebus cynosuros</i>	2	27	1	4
		Chacma Baboon	<i>Papio ursinus</i>	9	87	6	86
Struthioniformes	Struthionidae	Ostrich	<i>Struthio camelus</i>	77	379	72	263

Table S.4.4 – Parameter estimates (β), with respective posterior standard deviation (PSD) and 95% credible intervals (IC95) describing the effect of all considered covariates on our target species and livestock abundance during dry (grey) and wet (black) seasons, with the respective Goodness-of-fit statistics: Bayesian p-value (BPV) and overdispersion parameter (c-hat).

Group	Species	Covariate	Dry season		Wet season	
			$\hat{\beta} \pm PSD$	IC ₉₅	$\hat{\beta} \pm PSD$	IC ₉₅
Wild	Springbok	β_0^{2014}	2.58 ± 0.12	[2.29 - 2.71]	2.65 ± 0.12	[2.47 - 2.72]
		β_0^{2015}	2.99 ± 0.34	[2.37 - 3.7]	3.38 ± 0.34	[2.61 - 4.23]
		β_0^{2016}	3.87 ± 0.48	[3.00 - 4.88]	3.84 ± 0.48	[2.97 - 4.84]
		β_0^{2017}	3.89 ± 0.46	[3.06 - 4.84]	3.60 ± 0.46	[2.82 - 4.52]
		EVI	-0.02 ± 0.02	[-0.07 - 0.00]	-0.07 ± 0.05	[-0.2 - 0.00]
		EVI ²	-0.01 ± 0.14	[-0.28 - 0.27]	-0.75 ± 0.12	[-0.99 - -0.53]
		Distance to Water	0.43 ± 0.05	[0.32 - 0.53]	0.26 ± 0.06	[0.15 - 0.37]
		TRI	-0.56 ± 0.12	[-0.80 - -0.31]	-0.24 ± 0.12	[-0.49 - -0.03]
		BPV	0.19		0.06	
		C-hat	1.02		1.03	
	Gemsbok	β_0^{2014}	0.66 ± 0.25	[0.3 - 1.26]	1.72 ± 0.25	[0.83 - 2.62]
		β_0^{2015}	0.42 ± 0.16	[0.19 - 0.8]	1.26 ± 0.16	[0.67 - 2]
		β_0^{2016}	0.89 ± 0.33	[0.41 - 1.69]	1.6 ± 0.33	[0.85 - 2.55]
		β_0^{2017}	0.48 ± 0.18	[0.22 - 0.93]	1.37 ± 0.18	[0.73 - 2.19]
		EVI	-1.00 ± 0.22	[-1.45 - -0.57]	-0.75 ± 0.19	[-1.15 - -0.38]
		EVI ²	-1.83 ± 0.36	[-2.56 - -1.15]	-1.06 ± 0.22	[-1.50 - -0.66]
		Distance to Water	0.20 ± 0.10	[-0.01 - 0.40]	-0.15 ± 0.10	[-0.35 - 0.04]
		TRI	-4.22 ± 0.44	[-5.12 - -3.38]	-2.59 ± 0.35	[-3.31 - -1.94]
		BPV	0.24		0.18	
		C-hat	1.02		1.02	
	Zebra	β_0^{2014}	0.45 ± 0.54	[0.02 - 2.03]	0.49 ± 0.54	[0.06 - 1.86]
		β_0^{2015}	0.21 ± 0.26	[0.01 - 0.98]	0.29 ± 0.26	[0.04 - 1.04]
		β_0^{2016}	0.27 ± 0.37	[0.01 - 1.36]	0.33 ± 0.37	[0.04 - 1.18]
		β_0^{2017}	0.18 ± 0.21	[0.01 - 0.83]	0.26 ± 0.21	[0.03 - 0.92]
		EVI	-6.00 ± 0.58	[-6.95 - -5.05]	-3.54 ± 0.99	[-5.54 - -1.69]
		EVI ²	-3.50 ± 0.29	[-3.97 - -3.03]	-2.17 ± 0.73	[-3.56 - -0.77]
		Distance to Water	-1.04 ± 0.26	[-1.56 - -0.55]	-0.77 ± 0.20	[-1.17 - -0.39]
		TRI	-3.93 ± 1.01	[-5.91 - -2.04]	-4.60 ± 1.09	[-7.37 - -2.79]
		Proportion of Sand	-0.68 ± 0.40	[-1.55 - 0.03]	0.12 ± 0.20	[-0.28 - 0.50]
		BPV	0.41		0.37	
		C-hat	1.02		1.03	
Domestic	Sheep & Goats	β_0^{2014}	0.26 ± 0.13	[0.08 - 0.58]	0.51 ± 0.13	[0.14 - 1.25]
		β_0^{2015}	0.39 ± 0.16	[0.16 - 0.78]	1.37 ± 0.16	[0.59 - 2.92]
		β_0^{2016}	0.37 ± 0.17	[0.14 - 0.78]	1.03 ± 0.17	[0.35 - 2.43]
		β_0^{2017}	0.53 ± 0.24	[0.21 - 1.11]	2.05 ± 0.24	[0.89 - 4.36]
		EVI	-0.04 ± 0.04	[-0.16 - 0.00]	-0.03 ± 0.03	[-0.10 - 0.00]

