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Simulating the consequences of behavioural variation among African antelope populations under a changing climate and different land management scenarios

by

Graham John Elliott

Thesis for the degree of Doctor of Philosophy

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Abstract

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Although numerous predictions have been developed regarding climate change, many current tools and methods represent a reductionist approach and are insufficient to fully assess the ecological impact of climate change, and the adaptive capacity of species to mitigate these impacts. A complex systems approach is required: assessing the impacts of climate change on species is flawed without consideration of variation in behaviour and social organisation. The aim of this study is to evaluate the utility of using simulations to understand how the full range of behavioural variation, and social organisation, contributes to the adaptive capacity of species to respond to climate change. A high-resolution agent-based model was developed to simulate behavioural variation within a community of antelope species in Mokala National Park, South Africa, subject to different climate change scenarios. The model was then extended to evaluate and compare the effectiveness of two separate management interventions (habitat management and park expansion), in conserving the community under climate change. Comparisons were based on individuals' energy levels and whether there were selection pressures for specific behaviour or social groups. The results suggest both types of intervention show promise for mitigation of climate change effects but both schemes also selected for specific behaviour types and social groups. This may impact on populations ability to adapt to change and may affect the social cohesion of these populations.

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Research Thesis: Declaration of Authorship

Print name:	Graham John Elliott

Title of thesis:	Simulating the consequences of behavioural variation among African antelope populations under a changing climate and different land management scenarios

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;

None of this work has been published before submission

Signature:		Date:	

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Code for checking if an agent would cross the fence when going to waterhole or grazing patch was obtained from Geotechnical Software Services, http://geosoft.no.

The affine transform code which preserves the shape of the agent and the agent's view circles when turning were provided by Dr van der Vaart.

Abbreviations and Definitions

ABM	Agent-based model
ENM	Environmental Niche Model
EVI	Enhanced Vegetation Index
FMR	Field Metabolic Rate
GIS	Geographic Information System
GUI	Graphical User Interface
ha	Hectare
IQR	Interquartile range

MARSC	Modelling the Adaptive Response of Species under Climate change
MJ	Megajoules
NDVI	Normalised Difference Vegetation Index
ODD	Overview, Design concepts, and Details
PA	Protected area
SANParks	South African National Parks Authority
SDM	Species Distribution Model
UTM	Universal Transverse Mercator
WGS	World Geodetic System

Chapter 1 Introduction

1.1 Background

Global climate change is predicted to have a highly deleterious impact on ecosystems, communities and populations (IPCC, 2014a). The worst-case scenario is a global mean temperature increase of 4.7° C by 2100, compared with the mean temperature for 1986-2005, with temperature increases moving across landscapes at 70 km per decade by 2050 (IPCC, 2014a). Based on a worst-case scenario of maximum expected climate change and no species dispersal, it is predicted that 58% of all species will go extinct due to climate change by 2050 (Thomas et al, 2004). Regardless of whether the worst-case scenario materialises, predicted ecological impacts include species extinctions and shifts in biome distribution and species' distributions (IPCC, 2014b). In some cases, these changes are already happening (IPCC, 2014a & 2014b).

For example, to track climate change, species are moving to higher latitudes at a median rate of 16.9 km per decade (based on a meta-analysis of 764 terrestrial species from Europe, N. America and Chile) and to higher elevations at a median rate of 11.0 m per decade (based on 1367 terrestrial species from Europe, N. America, Malaysia and Marion Island), with distance moved correlating to temperature increase (Chen et al, 2011). However, large mammals are not generally tracking climate change, which is unsurprising given the challenge to large mammals of dispersing across fragmented landscapes that are densely populated by humans (Hetem et al, 2014).

In addition to the global impact of climate change, it is expected that mean temperature increases in southern Africa (the area of interest for this study – see Section 1.2) will exceed global mean increases and droughts will intensify (IPCC, 2014b). African national parks may experience unparalleled changes in species community composition (Thuiller et al, 2006). For example, Kruger National Park is predicted to lose 20 of its current species and gain 20 novel species by 2080 (Thuiller et al, 2006). In addition, it is predicted that an eastward range shift of species in southern Africa will contrast with a westward species range shift in equatorial Africa (Thuiller et al, 2006).

If their environments become less favourable due to climate change, species must either adapt to these changing conditions, or migrate to more favourable locations, in order to survive. Whilst some smaller species are evolving in response to climate change, for many species adaptation through evolution of novel phenotypes is unlikely, given the rate of climate change (Parmesan, 2006; Thomas & Gillingham, 2015). However, migration depends on the dispersal ability of the species; given the size and influence of the human population, migration may be difficult or not possible (Hetem et al, 2014).

Climate change and its future impacts on species represent a complex system (e.g. the whole is greater than the sum of its parts). The key issue which frames this study is that although many predictions on climate change have been made, many current tools and methods represent a reductionist approach and are insufficient to fully assess the ecological impact of climate change and the adaptive capacity of species to mitigate these impacts. When assessing a complex system, a complex systems approach is required. This is apparent in other disciplines: for example, predictive models in meteorology and sedimentology incorporate a high level of complexity to produce meaningful results (Stillman & Goss-Custard, 2010). Assessing the impacts of climate change on species is flawed without consideration of variation in behaviour and social organisation. Computer simulations facilitate this complex systems methodology.

1.2 Thesis aim, objectives and structure

The aim of this project is to evaluate how the full range of behavioural variation and social organisation contributes to the adaptive capacity of species to respond to climate change. The aim leads to three objectives. First, develop an agent-based model (ABM) to simulate the behavioural variation and social organisation of a community of antelope within Mokala National Park (hereafter ‘Mokala’), South Africa, under current and future climate change scenarios. Second, use the model to compare the impact of different habitat management schemes within Mokala on the antelope community, under the future climate change scenarios. Third, extend the model to compare the effects of expansion of Mokala on the antelope community under the future climate change scenarios. The issue, aims and overall methodology of this study are listed in the framework at the end of Section 1.2.

Thesis structure

Chapter 2 describes the development of the agent-based model used to simulate a community of four antelope species within Mokala National Park, South Africa, under current and future climate change scenarios. The species are blue wildebeest *Connochaetes taurinus*, black wildebeest *Connochaetes gnou*, tsessebe (also known as topi) *Damaliscus lunatus* and red hartebeest *Alcelaphus buselaphus.* Social organisation within these species is both flexible and responsive to environmental change (Estes, 1992), in accordance with the aim of this theses. Chapter 2 serves as a proof of concept of the model.

Chapter 3 builds on Chapter 2 to incorporate different habitat management schemes within the model, to compare their effect on the Mokala antelope community under different climate change scenarios. Comparisons of the habitat management schemes were based on individuals' energy levels and whether there were selection pressures for specific behaviour or social groups. The chapter provides an insight into how behavioural variation and social organisation contribute to the capacity of the antelope populations to adapt to climate change within the habitat management schemes.

Chapter 4 extends the model validated in Chapter 2 to compare the effect of expansion of Mokala on the antelope community under different climate change scenarios. Specifically, simulations were run for two different expansion configurations under climate change scenarios. One configuration favoured by park authorities, but with lower vegetation productivity, is compared with an alternative of similar size with higher vegetation productivity. Comparisons of the configurations were based on energy levels and selection pressure as described above.

Chapter 5 summaries the key findings and implications of the study. Limitations of the methodologies are discussed, along with future developments.

The following sections review the literature on aspects of conservation and ecology that are relevant to the thesis aims. Additional reviews relevant to the specific objectives are included in Chapters 2 - 4.

Chapters 2, 3, and 4 equate to the three objectives in the logical framework below. To meet the objectives, the results described above relate to the following comparisons within behavioural types and social groups:

- Exploratory v non-exploratory behaviour
- Cognitive ability: comparison between random foraging v memory-based foraging
- Interspecific differences
- Social classes: lone grazers, herd leaders and followers (note that the terms “grazers” and “agents” are used interchangeably throughout the thesis).
- Sociability: antisocial v social lone grazers

A logical framework linking the issue, aims and methodology of the thesis

Issue	Aim	Objective	Results	Methods
Current methods/tools represent a reductionist approach and are insufficient to fully assess the ecological impact of climate change and the extent to which species may mitigate these impacts.	Evaluate utility of a Complex Systems approach to better understand how the full range of behavioural variation and social organisation contributes to the adaptive capacity of species to respond to climate change.	Evaluate utility of simulating a community of antelope species as a complex system, incorporating variation in behavioural and social organisation and different climate change scenarios. (Chap. 2)	Variation in energy levels acquired by individuals.	Develop agent-based model to simulate the behaviour of antelope.
			Variation in energy levels between behavioural types and social groups	
			Selection pressure for specific behaviour and social groups	
		Quantify the effects of different levels of habitat management for species conservation on a community of antelope species within a protected area under climate change (Chap. 3)	Variation in individuals' energy levels between levels of habitat management.	Run model against future climate scenarios for different levels of habitat management.
			Energy levels vary between behavioural types, social groups and habitat management levels	
			Selection pressure for specific behaviour or social groups varies with type of habitat management	
		Quantify the effects of different expansion configurations of a protected area on a community of antelope species under climate change (Chap. 4)	Variation in energy levels acquired by individuals between park configurations.	Run model against future climate scenarios for different park configurations.
			Energy levels vary between behavioural types, social groups and park configurations	
			Selection pressure for specific behaviour or social groups varies with park configuration	

1.3 Challenges for climate change mitigation

The aspect of climate change that is of most concern, is the extent to which its future impact is unknown. Despite the numerous predictions that climate change will be deleterious for species, generally we do not know *how* climate change will actually cause extinctions, i.e. the proximate causes (Cahill et al, 2012; Román-Palacios & Wiens, 2020). If the impacts of, and responses to, climate change are non-linear, this would further confound attempts to predict the impact of climate change. In addition, the "cocktail" effect represents an additional confounding issue: climate change will not act in isolation, but rather its impact will combine with other issues such as range shifts, changes to community composition and changes in interspecific interactions (Thuiller et al, 2006; Heinz Centre, 2012; IPCC, 2019; IPCC, 2021).