	EVI ²	0.51 ± 0.17	[0.18 - 0.83]	0.15 ± 0.04	[0.07 - 0.23]
	Distance to Water	-2.06 ± 0.33	[-2.72 - -1.44]	-1.07 ± 0.22	[-1.53 - -0.67]
	TRI	-0.03 ± 0.03	[-0.09 - 0.00]	-0.10 ± 0.09	[-0.33 - 0.00]
	BPV	0.38		0.41	
	C-hat	1.01		1.01	
<i>Donkey</i>	β_0^{2014}	0.17 ± 0.11	[0.05 - 0.47]	0.19 ± 0.11	[0.08 - 0.39]
	β_0^{2015}	0.28 ± 0.16	[0.10 - 0.69]	0.21 ± 0.16	[0.11 - 0.41]
	β_0^{2016}	0.18 ± 0.10	[0.06 - 0.44]	0.34 ± 0.10	[0.17 - 0.65]
	β_0^{2017}	0.26 ± 0.14	[0.10 - 0.63]	0.24 ± 0.14	[0.11 - 0.49]
	EVI	-0.08 ± 0.07	[-0.26 - 0.00]	-0.04 ± 0.03	[-0.13 - 0.00]
	EVI ²	0.32 ± 0.16	[-0.01 - 0.61]	0.08 ± 0.03	[0.03 - 0.13]
	Distance to Water	-2.45 ± 0.36	[-2.97 - -1.66]	-2.70 ± 0.24	[-2.99 - -2.14]
	TRI	-0.03 ± 0.03	[-0.11 - 0.00]	-0.04 ± 0.04	[-0.15 - 0.00]
	BPV	0.48		0.45	
	C-hat	1		1.01	
<i>Cattle</i>	β_0^{2014}	0.46 ± 0.18	[0.20 - 0.91]	0.40 ± 0.18	[0.24 - 0.70]
	β_0^{2015}	0.80 ± 0.26	[0.40 - 1.41]	0.25 ± 0.26	[0.13 - 0.45]
	β_0^{2016}	0.48 ± 0.18	[0.22 - 0.89]	0.32 ± 0.18	[0.17 - 0.57]
	β_0^{2017}	0.71 ± 0.24	[0.34 - 1.26]	0.54 ± 0.24	[0.29 - 0.96]
	EVI	-0.09 ± 0.08	[-0.30 - 0.00]	-0.02 ± 0.02	[-0.08 - 0.00]
	EVI ²	0.24 ± 0.15	[-0.05 - 0.52]	0.12 ± 0.03	[0.05 - 0.19]
	Distance to Water	-2.16 ± 0.29	[-2.74 - -1.62]	-2.64 ± 0.23	[-2.98 - -2.12]
	TRI	-0.01 ± 0.01	[-0.05 - 0.00]	-0.02 ± 0.02	[-0.08 - 0.00]
	BPV	0.18		0.37	
	C-hat	1.02		1.01	

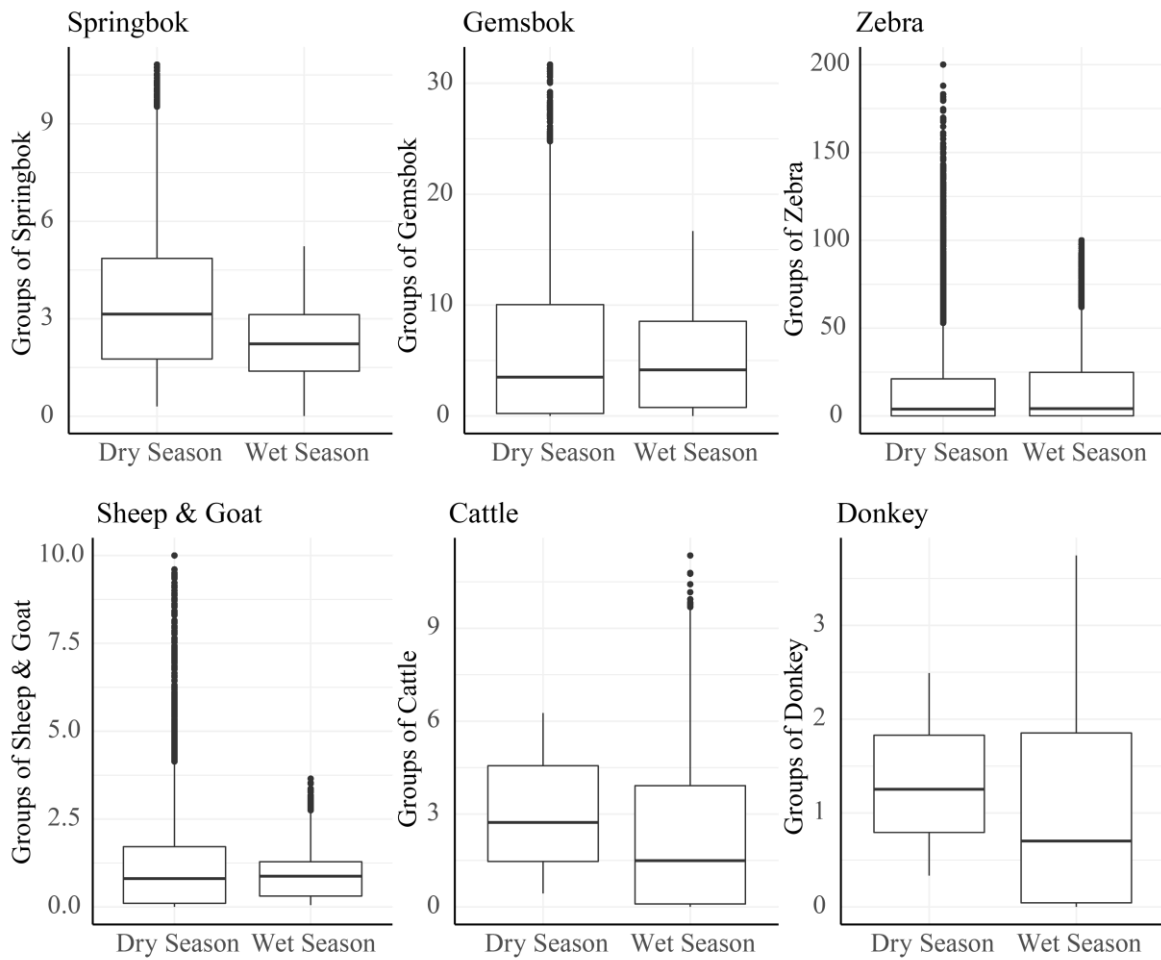


Figure S.4.4 – Distribution of the predicted number of groups of each target wild and domestic species in INP.