Predicting the ecological impacts of climate change is problematic, yet predictions are crucial to conservation planning and management (Suttle et al, 2007). At a regional scale, the vast amount of research on African megafauna includes very little research on the likely effects of climate change on species (Heinz Center, 2012; Owen-Smith et al, 2020).

An additional challenge relates to the scale of available predictions. As climate change represents a global threat to ecosystems (IPCC, 2014a; Chen, 2021), it is understandable that model predictions assessing possible scenarios under climate change, often take broad (i.e. global or continental) perspectives with coarse scales (Sinclair et al, 2010; Urban et al, 2016). This approach is useful when conveying information on large-scale trends to a wide audience of decision-makers, stakeholders and the general public. However, these models are less useful for conservation practitioners, as they lack specificity at the local scale, i.e. they fail to capture key local ecosystem dynamics (Pearson & Dawson; 2003; Sinclair et al, 2010) - this point is discussed further in Section 1.10. To inform management strategies, conservation practitioners need access to fine-scale data and models, for example focused on specific protected areas, but these are currently limited in number (Turner et al, 2015).

The current system of protected areas (PAs) globally does not adequately represent the environmental heterogeneity species experience across their range (Hanson et al., 2020). This inhibits the ability of populations to develop relevant local adaptations. A study of 19,937 vertebrate species found that for 4,608 (90.9%) terrestrial mammal, 4,836 (93.1%) amphibian and 8,653 (89.5%) bird species, the coverage of environmental heterogeneity was inadequate in PAs (Hanson et al., 2020). Of greater concern is the finding that 9,651 of all the included species (18.4%) did not have any of their environmental heterogeneity represented (Hanson et al., 2020). Increasing existing PAs to cover these shortfalls would require gazetting approximately 34% of the total land surface (Hanson et al., 2020) – twice the current target of 17% agreed under the Aichi Biodiversity Target 11 (CBD, 2018). South Africa was one of the priority countries identified by Hanson et al. (2020) for improvement of environmental heterogeneity within PAs.

1.4 Variation in exploratory behaviour

Differences in exploratory behaviour are associated with different personalities, e.g. exploratory, bold, aggressive, neophilic and risk-taking versus non-exploratory, shy, docile, neophobic and risk-averse (Careau et al., 2008). These groups are described as proactive and reactive respectively and the traits of the proactives are generally energetically costly, therefore as resources decline, the reactive group may fare better due to their reduced energy requirements (Careau et al., 2008).

Contrasting results exist in relation to exploratory behaviour among species. More exploratory grazers (also referred to as “fast explorers” - Rödel et al, 2015) should increase their chances of finding spatially dispersed resources and so acquire higher energy levels (Schuster et al., 2017; Schirmer et al, 2019). Therefore, as resources decline, individuals should exhibit more exploratory behaviour. However, golden-mantled ground squirrels *Callospermophilus lateralis* forage closer to their burrow as resource levels decline (Hefty & Stewart, 2019). Less exploratory individuals may garner more useful information from their more thorough search behaviour (Sulikowski, 2017). Consequently these “slow explorers” may exhibit more efficient foraging, develop a greater knowledge of their habitat and become more sensitive to changes in grazing quality. Both high and low levels of exploratory behaviour are beneficial compared with intermediate levels for some species (e.g. eastern chipmunks *Tamias striatus* - Bergeron et al., 2013; great tits *Parus major* - Zandberg et al., 2017).

Experimental evidence suggests fast explorers are faster learners, which leads to established routines and rigid predictions of their environment, ultimately promoting inflexible behaviour; whereas slow explorers are slower leaners but more responsive to their environment and therefore exhibit more flexible behaviour (Coppens et al., 2010; Mazza et al, 2018). Responding to change (as opposed to relying on routines) offers a flexible approach which should confer benefits as environments change, suggesting slow explorers may adapt better as resources decline.

However, Nawroth et al. (2017) reported no correlation between exploratory behaviour and learning and a meta-analysis of studies found equal numbers of studies reporting positive and negative correlations (Dougherty and Guillette, 2018). Within these contradictory views, the speed-accuracy trade-off is also disputed, with assertions of greater accuracy in making correct decisions by slow explorers (Mazza et al., 2018) and by fast explorers (Gomes et al., 2020).

Although much of this section relates to contradictory findings, these findings emphasise the behavioural plasticity present within species, which needs to be considered when assessing their adaptive capacity. Whilst these findings may be confounding for researchers, the presence of such flexibility within species offers hope that species may find ways to mitigate the impact of climate change.

1.5 Solitary v group foraging

Numerous advantages and disadvantages of both solitary and group foraging have been suggested, some suggestions being contradictory. Both exploitation and interference competition can reduce the energy intake of an individual. Exploitation competition reduces the amount of available resources (Hobbs et al, 1996), while interference competition reduces access to available resources. Group members may experience both types of competition directly from other group members, but lone grazers may also experience this if they are displaced by a herd (interference) or find that a grazing patch has been exhausted by a group (exploitation).

Comparisons have been drawn between producer-scrounger and leader-follower dynamics, i.e. the producer/leader finds the resource which is then also utilised by the scrounger/follower (King et al, 2009; Reebs, 2010). A contrary view is that the producer could be a subordinate group member that finds food and the dominant scrounger usurps the subordinate to monopolise the food (Thornton & Samson, 2012). Regardless, scrounging can benefit group foragers by taking advantage of grazing patches discovered by others. However, some of the advantages/disadvantages are interconnected: e.g. scrounging may benefit animal A as it moves to the patch occupied by B, but B is then disadvantaged due to exploitation competition, or interference if A displaces B.

Various theoretical studies have proposed information sharing as a key benefit of group foraging, e.g. individuals learn about the best grazing patches from conspecifics (Merkle et al, 2015). In contrast, an empirical study by Stutz et al. (2018) suggested that groups do not provide efficient (foraging) information transmission and instead may promote inefficient foraging (or more precisely poor diet selection) by prioritising herd cohesion. In other words, the need to remain close to neighbours inhibits spatial exploration of a patch. Information that is transferred could be deleterious, e.g. a population of bison *Bison bison* switched to foraging on agricultural land they previously avoided, after associating with different individuals that grazed the agricultural patches, and experienced increased mortality due to hunting (Sigaud et al, 2017).

The many wrongs principle (Bergman & Donner, 1964) suggests group navigation is more accurate than for a lone individual since the direction of travel of the group will be the average of the individual headings. Provided the errors of individuals’ estimates (of the correct heading) are distributed around the correct heading without bias and are not completely correlated with other, the mean heading of the estimates reduces the error (Berdahl et al., 2018). Therefore, groups should be able to locate previous foraging patches with greater accuracy than solitary animals.

Codling and Bode (2014) reported optimal navigation results from their model when individuals copied the direction of a subset of neighbours (up to seven neighbours - only limited increased accuracy derived from larger subsets) and applied only a small weighting (6%) to their own spatial knowledge. This method was consistently accurate regardless of the level of individuals' navigation error (Codling and Bode, 2014). Migrating caribou *Rangifer tarandus* copy the direction of a subset of neighbours but the subset is not based on distance (i.e. all individuals with X m) or the number of neighbours (i.e. the nearest Y individuals); instead the neighbours headings are weighted by distance from the target animal (Torney et al., 2018)

Whilst a group may navigate to grazing patches with greater accuracy than a solitary individual, the group will exhaust the available resources faster, so must then spend more time searching for other patches than a lone individual (Beauchamp & Ruxton, 2005). In any given patch, a group member will only acquire a fraction of the available resources due to the presence of other group members, whereas a lone grazer could consume all available resources.

1.6 The importance of behavioural variation within populations

In 1859, Darwin correctly predicted that novel traits within a species would initially be disregarded by researchers and would only be considered once the traits became widespread. The traditional approach to animal behaviour has focussed on the population mean, individual variation was considered to be noise that obscured the signal (Wolf & Weissing, 2012).

A focus on mean behaviour will not provide a complete picture of a species' or population's response in a given scenario (Moran et al, 2016). Indeed, concentrating on mean behaviour risks missing the most important behaviour. For example, in a population of eastern chipmunks, individuals that exhibited either a high or low tendency to explore were almost twice as likely to survive over a six-month period, compared with intermediate explorers (Bergeron et al., 2013). Among great tits presented with a novel foraging challenge, fast and slow explorers increased their success rate over time, compared with intermediate explorers (Zandberg et al., 2017). Among pumpkinseed sunfish *Lepomis gibbosus*, morphologically extreme individuals have the highest fitness levels, the mean morphology being maladaptive (Wilson, 1998). In a changing environment, individual variation will likely be more important than the average behaviour of a population. Indeed, Beever et al (2017) emphasize the importance of behavioural variation within populations as a means to mitigate climate change impacts.

Populations do not adapt by adopting novel behaviour at a specific moment in time *en masse*. Individuals adapt and beneficial adaptations may proliferate within a population over time via a genetic or cultural basis. For example, the ability to deactivate snares, initially acquired by one individual, spread through a mountain gorilla *Gorilla gorilla* population via a cultural process - learning (Diane Fossey Gorilla Fund International, 2016). Analysis of a population that only considers the behavioural mean may overlook an important beneficial adaptation, if that adaptation is only exhibited by a few individuals, i.e. the early stages of the adaptation's proliferation.

The importance of the individual, in terms of adapting to environmental change, highlights the benefit of incorporating individual variation within the study of species' response to climate change. Among 50 questions selected for their importance and relevance to conservation issues by a team of 85 experts in wildlife conservation and animal behaviour, six questions related to behavioural traits (Greggor et al, 2016).

When assessing animal behaviour, the "rule book" is only really a guidebook, due to behavioural plasticity, which in some cases may be extreme. For example, cannibalistic behaviour within hippopotamus *Hippopotamus amphibius* populations (Dorward, 2014); a lioness adopted different oryx *Oryx gazella* calves on multiple occasions, sometimes allowing the antelope mothers to nurse the calves (BBC News, 2002; The

Guardian, 2002); a lone female wild dog *Lycaon pictus* regularly associated with both spotted hyenas *Crocuta crocuta* and black backed jackals *Canis mesomelas* and regurgitated food for jackal pups (National Geographic, 2013); an estimated 49 white rhino *Ceratotherium simum* were killed in Pilanesberg National Park, South Africa, by young male elephants *Loxodonta africana* experiencing musth under abnormal conditions (Slotow & van Dyk, 2001). The will of subordinates in African wild dog society can override that of dominant dogs, if the subordinates achieve a consensus when they "vote" (by sneezing) on when to hunt (Walker et al., 2017).

These examples challenge our perception of species behaviour. Whilst these examples may be anecdotal, that simply reflects ecologists focus on mean behaviour; it does not mean they should be discounted; indeed, they provide an insight into the extent of behavioural plasticity. These examples demonstrate the need to consider the full extent of variation in behaviour and social organisation when researching species, particularly when assessing the impacts of climate change on species. Predictions of species response to climate change, based on (current) typical species behaviour, may produce results that are limited and inaccurate.

1.7 Advantages and disadvantages of memory when foraging

Memory use provides numerous benefits to animals including locating grazing patches (Boyer & Walsh, 2010; Bracis et al., 2015) and waterholes (Polansky et al., 2015), avoiding areas that were recently sampled (Van Moorter et al., 2009), avoiding difficult terrain (Fagan et al, 2013) and facilitating migratory behaviour (Bracis & Mueller, 2017). Spatial memory facilitates more efficient foraging through reduced search time and therefore reduced walking distance and energy expenditure, reduced residence time at a grazing patch and increased energy intake rate (Laca, 1998; Brooks & Harris, 2008). As resources decline, memory may guide animals to those areas still providing good grazing. These attributes offer the further benefit of reduced exposure time to elevated temperatures under climate change. Note that Boyer & Walsh (2010) suggested optimal foraging efficiency derives from a combination of memory use and random movement. An element of random foraging prevents over-reliance on the same patches (Merkle et al, 2016), which to some extent may reduce over-grazing.

There are also disadvantages to memory use. Memory use and maintenance is energetically costly (Dukas, 1999). Memory use could facilitate an ecological trap (Schlaepfer et al, 2002), if over-reliance on memory prevents an individual updating its spatial knowledge in a changing environment (Boyer & Walsh, 2010). For example, spatial memory may prompt an animal to move to a previously sampled patch because it (incorrectly) assumes the patch is still of good quality grazing.

Cognitive flexibility is the ability to learn and respond to new information, typically tested using reversal learning: an animal learns an association, e.g. location A yields a reward, location B does not, and then the association is reversed (Tello-Ramos et al., 2019). Cognitive flexibility varies between and within species and experimental evidence suggests it is negatively correlated with memory retention (Tello-Ramos et al., 2019). Therefore animals that make extensive use of memory *may* exhibit behavioural inflexibility in changing environments and suffer reduced fitness or survival.

However, binary, mutually exclusive choice experiments such as reversal learning are poor representations of actual behaviour (Stephens, 2008). Many types of behaviour are not mutually exclusive, but rather foreground-background, e.g. whist foraging patch A, patch B is still a (background) option that can be foraged at any time (Stephens, 2008). Individuals that made apparently rash, inefficient decisions in binary, mutually exclusive choice experiments, performed better in experiments that incorporated a more realistic representation of foraging behaviour (Stephens, 2008).

Animals are able to remember not only the location but also the relative value of resources, enabling efficient foraging through selection of the most profitable grazing patches (Fagan et al, 2013; Merkle et al., 2014; Soldati et al., 2017). In the case of red-footed tortoises *Chelonoidis carbonaria*, this spatial/attribute memory was accurate for at least 18 months (Soldati et al., 2017). This combination of memory retention and selective use of memory demonstrates cognitive flexibility (e.g. recently acquired grazing information may be preferred over less profitable older information), contradicting the negative correlation between cognitive flexibility and memory retention suggested by Tello-Ramos et al. (2019).

1.8 Benefits and limitations of agent-based models for conservation

An ABM is a computer simulation based around an individual (Stillman et al, 2015) and, from an ecological or conservation perspective, is typically designed to simulate how the agent (i.e. the individual) behaves, moves and interacts with other agents and its environment, across time and space. Generally an ABM will incorporate many agents and each agent can be given different attributes e.g. bold or timid, exploratory or non-exploratory, aggressive or submissive, and rules which govern its behaviour and interactions. Through the use of this bottom-up approach (i.e. focused on the individual), differences in behaviour and attributes between individuals lead to population level effects (Stillman et al, 2015) and are fundamental to the ability of ABMs to simulate complex systems (Cartwright et al, 2016). At the same time, the bottom-up approach represents an advantage when explaining results and methodologies to stakeholders. It may be easier for stakeholders to understand the behaviour and properties of individuals than of populations (Cartwright et al, 2016) and therefore also to understand the results or predictions of the model (Stillman et al, 2016).

Agent-based models (also known as individual-based models - Grimm et al, 2010; Wood et al, 2015) represent useful, flexible, analytical tools which have been used to simulate a range of ecological subjects. These include migration (Bennett & Tang, 2006; Bracis & Mueller, 2017), dynamics of marginal populations (Vale et al, 2014), dispersal across heterogeneous landscapes (Revilla et al 2004; Gilroy & Lockwood, 2016), responses of species to changes in habitat and competition (Wood et al, 2021), and animal cognition (van der Vaart and Verbrugge, 2008).

As these examples indicate, ABMs may cover different conservation issues at a range of spatial and temporal scales, e.g. assessing fine-scale foraging behaviour, determining home ranges at a coarser scale, or simulating migratory behaviour which may be at regional or continental scales (Malishev & Kramer-Schadt, 2021). It is worth noting that agents' energy requirements will vary across these scales, e.g. individuals foraging locally will require less energy than those undertaking long-distance migrations (Bauer

& Klaassen, 2013; Enstipp et al, 2016). However, energy acquisition is often neglected in models (see Section 2.2.1).

Animals' awareness of their environment and our ability to predict their behaviour also varies with scale (Brooks & Harris, 2008). For example, within its home range an individual may have a good knowledge of available resources (Fagan et al, 2013; Merkle et al, 2016), and from a modelling point of view, variation in vegetation, land use and climate may be relatively limited at this scale. In contrast, broad-scale models (e.g. regional or continental) need to incorporate the greater levels of variation typically evident within these three factors within the target area. Consequently, broad -scale models also need to incorporate the additive and relative effects of these three factors and how they interact (Graham et al, 2019). An example of the contrast between the complexity levels present at different scales would be modelling the dynamics of a single population in one PA, compared with modelling a metapopulation of numerous populations across a country or countries.

Key advantages of ABMs are their ability to simulate the following: individual variation in behaviour and ability; interactions within and between species; interactions between agents and their environment; dispersal ability (Bennett & Tang, 2006). These aspects are important in terms of ecological responses to climate change (Cahill et al, 2012).