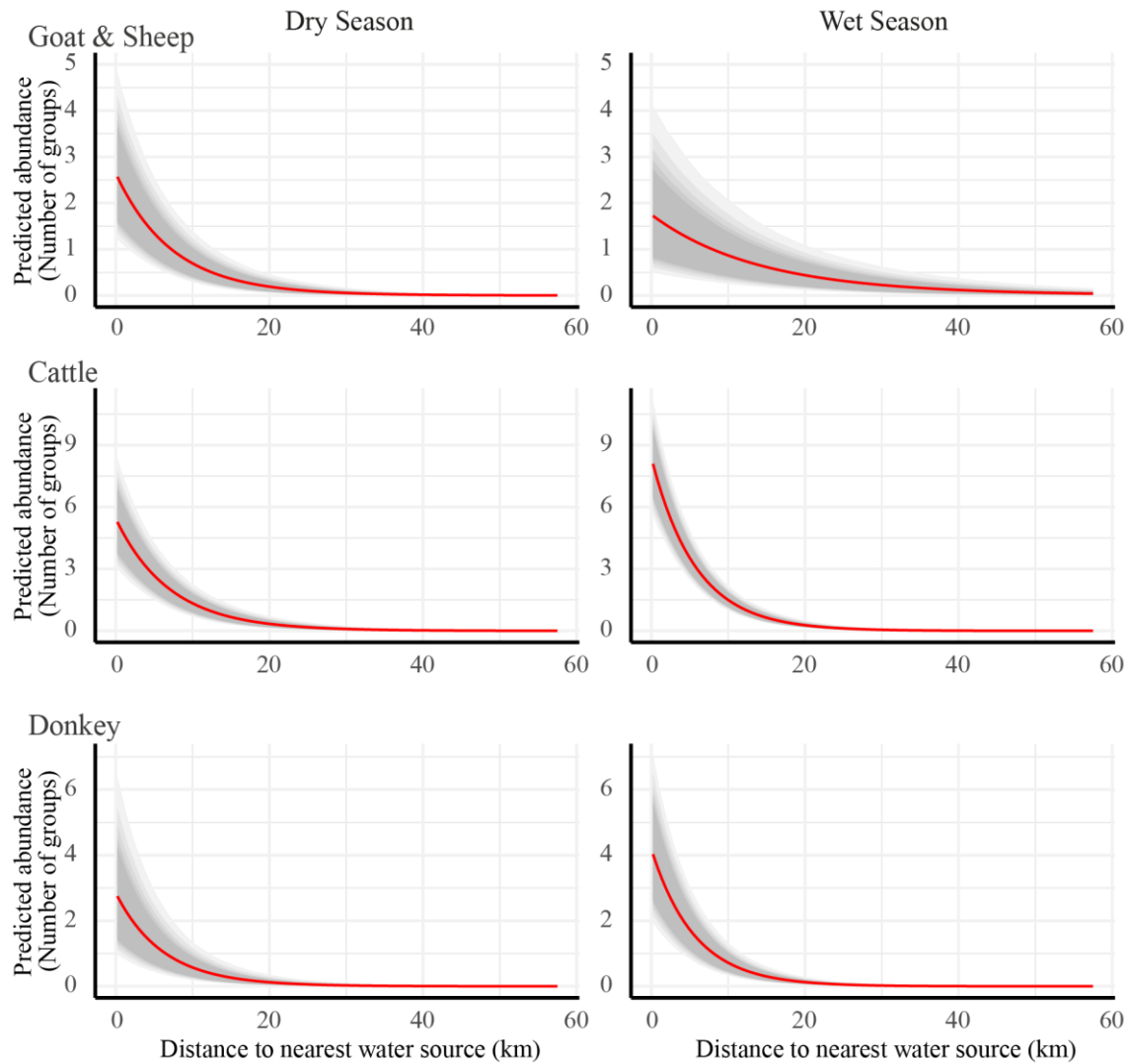


Figure S.4.5 – Maximum expected abundance of groups of domestic species in response to the distance to permanent water points, during dry and wet seasons. The different shades of grey represent the 95%, 90%, 85%, 80% and 75% credible intervals.

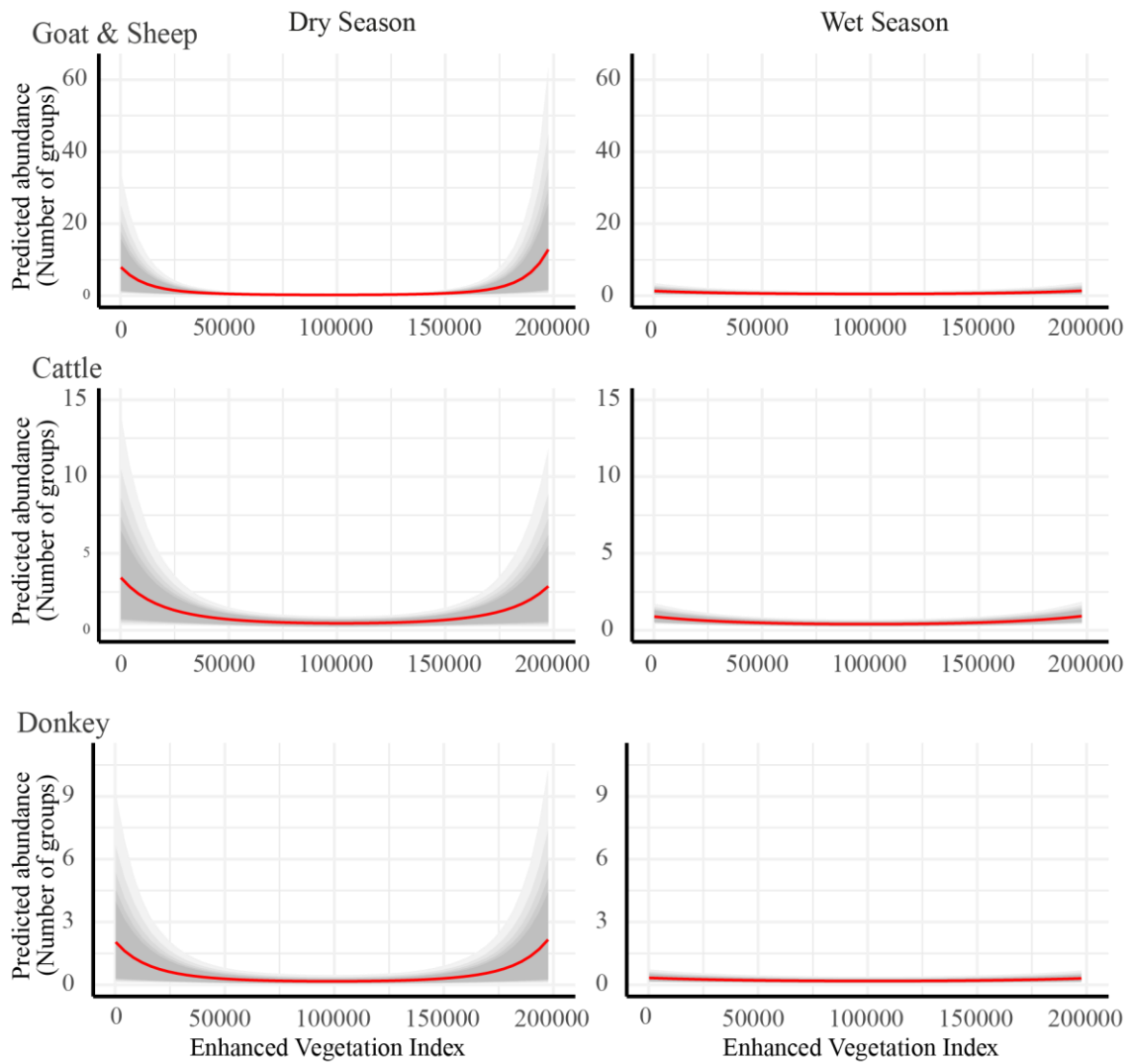


Figure S.4. 6 - Maximum expected abundance of groups of domestic species in response to the proportion of grass in the land cover during dry and wet seasons. The different shades of grey represent the 95%, 90%, 85%, 80% and 75% credible intervals.