Successful, yet unexpected and counter-intuitive behaviour has been identified by ABMs. For example, apparently overly cautious grazers in a predator-prey model were less efficient foragers, but lived longer (van der Vaart and Verbrugge, 2008). By taking an holistic approach to complex systems, ABMs can reveal emergent system properties, i.e. the system is more complex than the sum of its components.
By incorporating actual landscape features, for example as GIS layers (i.e. Oloo & Wallentin, 2017), ABMs can simulate a range of responses by agents to actual environmental cues and assess whether areas of favourable habitat are actually accessible to the target species. Behavioural responses to environmental variation can be identified at different scales (e.g. moving from a low resource area to a nearby high resource area, or migrating between winter and summer ranges). Simulations of

management interventions can inform an adaptive management approach to conservation, by indicating possible results of the interventions.

Another advantage of ABMs is their capacity to include a range of sensory and cognitive abilities for agents; this mitigates the discrepancy between our theoretical assessment of adaptive behaviour and the adaptive behaviour that can actually be achieved by an individual (Jordan & Ryan, 2015; this discrepancy is discussed further in Section 2.2). Furthermore, ABMs could provide a more flexible and realistic insight into animal behaviour.

Agent-based models can offer flexibility through incorporating other methodologies such as dynamic energy budget theory (Chimienti et al, 2020) or aspects of machine learning (DeAngelis & Diaz, 2019) - examples are discussed in Section 2.2.1. Agent-based models that incorporate machine learning techniques (such as artificial neural networks or genetic algorithms) can simulate greater levels of behavioural variation (DeAngelis & Diaz, 2019). For example, genetic algorithms allow individuals to learn and adapt from their experiences, resulting in a population of individuals that make different decisions and exhibit different behaviour (DeAngelis & Diaz, 2019), due to their individual experiences and circumstances, as opposed to individuals exhibiting rules-based decisions and behaviour imposed by the modeller. The results may more accurately reflect the populations being modelled, although the model is still subject to assumptions by the modeller, which may affect model accuracy (in this respect see Section 2.2.1, regarding Morales et al, 2005).

However, ABMs do have disadvantages. Despite the previous comment that stakeholders may find it easy to understand the basic principles, attempts to go beyond basic principles and explain the complexity inherent within ABMs may be incomprehensible to stakeholders, due to insufficient knowledge of computer modelling. This could have implications for stakeholder acceptance and the model's credibility (Cartwright et al, 2016). Development of ABMs require a steep learning curve or experience in programming (Wood et al, 2015). Likewise, understanding other researcher's models is also difficult and time-consuming, even for experienced programmers, which represents a challenge for making models transferable. There may be a tendency to strive for perfection in a model that is already adequate (Cartwright et al, 2016). Furthermore, ABMs that contain errors can produce reasonable but erroneous results, leading to invalid conclusions, with the errors remaining unidentified.

ABMs are typically data intensive and time-consuming in terms of their development and run time (Cuddington et al., 2013). Prior to refinements, the model developed for this research (called MARSC - Modelling the Adaptive Response of Species under Climate change) would have taken 130 days (running 24 hours/day) for a run size of 10,000. In their review of different model types, Cuddington et al. (2013) assert that ABMs lack transparency; but key information such as parameters and assumptions can simply be provided, for example by following the ODD protocol (Overview, Design concepts and Details - Grimm et al, 2010). Cuddington et al (2013) suggest process-based models are superior to simulations, statistical and rule-based models, due to their transparency and ease of interpretation; however, the authors blur the distinction between process-based models and simulations and acknowledge that simulations can actually be process-based.

1.8.1 A brief overview of two alternative ecological ABMs

There are existing ABMs which assess broadly similar ecological aspects to MARSC, e.g. RangeShifter (Bocedi et al, 2014; Bocedi et al, 2021) and SEARCH (Spatially Explicit Animal Response to Composition of Habitat - Pauli et al, 2013), both of which incorporate user-defined parameters. Note that other ABMs which simulate the behaviour of similar species to MARSC are discussed in Section 2.2.1.

RangeShifter facilitates modelling of how species and populations respond to environmental change or management interventions, for example through range expansion or shifting, and changes in population dynamics (Bocedi et al, 2014; Bocedi et al, 2021). RangeShifter incorporates a cost analysis approach to agents’ movement across a landscape (e.g. urban landscapes would have a higher movement cost than woodland or grassland) (Bocedi et al, 2014). The model includes the option to subject ecological processes to density dependence, with the density dependence acting at two possible levels: either on individual cells or on patches of cells (Bocedi et al, 2014). Key aspects of the model relate to dispersal behaviour, habitat connectivity and land-use, while a new version (RangeShifter 2.0) can incorporate temporally changing landscapes (i.e. the landscape can be altered during the simulation) and genetic adaptation to control dispersal behaviour (Bocedi et al, 2021).

However, the model does not incorporate foraging behaviour or energy acquisition and agents do not possess any spatial memory (Bocedi et al, 2014; Bocedi et al, 2021). In addition, the model does not establish functional relationships between population and dispersal parameters and climate variables, thus inhibiting simulations of population responses to climate change (Bocedi et al, 2020).

SEARCH models the dispersal behaviour of juvenile individuals seeking to establish a home range within actual or theoretical landscapes, which have adult resident conspecifics with established home ranges (Pauli et al, 2013). Offspring of adult females become the dispersing juveniles in the next cycle (Pauli et al, 2013). SEARCH highlights dispersal patterns and population-level responses that emerge from the movement of individual animals. User-supplied GIS layers allow agents to build a memory of habitat characteristics encountered, including whether the habitat is occupied (Pauli et al, 2013). A useful feature of the model is the ability to output GIS shape files reflecting agents’ movements, spatial memory and their home range (Pauli et al, 2013).

However, there are limitations. The size and location of home ranges are fixed, regardless of changes in habitat or the population, and females’ litter size does not reflect the condition of individual females or habitat quality, but are randomly selected from a distribution based on a user-defined mean litter size (Pauli et al, 2013). Ecological processes are not density dependent - the carrying capacity of the target location is not considered (Pauli et al, 2013). Unlike MARSC, there is no direct conversion between actual food items and actual energy input: instead, energy levels (which have no units) are based on the size of food items (which have no units) randomly selected from a distribution of size classes (Pauli et al, 2013).

1.9 Alternative modelling approaches

Alternative modelling approaches to ABMs - such as Species Distribution Models (SDMs) and Environmental Niche Models (ENMs) - typically relate correlations of population or species occurrences with environmental attributes (Peterson & Soberón, 2012). Whilst SDMs and ENMs are similar in their approach, they differ in that the former is focussed on the realised niche and the latter is focussed on the fundamental niche (Peterson & Soberón, 2012). Given this distinction, much of the following text focuses on SDMs, however both ENMs and SDMs are discussed with regard to recent hybrid models.

Species distribution models have been widely used to identify suitable habitat for species and to predict future distributions. Applications include species response to climate change (Taylor et al., 2017); assessing the distribution of invasive species (Marcantonio et al., 2016); predicting the range expansion of reintroduced species (Smeraldo et al., 2017); assessing the impact of changes in land use (Guisan & Zimmermann, 2000) and conservation planning for migratory species (Singh & Milner-Gulland, 2010).

Although SDMs have been important in understanding and predicting species distributions, they have limitations. Traditional SDMs focus on environmental suitability but exclude relevant factors such as biotic interactions, species life histories, the emergent qualities of biological systems and, perhaps of most concern, dispersal abilities (VanDerWal et al, 2009; Sinclair et al., 2010; Araújo & Petersen, 2012). Predictions which discount dispersal ability and simply assume species can migrate to more suitable areas could overestimate the ability of species to mitigate the impact of climate change. The assumption that predicted areas of suitable habitat are accessible to the target species may not be valid (Araújo & Petersen, 2012; Mestre et al., 2017). SDMs assume that the species is in equilibrium with its environment (Guisan & Zimmermann, 2000), which is unlikely under climate change. It is argued that predictive (as opposed to descriptive) model accuracy should be tested on independent data (Houlahan et al., 2017); though for logistical and financial reasons this frequently does not happen. However, if the independent data is obtained from a different location, there may not be continuity of model accuracy between the data sets. In other words, a model developed for area A may not be applicable to area B (Osborne & Suárez-Seoane, 2002).

Manel et al (2001) found that many model evaluations were “inherently misleading” and may overestimate the true occurrence of rare species - which is of particular concern for conservation. Likewise, models tend to over-predict the distribution of species with limited ranges and under-predict the distribution of widespread species (Márcia Barbosa et al., 2013). VanDerWal et al (2009) concluded that SDMs were more suited to predicting the upper limit of abundance, rather than mean abundance, due to the omission of key factors.

Predictions of SDMs typically define distinct distribution borders; this assumption - that species’ distributions are precisely constrained by the predictor variables - is questionable (Pearson & Dawson, 2003). Broad, continental-scale SDMs with coarse resolution lack accuracy regarding marginal populations (Pearson & Dawson, 2003; Araújo and Rahbek, 2006; Vale et al, 2014). Yet marginal populations, for which SDMs are least able to provide accurate predictions of future distributions, may be critical for a species’ survival (Calkins et al, 2012). These points may explain why a review of 116 SDMs found that 90% of the models showed marked differences between predicted and actual ranges of species (Araújo & Rahbek, 2006).

More recently, hybrid models have been developed that address some of these points, with noteworthy results. For example, Bush et al (2016) incorporated dispersal ability and local variation in the maximum temperature tolerance threshold of Australian fruit flies *Drosophilidae* within an SDM, which reduced the projected range loss by 33% by 2105. Similarly, incorporating local adaptation within an ENM reduced the projected range loss for two forest bat species, whilst increasing the projected range overlap for the species, suggesting increased interspecific competition (Razgour et al, 2019).

Incorporating phylogeography (the study of the spatial distribution of species lineages (Elith & Leathwick, 2009)) within correlative models is an interesting alternative for considering local adaptation. Different lineages (e.g. subspecies) may experience different climates (D'Amen et al, 2013), resulting in local adaptation. D'Amen et al (2013) developed ENMs for nine African mammal species (comprising 32 subspecies or geographically distinct distributions) that projected the shift of currently suitable, occupied climates for the 32 different lineages, under two future climate scenarios.

Results were compared with species-level ENM's which did not include phylogeography. The predicted percentage of the current geographic ranges that were climatically suitable by 2080, using the lineage-based ENMs, was approximately half that predicted by the species-level ENMs (D'Amen et al, 2013). When considering only the protected range (i.e. PAs), the percentage predicted by the lineage-based ENMs was only a third of that predicted by the species level ENMs (D'Amen et al, 2013). In practical terms, species-level models may (erroneously) identify PA's that remain suitable for a species under climate change (based on species-level predictors), but the PA's may be unsuitable for the species' lineages that actually live within them (D'Amen et al, 2013).

For all these reasons, basic (i.e. non-hybrid) SDMs and ENMs do not incorporate the level of complexity required for accurate predictions of how populations and species will be affected by, and respond to, climate change.

1.10 The benefits of an area-specific, small-scale case study

The fine-scale, area-specific (hereafter "area-specific" explicitly incorporates the term "fine-scale" - in other words, closely tailored to a specific location) approach has advantages and disadvantages, which need to be considered. However, I will argue that a fundamental disadvantage of area-specific models does not apply to the Mokala model, due to its design and intended purpose. I will further argue that in this instance, compared with a broader multi-site research approach, the area-specific approach is more efficient and removes confounding aspects. Threats to species such as climate change are not constant across the species range (Scheele et al., 2017) - local environmental conditions result in local adaptations (Savolainen et al. 2013).

By omitting influential local detail such as ecosystem dynamics and biotic interactions (Pearson & Dawson; 2003; Sinclair et al, 2010), broad, coarse-scale models may overestimate or underestimate both the future distributions of species (Sinclair et al, 2010) and the effectiveness of protected areas (Velazco et al, 2020). The size of the error (e.g. the difference between the predicted distribution and the actual distribution) reduces with the extent of the study area (Velazco et al, 2020). A key advantage of the area-specific ABM is that it incorporates high levels of detail on species behaviour, variation in behaviour, and also high-resolution spatial data, all specific to Mokala (see Section 2.3). Therefore the models will be more accurate representations of Mokala and the antelope community than broad, coarse-scale models.

A likely problem with area-specific models is that of overfitting (to the target area), i.e. the models would not be transferable to other scenarios (Araújo et al., 2005; Huang & Frimpong, 2016) and as such, they are limited in their benefit to the broader conservation community. Whilst this criticism was specifically aimed at correlative models, it is reasonable to assume that any type of model that has been “overfitted” to a specific location would not represent the ecology of a different location. I would argue that whether overfitting is a problem depends on the context. If the intention is to predict survey areas for the presence of an endangered species beyond its known range, then overfitting the predictive model to the known range would be ill-advised. However, if the intention is to assess the response of species to climate change, then expecting that the modelled response of species at location A will also apply at location B is I believe unreasonable, based on the following points.

Although numerous SDMs have been found to be transferable and this is generally considered advantageous, various SDMs have exhibited poor transferability, e.g. Barbosa et al. (2009) - models for Spain showed good predictive power when transferred to Portugal, however models for Portugal were poor predictors when transferred to Spain; Murray et al. (2011) - models were transferable at local scale but were poor predictors at landscape scale; Gies et al (2015) - model transferability was low between two adjacent watersheds in Germany; Roach et al (2017) - poor model transferability was evident between two US states having similar habitat, climate and species. Roach et al. (2017) suggests that effective conservation may require area-specific models.

It can be further argued that extrapolation of species behaviour between sites is unrealistic (despite the fact that this approach is often used) because behaviour is locally adapted. Whilst translocation programs have met with varying success, various translocated populations that persisted have adopted similar behaviour to resident conspecific populations, e.g. Warren et al (1996) - caribou; Richard-Hansen et al (2000) - howler monkey *Alouatta seniculus*; Pinter-Wollman et al (2009) - African elephant; Scillitani et al (2012) - Alpine ibex *Capra ibex;* Weise et al (2015) - leopard *Panthera pardus*). To further confound the use of spatial extrapolation, persistent behavioural differences exist among neighbouring chimpanzee *Pan troglodytes* populations, despite the fact that ecological conditions are similar among the populations (Luncz & Boesch, 2014).

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Chapter 2 Simulating a complex ecological system - model development and evaluation

2.1 Abstract

Species exhibit behavioural variation among individuals which can facilitate adaptation to climate change. Investigation of behavioural variation can inform conservation initiatives; yet research has typically ignored variation in favour of the behavioural mean. This reductionist approach may also omit other key aspects, i.e. cognitive ability, personality and emergent properties of the system. However, agent-based models (ABMs) can incorporate these aspects to offer a more complete picture of species' adaptive capacity. The aim of this study was to develop an ABM to simulate how antelope species within Mokala National Park, South Africa, may adapt to climate change, through behavioural variation. The ABM simulated key components of herbivore ecology that have been largely ignored by the modelling community (i.e. variation in foraging, sociability and cognitive ability) under current and projected future climate change scenarios. Several emergent properties were identified. Variation in all behavioural traits affected grazers' energy levels for the current and intermediate climate scenarios but this effect was greatly reduced for the worst-case climate change scenario. Although most lone grazers were programmed to be antisocial, some were social grazers that failed to join herds. Antisocial lone grazers acquired higher energy levels than social lone grazers. Herd leaders generally obtained higher energy levels than followers, who generally obtained higher energy levels than lone grazers. However, under the worst-case climate scenario, lone grazers had slightly higher energy levels than herd followers (but not herd leaders). The least water-dependent species had the highest energy levels. The ABM facilitated an holistic analysis of a complex ecological system, identified emergent properties of the system and revealed how behavioural variation impacts the fitness of individuals and populations.

2.2 Introduction

This chapter begins with a brief introduction to set out key issues which represent gaps in our knowledge or contested areas of research, and to explain why these issues matter. These issues provided the focus for development of the agent-based model MARSC, and features were incorporated within the model to allow investigation of these issues. There is also an explanation on the benefits of using antelope as the focal subjects when researching the impact of climate change, and a brief overview of other herbivore-based ABMs. Subsequent sections provide a brief description of Mokala National Park, South Africa and describe MARSC in greater detail. Simulation results are presented and discussed. Note that a brief description of the four antelope species simulated within MARSC is included in the Appendix.

One way animals can mitigate the negative impact of climate change is through changes in behaviour. Species exhibit a high degree of behavioural variation among individuals, which can facilitate adaptation to climate change (Wolf & Weissing, 2012; Sih, 2013; Merrick & Koprowski, 2017). However, adaptation represents a scale: while the responses of some individuals may mean they thrive in changed environments, the response of others may be maladaptive (Sih, 2013). Furthermore, animals' perception of threats and other cues may be imperfect (Wolf & Weissing, 2012; Sih, 2013; Jordan & Ryan, 2015; Keith & Bull, 2017). Conspecifics may exhibit adaptive or maladaptive responses to novel situations, based on their experiences (Sih, 2013). Therefore, behaviour that may appear maladaptive, may actually be the optimal response given an individual's sensory and cognitive limitations (Sih, 2013; Jordan & Ryan, 2015).

The issue of imperfect perception is particularly relevant as species are exposed to environmental change due to climate change. In addition, animals may not have the capacity to consider the costs and benefits of all possible behavioural responses to changing environments (Jordan & Ryan, 2015). Therefore, when assessing possible responses to climate change, it is important to consider a broad range of behaviour (Greives & Bowden, 2019) and look beyond 'the tyranny of the Golden Mean' (Bennett, 1987), i.e. consider additional metrics rather than just one measure of central tendency when assessing data (see Section 2.3.5).

Since we cannot know how well animals will perceive threats derived from climate change (Sih, 2013), perception not only constrains animal behaviour, but also our ability to predict the responses of species and individuals to climate change. Consideration of a wide range of behaviour should also reduce the impact of the disparity between human and animal perception of climate change-derived threats.

However, our understanding of the role of behavioural plasticity in mitigating climate change is still emerging (Beever et al, 2017). In addition, the impact of climate change on mammals within PAs - particularly in Africa - has been neglected by the modelling community (Sieck et al, 2011; Okayasu et al, 2019). It is clear there is a pressing need to fill these gaps in our knowledge.