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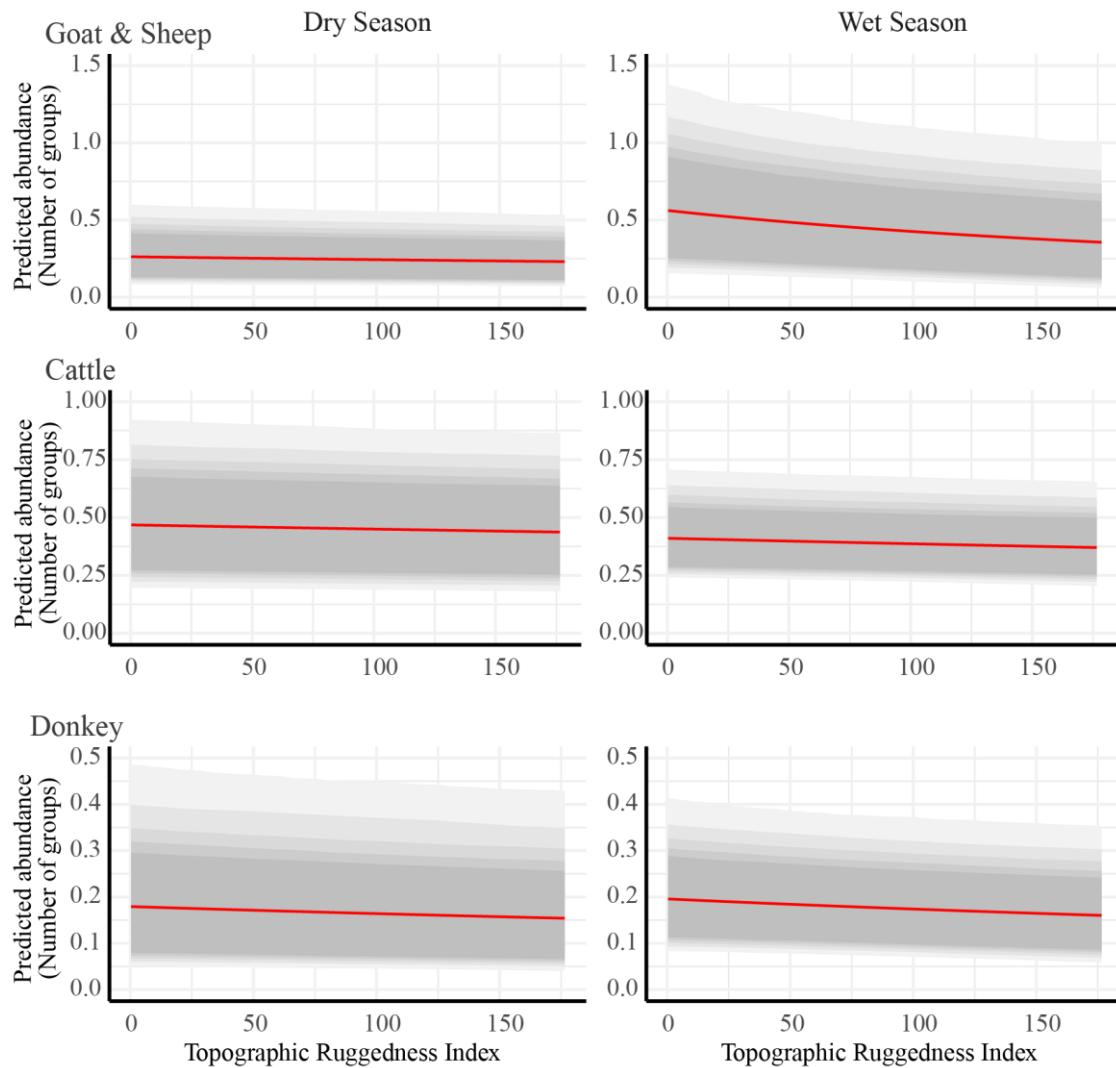


Figure S.4.7 - Maximum expected abundance of domestic species in response to the topographic ruggedness index (TRI) during dry and wet seasons. The different shades of grey represent the 95%, 90%, 85%, 80% and 75% credible intervals.

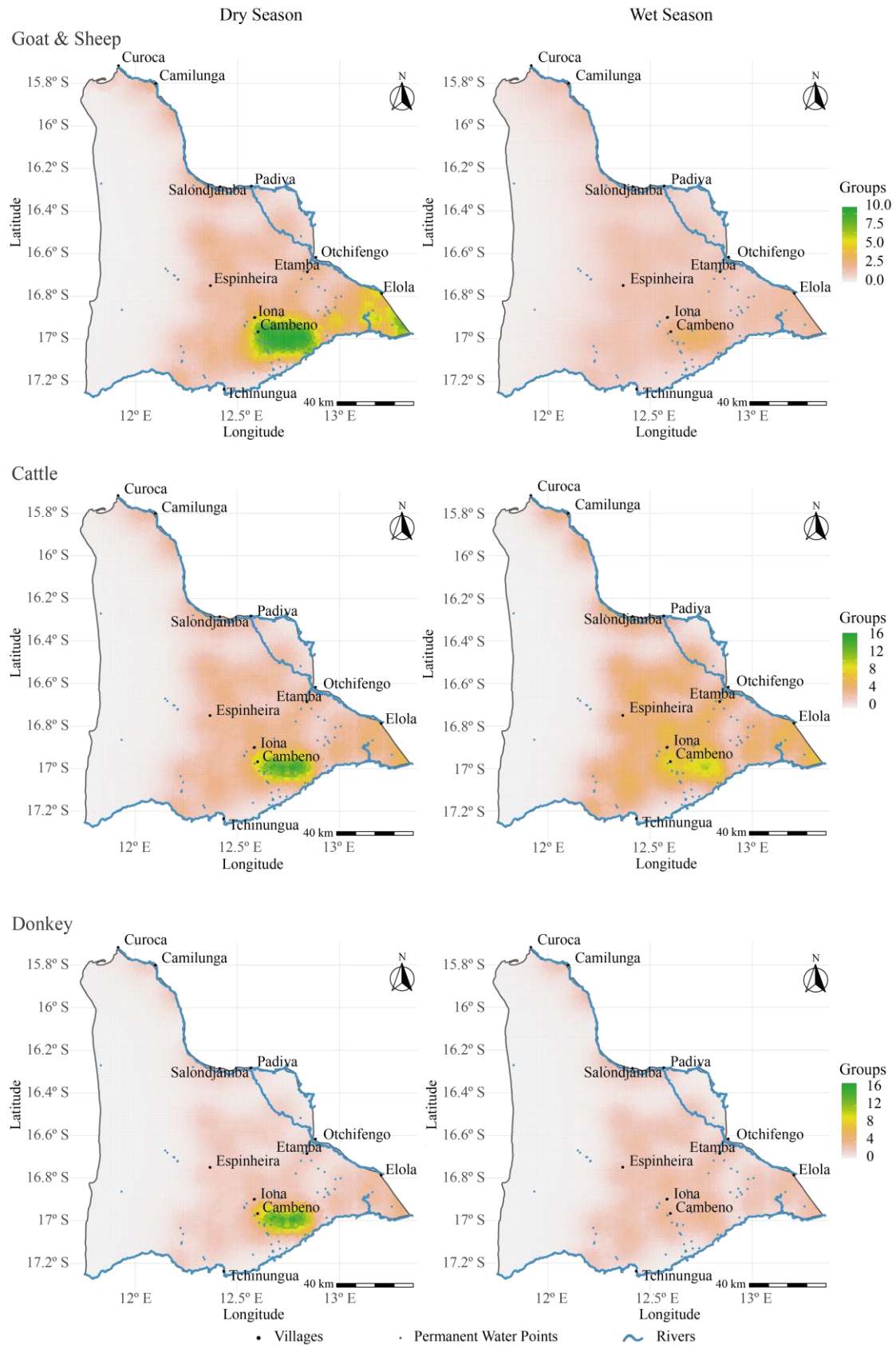


Figure S.4.8 - Maximum expected number of groups associated to each site of livestock species in Iona National Park.

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Appendix 5 - Supporting information for Chapter 5

Table S.5.1 – Number of independent detections of each mammal species recorded during our surveys in Bicular National Park and Cuatir Conservation Area. The species are sorted by order, family, and body weight.

Family	Species	Bicular National Park	Cuatir Conservation Area
Bovidae	<i>Raphicerus campestris</i>	113	1627
	<i>Sylvicapra grimmia</i>	33715	7078
	<i>Aepyceros melampus</i>	0	128
	<i>Redunca arundinum</i>	0	279
	<i>Tragelaphus spekii</i>	0	2
	<i>Tragelaphus strepsiceros</i>	1560	106
	<i>Hippotragus equinus</i>	2981	320
	<i>Taurotragus oryx</i>	1194	91
	<i>Syncerus caffer</i>	1	1
Giraffidae	<i>Giraffa camelopardalis</i>	0	69
Suidae	<i>Potamochoerus larvatus</i>	3060	121
	<i>Phacochoerus africanus</i>	688	289
Canidae	<i>Otocyon megalotis</i>	52	149
	<i>Canis mesomelas</i>	2	0
	<i>Canis adustus</i>	2	535
	<i>Lycaon pictus</i>	104	1
Felidae	<i>Felis silvestris</i>	121	137
	<i>Caracal caracal</i>	460	62
	<i>Leptailurus serval</i>	109	128
	<i>Acinonyx jubatus</i>	0	48
	<i>Panthera pardus</i>	640	78
Herpestidae	<i>Helogale parvula</i>	22	0
	<i>Galerella sanguinea</i>	70	4
	<i>Paracynictis selousi</i>	21	1
	<i>Bdeogale nigripes</i>	0	1
	<i>Atilax paludinosus</i>	0	8
	<i>Ichneumia albicauda</i>	122	28
Hyaenidae	<i>Proteles cristata</i>	2	0
	<i>Crocuta crocuta</i>	2271	2
Mustelidae	<i>Ichonyx striatus</i>	105	66
	<i>Mellivora capensis</i>	101	29
Viverridae	<i>Genetta genetta</i>	592	77
	<i>Genetta angolensis</i>	78	14
	<i>Civettictis civetta</i>	1	2
Leporidae	<i>Lepus saxatilis</i>	1948	567
Equidae	<i>Equus quagga</i>	0	90
Manidae	<i>Manis temminckii</i>	9	1
Cercopithecidae	<i>Chlorocebus cynosuros</i>	2755	370
Elephantidae	<i>Loxodonta africana</i>	6639	0
Hystriidae	<i>Hystrix africaeaustralis</i>	358	195
Pedetidae	<i>Pedetes capensis</i>	113	358
Sciuridae	<i>Funisciurus congicus</i>	21	0
Orycteropodidae	<i>Orycteropus afer</i>	777	89

Table S.5. 2 - Estimated effects of each tested covariate in the probability of colonization of each target species. 'Mild Fire' and 'Severe Fire' are compared to 'No Fire' areas and the results for 'Cuatir' reflect the difference to 'Bicuar'.