Antelope represent a useful group for the study of behavioural variation as they exhibit wide variation in behaviour (e.g. sedentary/migratory populations, territorial/lekking reproductive strategies, and hider/follower strategies among calves) and social organisation (Estes, 2014). Their social organisation typically comprises territorial males, bachelor groups, and groups of females with young (Estes, 1992). However, amongst migratory populations during the migratory phase, all these groups will travel together and the only associations that are maintained are between mothers and their young (Estes, 1992). At other times, the groups of females are based on dominance hierarchies and described by Estes (1992) as “semiclosed”, meaning that groups will often (initially) reject newcomers, who therefore remain solitary, at least temporarily, but on occasion outsiders may be accepted (Estes, 1992).

This makes antelope a realistic model system when investigating the extent to which behavioural variation may offer mitigation against climate change. The focal species are savanna antelope. Savannas are already subject to spatial and temporal variation in rainfall, furthermore rainfall is unpredictable (Owen-Smith et al, 2020). These factors drive the spatiotemporal variation in vegetation and available surface water (Owen-Smith et al, 2020). Antelope have had to adapt to these conditions - again making them a realistic subject.

Antelope represent a key, intermediate trophic level within food webs and are often the dominant group within large herbivore communities (Bro-Jørgensen, 2016). As herbivores they influence, and are influenced by, the plant community; as prey they influence, and are influenced by, the predator community (Bro-Jørgensen, 2016). For antelope the outlook under climate change is bleak: a reduction in climatically suitable habitat is forecast for 59 of the 72 African antelope species by 2080; for 19 of the 59 species the predicted reduction is greater than 50% (Payne & Bro-Jørgensen, 2016). Any negative impact on antelope biodiversity will have far-reaching effects given their role in seed dispersal, nutrient cycling and shaping habitat (Bro-Jørgensen, 2016).

Very little empirical research exists on fitness differences between herd members and lone grazers; where available, the research typically compares gender differences, i.e. territorial males and female herds. In a comparison of a lone male, a male and female pair and a group of one male with three females, Seri et al (2018) found no difference in diet or time spent grazing or moving, between these three groups of addax antelope *Addax nasomaculatus*. Abaigar et al (2019) reported different activity patterns for a lone female mhorr gazelle *Nanger dama mhorr* compared with conspecifics, but this was under abnormal circumstances.

Similarly, our understanding of the costs and benefits of herd leadership is limited (Strandburg-Peshkin et al, 2018). However, it seems reasonable to assume that leaders may benefit from increased fitness over followers (Smith et al, 2016). Leaders had higher fitness levels than both followers and lone grazers in a model developed by Patin et al. (2019).

The aim of this study was to evaluate the potential of a fine-scale, area-specific, agent-based model to assess how variation in behaviour and social organisation among an antelope community in Mokala National Park may mitigate the impact of climate change. The antelope species are blue wildebeest *Connochaetes taurinus*, black wildebeest *Connochaetes gnou*, tsessebe (also known as topi) *Damaliscus lunatus* and red hartebeest *Alcelaphus buselaphus.* The model served as a proof of concept of modelling a complex system, in order to explore the effectiveness of management interventions in Chapters 3 and 4. However, the model was exploratory in its own right and revealed interesting insights which were developed further in the subsequent chapters.

To meet the aim, this study involved three key objectives. First, to confirm that individuals varied in energy levels across the climate scenarios and behavioural types as a basic validation of the model. Second, to assess how variation in behaviour and social organisation within the antelope populations contributes to their adaptive capacity, and how this capacity responds to different climate change scenarios. Third, to determine the presence of selection pressures on behavioural types and social groups (e.g. lone grazers, herd leaders and followers). Objectives two and three provided further validation of the model but also highlighted interesting and unexpected results which were explored in Chapters 3 and 4 (e.g. comparisons between the social groups – Section 2.4.5 and the sociability of lone grazers – Section 2.4.6).

2.2.1 Other agent-based models of large herbivores

Other agent-based models of large herbivores have been developed, but unlike MARSC, few have incorporated energy intake. Falcón-Cortés et al (2021) compared the effect of different memory classes on the foraging behaviour of elk *Cervus canadensis*. However, the model was based on occupancy, derived from GPS location data; there was no analysis of energy intake, and they did not include random foraging. Furthermore, they incorporated different habitat types into a single habitat class that was deemed suitable for elk, and discounted patches that were smaller than 0.27 hectares. Ranc et al (2021) developed a model which demonstrated the importance of memory-based foraging among roe deer *Capreolus capreolus*, but also did not incorporate energy acquisition.

Chimienti et al (2020) incorporated dynamic energy budget theory into an individual-based model, to assess how the activity budget affected the survival of musk ox *Ovibos moschatus*. The model did not calculate energy intake directly, but used a single average value of snow depth across the study area as a proxy for food availability and energy assimilation (Chimienti et al, 2020). Semeniuk et al (2012) assessed the strategy used by caribou when selecting their winter habitat within an industrialised landscape. Their model incorporated energy intake, but each class of habitat (e.g. conifer forest, deciduous forest, shrub) was given a single value representing energy intake per foraging bout. In other words, they did not allow for variation in productivity within each habitat class. Merkle et al (2016) developed an agent-based model to assess the benefit of memory-based foraging among bison, based on energy intake per distance travelled. Although their model did not assess future scenarios under climate change.

Rather than the rules-based behaviour often used within ABMs, Morales et al (2005) incorporated artificial neural networks that were further refined by a genetic algorithm to simulate decision-making by elk. Although the simulated elk frequently returned to areas that had been previously visited (which is also evident within actual elk populations), there was “considerably less” movement exhibited by the simulated elk compared with actual elk (Morales et al, 2005). This could be down to an overestimation of available resources (Morales et al, 2005) and the fact that vegetation regrowth occurred at the end of each day within the model. The reduced movement by the simulated elk could also be due to limited variation in vegetation within the model (i.e. there is less need to explore a landscape that is relatively homogenous, when foraging). The simulated landscape comprised just one generic type of grass with a fixed energy value per unit of mass, and each individual plant was assigned to one of three different size classes (Morales et al, 2005).

2.3 Methods

2.3.1 Mokala National Park

The MARSC model was based specifically on Mokala National Park, which is located centrally within South Africa, in the Northern Cape province approximately 80 km south-west of Kimberley. Mokala provides unique habitat types not represented in any other national parks within South Africa (Bezuidenhout et al., 2015). The newest National Park in South Africa (gazetted in 2007), Mokala straddles the Savanna and the

Nama-Karoo Biomes, as such the park provides the only designated protection for this ecotone (Bezuidenhout et al, 2015). However, it is predicted that increased temperatures due to climate change will result in Mokala tending towards arid savanna in the future (Mokala National Park, 2017).

Currently the park size covers 32,445 hectares, of which 28,548 hectares have been declared and 3,897 hectares are in the process of being declared (Mokala National Park, 2017). The park has an ongoing expansion programme, in part due to its “inefficient shape” (Mokala National Park, 2017); by 2027 the intention is to add a further 25,000 hectares, which to some extent will address the shape issue, and the ultimate aim is for Mokala to have a footprint of about 140,000 hectares (Mokala National Park, 2017). Topographically, the south-central and southern areas of the park comprise rolling hills, contrasting with the open plains of the west, north and north-east (Mokala National Park, 2017; see Appendix Fig 1).

Professor Owen-Smith (Wits University, S. Africa; pers. comm.) suggested researching the antelope species but pointed out there were few locations where they were all present. However, all these species are present in Mokala National Park; Dr Ferreira (SANparks) also recommended researching these species in Mokala (pers comm). Currently there are no large carnivores within the park although their reintroduction is expected in the future (Mokala National Park, 2017). Since an objective of this study is to assess the impact of climate change and management interventions on social cohesion among antelope populations, these species represent a good choice to study as they encompass a range of social organisation that is flexible and responsive to environmental change (Estes, 1992).

2.3.2 Data collection

Data collection was carried out in Mokala between 13-3-18 and 10-5-18 in order to aid parameterisation and validation of MARSC. Behavioural observations were made from a vehicle, either with or (more frequently) without binoculars - the majority of animals appeared relatively habituated to vehicles. Furthermore, observations were delayed for several minutes with the vehicle stationary and the engine stopped to minimise possible disturbance to the animals.

Focal sampling comprised 10 minutes of recording an individual’s behaviour based on the following behavioural types: vigilant, resting, grazing, ruminating, standing, moving, flight, not visible, other (i.e. none of the previous types) (see Appendix - Table 1). Data on some of these behavioural types that were fundamental to the simulation are compared with alternative sources in Table 2.9. The following additional information was also recorded: date, time, GPS co-ordinates, group size (and whether this value was estimated or actual), weather description, group description (e.g. mixed species, whether calves were present), brief description of habitat, and additional notes (e.g. whether other species were nearby, or if a vehicle approached, which might illicit a vigilant response from the target individual). A total of 165 behavioural observations were recorded, broken down by species as: blue wildebeest - 40, black wildebeest - 41, hartebeest - 40, topi - 44.