Species	Covariate	Estimated Effect
Common Warthog	Trend	-3.23 [-4.84, -1.34]
	Mild Fire	-0.39 [-3.86, 1.33]
	Severe Fire	0.41 [-1.51, 1.79]
	dEVI	0.97 [-0.21, 1.95]
	Distance to Unburn	0.00 [-1.07, 1.05]
	Cuatir vs. Bicuar	-1.88 [-2.73, -1.19]
	Trend * dEVI	-1.57 [-3.41, 0.38]
	Trend * Distance to Unburn	-0.76 [-4.33, 1.61]
Roan Antelope	Trend	-1.57 [-3.80, -0.02]
	Mild Fire	-1.11 [-3.93, 0.68]
	Severe Fire	-0.57 [-3.78, 0.99]
	dEVI	0.05 [-1.08, 1.09]
	Distance to Unburn	0.27 [-0.57, 1.19]
	Cuatir vs. Bicuar	-1.21 [-2.20, -0.52]
	Trend * dEVI	0.02 [-1.80, 1.84]
	Trend * Distance to Unburn	-0.14 [-3.08, 1.42]
Steenbok	Trend	-0.37 [-1.36, 0.61]
	Mild Fire	-0.02 [-1.12, 0.93]
	Severe Fire	-0.58 [-1.75, 0.44]
	dEVI	0.53 [-0.51, 1.45]
	Distance to Unburn	0.12 [-0.51, 0.72]
	Trend * dEVI	-0.98 [-2.47, 0.62]
	Trend * Distance to Unburn	-0.03 [-1.18, 0.92]
Common Eland	Trend	-2.80 [-4.9, 0.96]
	Mild Fire	1.22 [-1.76, 3.79]
	Severe Fire	-2.43 [-4.89, 1.18]
	dEVI	-0.68 [-3.54, 1.52]
	Distance to Unburn	-0.37 [-1.76, 1.33]
	Trend * dEVI	-0.88 [-4.69, 4.04]
	Trend * Distance to Unburn	1.65 [-1.15, 2.95]
African Savanna Elephant	Trend	-1.33 [-3.58, 0.90]
	Mild Fire	-0.72 [-4.32, 2.16]
	Severe Fire	0.20 [-1.77, 2.10]
	dEVI	-2.17 [-3.79, -0.01]
	Distance to Unburn	1.07 [-0.32, 2.57]
	Trend * dEVI	3.04 [-0.01, 4.91]
	Trend * Distance to Unburn	-2.91 [-4.91, -0.04]
Bushpig	Trend	1.00 [-0.12, 2.14]
	Mild Fire	-0.33 [-1.37, 0.61]
	Severe Fire	0.33 [-0.73, 1.30]
	dEVI	-0.40 [-2.11, 1.00]
	Distance to Unburn	0.29 [-0.32, 0.92]

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	Cuatir vs. Bicular	0.83 [0.38, 1.31]
	Trend * dEVI	0.54 [-1.82, 3.15]
	Trend * Distance to Unburn	0.07 [-1.00, 1.16]
Greater Kudu	Trend	-0.02 [-2.40, 2.11]
	Mild Fire	-1.22 [-4.76, 1.80]
	Severe Fire	-2.68 [-4.88, 0.34]
	dEVI	-0.94 [-2.51, 0.86]
	Distance to Unburn	0.69 [-1.20, 1.93]
	Cuatir vs. Bicular	0.25 [-0.51, 1.01]
	Trend * dEVI	0.87 [-2.33, 3.48]
	Trend * Distance to Unburn	-2.83 [-4.92, 0.32]
Common Duiker	Trend	-0.72 [-1.38, -0.07]
	Mild Fire	0.11 [-0.55, 0.77]
	Severe Fire	-0.58 [-1.39, 0.16]
	dEVI	-0.05 [-0.48, 0.38]
	Distance to Unburn	-0.21 [-0.60, 0.15]
	Cuatir vs. Bicular	0.20 [-0.11, 0.51]
	Trend * dEVI	-0.18 [-0.94, 0.55]
	Trend * Distance to Unburn	0.61 [0.00, 1.24]

Appendix 6 - Supporting information for Chapter 6

Appendix 6.1 – Multicollinearity analysis

Multicollinearity among continuous covariates was assessed through a nonparametric Spearman's correlation analysis using the “psych” R package (Revelle, 2020). Among correlated covariates ($|\rho| \geq 0.5$; Zuur *et al.* (2009a), the covariate less correlated with the dependent variable or for which the predicting hypothesis had less empirical support was excluded from the subsequent modelling procedure.

The multicollinearity analysis failed to detect significant correlation among potential covariates, and only distance to water showed a slight negative correlation with the proportion of grassland cover ($\rho = -0.51$). Given the low correlation factor among these covariates, and their biological importance for species resources acquisition, all were retained for subsequent analyses (Appendix 6: Table S.6.1).

Table S.6.1 – Correlation matrix between the covariates considered in the analysis.

	Distance to Water	Shrubland Cover	Grassland Cover
Distance to Water	1	0.25	-0.51
Shrubland Cover	0.25	1	-0.08
Grassland Cover	-0.51	-0.08	1

Table S.6.2 - Goodness-of-fit (Bayesian p-value and c-hat) of each model.

Model	Parameter	Dry	Wet
Roan antelope	Bayesian p-value	0.48	0.83
	$\hat{c}$	1.14	0.85
Greater kudu	Bayesian p-value	0.38	0.66
	$\hat{c}$	1.54	0.94
Warthog	Bayesian p-value	0.47	0.67
	$\hat{c}$	1.20	0.93
Bushpig	Bayesian p-value	0.62	0.68
	$\hat{c}$	1.06	0.93
Common duiker	Bayesian p-value	0.73	0.99
	$\hat{c}$	0.94	0.87
Malbrouck monkey	Bayesian p-value	0.52	0.48
	$\hat{c}$	1.03	1.05
Scrub hare	Bayesian p-value	0.52	0.73
	$\hat{c}$	1.04	0.89

Table S.6.3– Number of occasions with detection and with non-detections of each target species in each season considered in the modelling.

	Year	2017		2018		2019
	Season	Dry	Wet	Dry	Wet	Dry
Leopard	Detection	99	75	25	91	93
	Non-detection	4420	7947	1656	13763	13357
Spotted-hyaena	Detection	186	228	48	366	236
	Non-detection	4332	7793	1636	13488	13222
Malbrouck monkey	Detection	133	92	16	114	86
	Non-detection	4386	7929	1666	13740	13366
Common duiker	Detection	730	1092	255	2260	2139
	Non-detection	3793	6947	1443	11596	11332
Bushpig	Detection	65	86	34	193	122
	Non-detection	4453	7934	1648	13661	13330
Warthog	Detection	21	34	11	68	53
	Non-detection	4497	7986	1671	13786	13396
Greater kudu	Detection	18	7	5	62	63
	Non-detection	4500	8013	1676	13792	13386
Roan antelope	Detection	98	94	28	249	257
	Non-detection	4420	7926	1653	13605	13196