In addition to informing parameterisation of MARSC, data collection also provided a valuable insight of Mokala, in terms of the habitat heterogeneity and additional details on the target species, which was useful when developing MARSC. For example, black wildebeest range across the north and west of the park, but avoid the central area (pers. obs., pers. comm., see Section 2.5.1). Nonetheless, one black wildebeest was observed several times in the central area of the park; in effect it appeared to have established a territory in this atypical habitat. Furthermore, many large (predominantly) plains species, including the target species, forage among supposedly unsuitable habitat - the park’s rocky outcrops (pers. obs., pers. comm.), providing further evidence of the broad range of behavioural variation among species.

2.3.3 The MARSC agent-based model - ODD protocol

The following model description is framed within the ODD protocol (Grimm et al, 2010; Grimm et al, 2020). The MARSC model was written in the Java programming language (Java 8 -http:// java.sun. com), within the IntelliJ IDEA agent-based modelling framework (https://www.jetbrains. com/idea/). The use of Java was based on experience of developing a model previously in this language and because as an object-orientated programming language, Java lends itself to agent-based modelling. Key components and outputs of MARSC are shown in Fig 2 of the Appendix.

1. Purpose

The overarching aim of the model was to adopt a complex systems perspective to explore facets of animal personalities (i.e. the range of behavioural variation) which have previously been ignored, but which may influence the survival of individuals and populations.

The MARSC model simulates variation in behaviour, social organisation and interactions with conspecifics within a community of antelope species within Mokala National Park, South Africa, to investigate how this variation may mitigate the negative impact of climate change on this community. Agents move across the Mokala landscape, gaining knowledge of the location of resources (grazing patches and waterholes) and making use of those resources, and responding to environmental and internal physiological cues and to conspecifics. The model used parameters gleaned from relevant literature where possible, field observations or else arbitrary parameters. Agents’ energy levels were used to compare variation in behaviour, cognitive ability and social organisation, and the effect of different environmental scenarios and differences between the species. By converting the Enhanced Vegetation Index (EVI) to energy intake (see Appendix, Box 1) at high resolution, incorporating variation across a range of behavioural traits and considering variation within groups (i.e. the use of three medians - see Section 2.3.5), MARSC provides a means to assess the consequences of agents’ decisions, behaviour and movements in time and space.

2. Entities, state variables and scales

Agents represent the four species of antelope: blue wildebeest, black wildebeest, tsessebe and hartebeest. Agents can travel in any direction and occupy any position within the park. Agents can occupy any position within an individual 10m x 10 m cell (e.g. agents' X and Y coordinates have 14 decimal places) or, in the case of a herd, several agents can occupy a single cell - multiple agents occupying the same cell are superimposed over each other. An advantage of this approach is that it allows a more realistic representation of herds. For example, a grazing herd of 25 individuals would occupy 25 cells - an area of 50 m x 50 m (a square formation of 5 cells x 5 cells) if each cell could only accommodate one agent. Yet in reality 25 individuals could occupy a much smaller area when grazing (pers. obs.) of perhaps four or five cells. The quality of grazing (and therefore energy intake levels) may vary considerably more across 25 cells than four cells. In addition, if the model were restricted to one agent per cell, any prolonged grazing may result in the herd becoming dispersed across a much wider area as agents could only graze in unoccupied cells.

Agents' key variables are listed in the Appendix (Tables 2 and 3). Agents could be lone grazers or form herds - which effectively act as a unit comprising a leader and followers, with behaviour and movement controlled by the herd leader.

The park landscape is an entity that varies across the EVI scenarios. The park landscape was developed in ArcGIS Desktop version 10.6.1 (www.arcgis.com) as a 2876 x 2696 grid of cells (each 10 m x 10 m) which was accessed by MARSC. The GIS map displayed within MARSC as a 1087 x 1019 grid of cells of approximately 26.5 m x 26.5 m, therefore X,Y coordinates within MARSC were multiplied by a factor of 2.64573 to convert to the actual GIS map locations when obtaining EVI values.

Cells represent vegetation productivity (EVI) or waterholes or the park boundary. EVI values were converted to agents' energy intake values using the formula described in Box 1 (see Appendix). To my knowledge, MARSC is the only application to provide this functionality. There is a fundamental need to understand the extent to which individuals acquire resources (Chimienti et al, 2020). Without this information, models that inform on other aspects are less useful for applied conservation. For example, a model may predict a range shift for a population under climate change. However, without information on energy acquisition, it may be the case that no individuals can acquire sufficient energy to actually survive within the new range.

The environmental scenarios were: current scenario (2018); an intermediate future scenario (current EVI values reduced by 30%); a worst-case future scenario (current EVI values reduced by 60%). The EVI-30% level was used because 30% was the highest deviation recorded during Jan 2012 - Mar 2015 from a long-term mean for Mokala (Feb 2000 - Mar 2015) (Smit & Simms, 2015). The EVI-60% level was selected as an arbitrary extreme future scenario, representing twice the reduction of the intermediate scenario. The full simulation included nine maps – the three environmental scenarios with each scenario comprising three maps representing March, April and May (these months represent the period of fieldwork). Simulations were run for current EVI conditions and EVI-30% and EVI-60% (representing future scenarios).

Spatial memory

Grazers have two long-term memories: one for grazing patches, one for waterholes, and also a short-term memory which directs grazing behaviour. Note: the short-term memory exists only for programming purposes. Long-term memory has been reported in various species such as prairie voles *Microtus ochrogaster* (Paz-Y-Miño C. et al., 2002), elephants (Hart et al., 2008), parasitic wasps (Smid et al., 2007) and numerous primate species (Trapanese et al., 2019). Some species are able to remember not only the location but also the relative value of resources for at least 18 months (Soldati et al., 2017). Cattle avoid poor foraging areas for 21 consecutive days, opting instead for areas of better forage, suggesting discriminatory memory use (Bailey, 1995).

Grazers' long-term memories contain only unique records. Grazers can only access their grazing memory from day ten of the simulation period and if the memory contains more than nine records; this reflects the fact that animals in a novel habitat will initially have no spatial memory of available resources. Thereafter, grazers' foraging is based on their personality, e.g. risk-averse individuals use their memory to return to known resources, whereas risk-takers are more exploratory. When using memory, the choice of grazing patch to use is based on the following formula and grazers select the highest pixscore that does not entail crossing the park fence:

$$pixscore = pixcount * \frac{1}{dist}$$

where pixcount = the number of suitable pixels at a patch, and dist = distance to the patch from the grazer’s current location. Details of the variables contained within the memories are listed in Table 3 of the Appendix.

Simulations included four grazing memory strategies: no memory - foraging is random; basic memory - grazers make use of all memory records, and two smart memory options: “smart03” and “smart06” - grazers consider only records with a pixscore above 0.03 and above 0.06 respectively. The ‘smart’ memory options represent a cost/benefit approach with animals filtering memory records based on their relative value (Soldati et al., 2017), i.e. distance to resource compared with the quality and quantity of the resource. The no memory grazers can be thought of as animals that are in unfamiliar territory (i.e. if a population were regularly moving due to tracking climate change).

Grazers were assigned a “memory distance” value of either 500 m or 3 km - a grazer with a memory distance of 500 m would only use memory records that were within 500 m of its current location. This was to differentiate between personality type, i.e. bold, exploratory grazers and timid non-exploratory grazers. Non-exploratory grazers (memory distance = 3 km) would access memory records from a much wider area and therefore were more likely to remain within the same local area – their home range, whereas a memory distance of 500 m would promote more exploratory behaviour due to the reduced number of available memory records. Exploratory grazers could be considered as nomadic opportunists, roaming the park and only making use of their localised spatial memory if they happen to be in a location they have previously visited.

3. Process overview and scheduling

The schedule of processes within MARSC is generally as shown in the order listed below and in the MARSC cycle flowchart (see Appendix, Fig 3).

Go to water
Rest
ScanWater
ScanFence
ScanConspecifics
ScanEVI
Move
Forage
Output

The names are those of the submodels which are then described in Section 7 of this ODD protocol. Note that the 'Move' submodel is called 'Move away' in the flowchart, likewise the 'ScanEVI' submodel is called 'Scan local forage'. However, the sequence of processes and submodels varies among lone grazers and between herds, e.g. the timing and duration of trips to waterholes varies (moving to a local waterhole may only require one "move" cycle, whilst a more distant waterhole may take two or more consecutive "move" cycles to reach); if a grazer scans a patch, the next activity could be 'forage' or (if the patch is barren) 'move'.

State variables were updated on an individual basis dependent on the process undertaken, e.g. when foraging, an individual would then update its energy levels, but while resting no state variables would be updated. Some behaviour is context-dependent: e.g. agents do not go to waterholes during night-time, random foragers do not update their grazing memory, whereas memory-based foragers do. The model simulated behaviour over a 30 day period, with each discrete time step (cycle) representing 1 hour, note that "cycle" and "hour" are used interchangeably within this thesis. There were three periods covering March, April and May.