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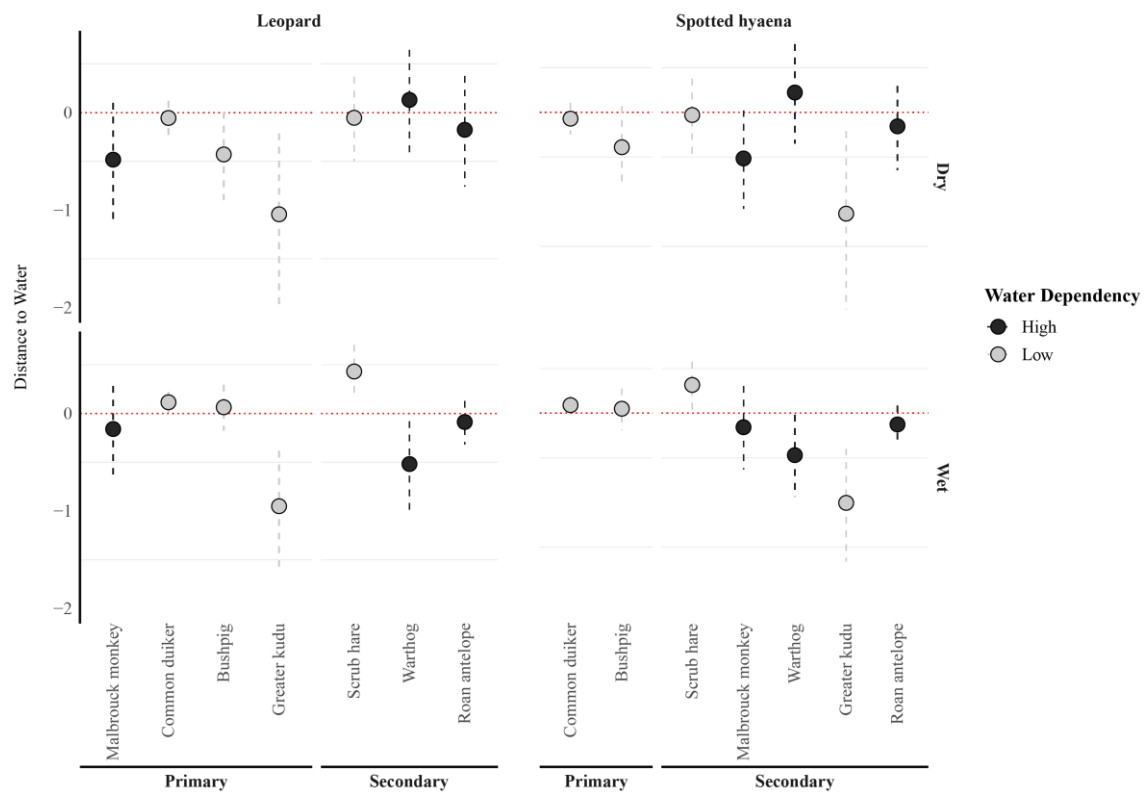


Figure S.6. 1 – Untransformed coefficient estimates (and respective 95% credible intervals) of the distance to the nearest water source effect on prey species' local abundance, based on leopard and spotted-hyaena dominance models. Prey species are classified according to: i) water dependency – high, if requiring near daily access to drinking water; low, if able to obtain sufficient water from forage or only requiring access to drinking water irregularly (Kihwele et al., 2020); and ii) importance for each predator's diet – Primary if the Frequency of Occurrence (FO) > 5%; Secondary if FO < 5%.

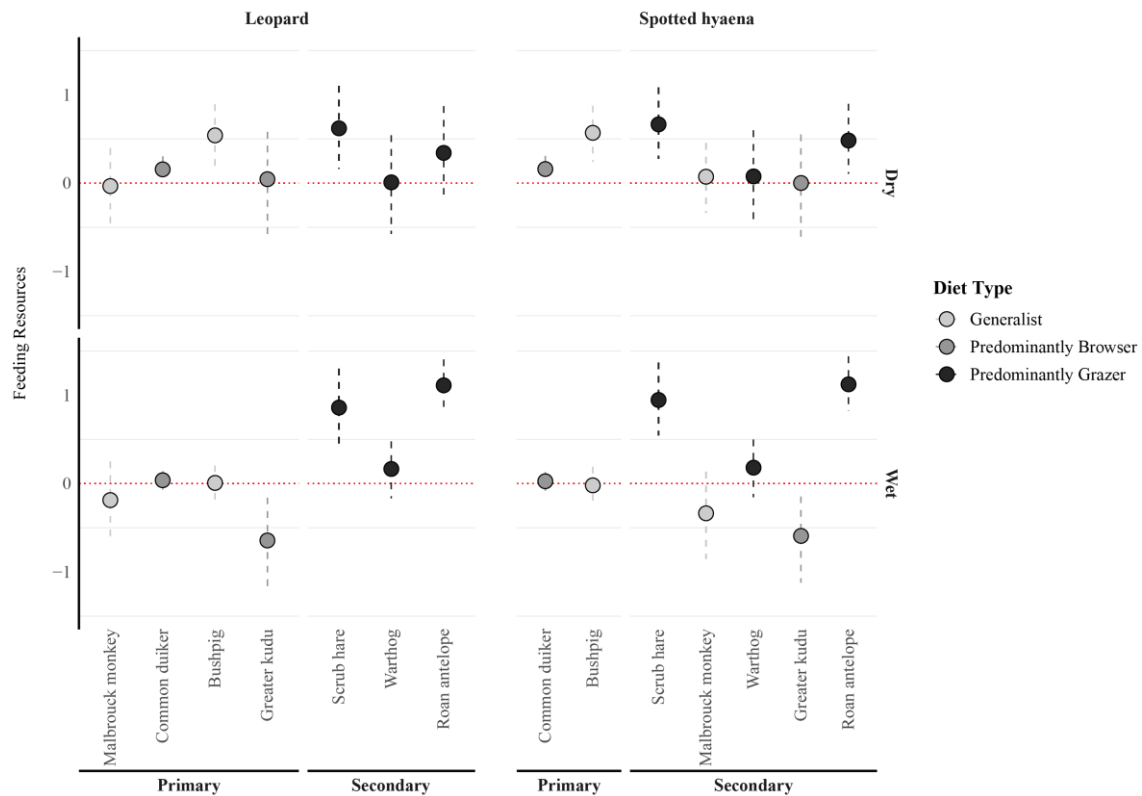


Figure S.6.2 – Untransformed coefficient estimates (and respective 95% credible intervals) of the proportion of grassland or shrubland cover effect (as a proxy for food availability for predominantly grazer species and generalist and predominantly browser species) on prey species' local abundance, based on leopard and spotted-hyaena dominance models. Prey species are classified according to: i) diet type – predominantly grazer, if more than 60% of their diet is comprised by monocots; generalists, if they consume more than 20% of a variety of food, i.e. monocots, dicots or fruits; predominantly browser, if more than 70% of their diet is comprised by dicots (Hempson et al., 2015); and ii) importance for each predator's diet – Primary if the Frequency of Occurrence (FO) > 5%; Secondary if FO < 5%.

Table S.6.4 - Temporal activity overlap between predator and prey species pairs and the p-value of the Watson's U^2 test for the differences between activity patterns.

Prey Species	Leopard		Spotted-hyaena	
	Dry	Wet	Dry	Wet
Scrub hare	0.77 [0.70; 0.83] ***	0.66 [0.58; 0.75] ***	0.92 [0.88; 0.96]	0.86 [0.79; 0.92] **
Malbrouck monkey	0.44 [0.38; 0.51] ***	0.49 [0.41; 0.57] ***	0.28 [0.23; 0.32] ***	0.28 [0.23; 0.33] ***
Common duiker	0.76 [0.72; 0.81] ***	0.78 [0.71; 0.84] ***	0.60 [0.56; 0.63] ***	0.55 [0.52; 0.58] ***
Warthog	0.42 [0.35; 0.51] ***	0.46 [0.37; 0.54] ***	0.25 [0.19; 0.31] ***	0.25 [0.20; 0.31] ***
Bushpig	0.84 [0.75; 0.91] **	0.87 [0.80; 0.94] **	0.74 [0.68; 0.80] ***	0.81 [0.75; 0.85] ***
Greater kudu	0.61 [0.51; 0.71] ***	0.61 [0.50; 0.72] ***	0.44 [0.35; 0.51] ***	0.40 [0.32; 0.48] ***
Roan Antelope	0.84 [0.77; 0.90] ***	0.86 [0.80; 0.92] ***	0.66 [0.62; 0.71] ***	0.66 [0.62; 0.72] ***

Significance codes: * p-value < 0.05; ** 0.001 < p-value < 0.01; *** p-value < 0.001

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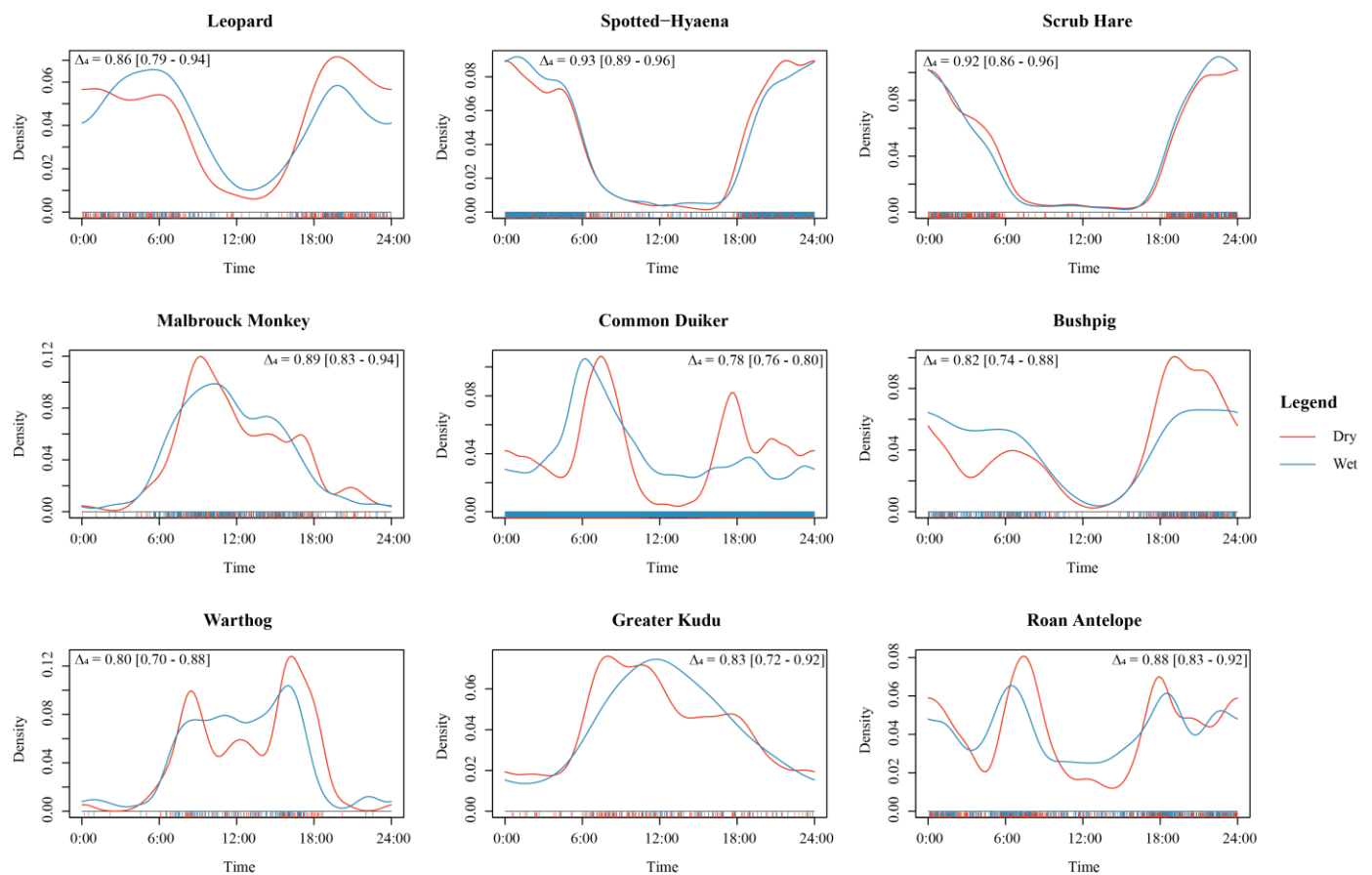


Figure S.6.3 - Activity plot of all the target predator and prey species, during dry (red) and wet (blue) seasons. We also present the overlap coefficient (Δ_4) between the activity of each species across season.