The ScanFence submodel is actually called from several sections of the code (e.g. after drinking and after foraging), although for simplicity ScanFence is only shown once below and in the flowchart. Similarly, the “Move” submodel is also called from several sections of the code (see Appendix, Fig 3).

Herd members and lone agents are processed as two separate groups - herd members first, as lone agents that joined a herd in the previous cycle are transferred to the herd members group. All herd members are updated to match the herd leader in terms of activity, the time to go to water and heading. Within each herd the leader executes an activity first, the order in which the other herd members execute the same activity is the order in which they were created within MARSC. Lone grazers are also processed in the order in which they were created.

The total run size was 1080 runs (324,000 grazer records), broken down as 360 runs for each of the three EVI scenarios. Each EVI scenario comprised 120 runs for each of the three months, made up of 30 runs per memory type (there are four memory types) within each month.

4. Design concepts

Basic principles.

Variation across a broad range of behaviours (i.e. variation in personality) can contribute to the adaptive capacity of individuals, populations and species to mitigate the negative impacts of climate change (Beever et al., 2017). A complex systems approach (the sum of the whole is greater than the sum of the parts) to ecological, climate change and conservation issues can incorporate behavioural variation and highlight important emergent properties of ecosystems, which would not be revealed by a reductionist approach (Ruddell et al., 2016). ABMs can facilitate a complex systems methodology to assess the effectiveness of, and interactions between, behavioural variation and management interventions in mitigating climate change impacts.

Emergence.

Several emergent results were expected due to behavioural variation, rather than being programmed within the model. It was expected that correlations between energy intake and different behavioural traits would vary across different EVI scenarios. In particular, it was assumed that the ‘smart’ memory types would emerge as more efficient foraging strategies as resources declined. Agents were expected to form herds and the size and social structure of herds would vary, i.e. leaders may be bold or timid, followers in a herd may show wide variation in boldness or be mostly bold or mostly timid, leaders may persist or be usurped. Herd leaders should obtain higher energy levels than followers, who should obtain higher energy levels than lone grazers.

Adaptation and objective.

Agents adapt to the vegetative heterogeneity by filtering possible grazing patches (in memory) based on their pixscore - in effect applying a cost/benefit analysis to grazing decisions. The more selective “smart” agents only consider patches that exceed a specific pixscore threshold. When foraging, agents evaluate whether a patch is worth grazing based on the productivity level (EVI value) of each cell within the patch. Exploratory agents filter their spatial memory to access only local grazing patches, if none are available, they forage across a wider area, whereas non-exploratory agents use their spatial memory across a broader area and therefore remain within a familiar home range. Agents adapt to the distribution of waterholes and their spatial location by accessing the nearest waterhole from memory (but see Learning below).

The objective of these adaptations is to maximise their energetic gain. Grazers’ energy levels allow comparison between the different levels of memory use to evaluate whether this adaptation achieves the objective.

Learning.

Agents learn the location (and value, in the case of grazing patches) of resources and can then filter this information when deciding where to graze or drink. Given the shape of the park (Appendix, Fig 1), memory records are further filtered to discount resources where straight-line movement to the resources is not possible, i.e. the path is blocked by the fence. Agents learn the most direct (straight) path for foraging at each patch they graze – avoiding turns.

Prediction.

The implicit prediction in memory use by agents is that resources will be consistent, i.e. an agent predicts that the level of available grazing at a patch will be consistent with the memory record, or that a waterhole will still have water.

Sensing.

Grazers perceive their surrounding environment at two levels, evident within the model as 2 concentric circles. The smaller circle (hereafter “short view circle”) represents the grazers visual perception of available forage and extends to a radius of 4 pixels (106 m). Within this circle the grazer is able to discern different quality of vegetation (EVI value). The larger circle (hereafter “long view circle”) has a radius of 15 pixels (400 m) and represents the grazers wider perception with regard to waterholes and conspecifics and the park boundary. Agents sense their internal energy levels and their social status (herd members).

Interaction.

Lone agents choose to join (if social) or avoid (if antisocial) herds or conspecifics they see. The behaviour of followers replicates the leaders’ behaviour. When moving or grazing, the leader and bolder individuals occupy central positions within the herd, whereas timid individuals occupy the margins (based on the fact that these species form dominance hierarchies within herds - Estes, 1992). All grazers are assigned boldness values on a scale of 1 - 10 (timid - bold), selected from a normal distribution with mean = 5.5 +/- 3 (SD). Followers' positions are offset, relative to the leader's position, the offset (measured in 10m cells) is calculated as:

$$offset = (1/bold\ score) * 2$$

A new herd member will usurp the incumbent leader if the newcomer has a higher boldness score. On detecting the park boundary, agents move away from fence.

Stochasticity.

Across the species the initial location and heading of agents within the park is random, as is their boldness score and sociability. The time at which lone agents and herd leaders visit waterholes is also random. The attribution of memory class and memory distance is also random.

Collectives.

Grazers may form hierarchical herds or remain as solitary grazers. Herd movements and behaviour are directed by the herd leader. Although leaders do exist among social species (Fischhoff et al. 2007; Smith et al. 2016), the decision to have a single leader for herds which dictated the herd's movements was also done for convenience. This approach was also adopted in a model developed by Patin et al (2019). Given the flexible social organisation within the target species (Estes, 1992), the contrasting basis for leadership among social species (i.e. personality, knowledge, state - Fischhoff et al. 2007) and whether leadership is ephemeral or consistent (Ioannou et al, 2015), I concluded that trying to incorporate this degree of variation would make the model intractable and greatly increase the runtime. Although most lone grazers are programmed to be antisocial, some lone grazers are social grazers that do not locate herds to join.

Observation.

Energy level was the main metric within the model. For testing, the Graphical User Interface of MARSC facilitated inspection of behaviour and spatial utilisation of individuals and herds.

5. Initialisation.

Initially the 300 agents are positioned randomly within the park with random headings (75 agents per species) and have no knowledge of the landscape; as the simulation proceeds grazers accumulate spatial memory of resources. Day and hour are set to zero. Boldness scores, which range from one (timid) to ten (bold), are selected from a normal distribution. Grazers are initially assigned within the species to the following social groups: antisocial - 12.5%; intermediate - 12.5%; and social - 75%. After day 9, all intermediate grazers are changed to social grazers, in order to potentially introduce new members into herds with different spatial memories.

The type of memory for all agents is set at initialisation, i.e. a run will feature all agents using only basic memory or only no memory. Different memory types among agents within a run would be negated within herds, as their behaviour is dictated by the leader. At the start of each day, each agent’s energy level was reset to 0.

6. Input data

The park boundary and waterhole locations were provided by SANParks; see also Section 2.3.4 GIS data processing.

7. Submodels

Submodels are briefly described below using pseudo-code (indented) along with additional information where appropriate. Submodel names are in bold, submodel names in normal text means that the submodel is being called by another section of code.

Go to water

```
If daytime, and agent has waterhole records in memory, and current hour is time when agent goes to waterhole,
    then using memory, move to nearest waterhole
    then move away from waterhole
```

Blue wildebeest visit waterholes every fourth day (Curtin et al, 2018); hartebeest visit waterholes every second day; black wildebeest and tsessebe visit waterholes daily (Estes, 1992). After drinking, grazers instinctively move away from the immediate area, as predators use waterholes as ambush sites (Estes, 1992). Grazers visit the nearest waterhole that does not entail crossing the park fence.

Rest

```
Rest if hour is 12:00 or 13:00 or 21:00 - 23:00 or 02:00 - 06:00 (inclusive)
```

The periods of rest, which include rumination, are based on Estes (1992) and Berry (1980). Although most resting occurs at night, some nocturnal activity occurs, likewise the species rest during the hottest time of the day (Estes, 1992)

ScanWater

```
Scan for waterholes and if waterhole is seen
If waterhole is first waterhole seen,
    then go to waterhole and drink,
    then update waterhole memory record
    then assign time agent goes to water hereafter
If agent already has waterhole records in memory,
    then update memory record if this waterhole is new to the agent
```

The time assigned for going to water is randomly selected for each grazer but within daylight hours (06:00 to 20:00); the grazer then visits a waterhole at that same time throughout the simulation.

ScanFence

```
If grazer is outside "internal border" but still within the park,
    then calculate heading to move grazer back inside the "internal border",
If grazer is inside "internal border" but next move will take it outside the "internal border",
    then change heading by $180^0$,
else resume code
```

Due to initial issues with grazers leaving the park (i.e. “escaping”), a virtual “internal border” was created just inside the actual park border, to help identify when grazers were near the park fence. In reality, animals do leave and enter Mokala through various holes in the fence (pers. obs.; pers. comm.).

ScanConspecifics

```
If see conspecific(s)
  then if antisocial, move away
Else
  join conspecific(s)
If joined conspecific(s) & have highest boldness value in group
  then become leader
```

ScanEVI

```
Scan local habitat patch
If scanned patch includes cells > EVI threshold,
    then rank each cell by distance from agent
    then update short-term grazing memory
If scanned patch has no cells > EVI threshold
    then Move
```

Each grazer scans the immediate area within its short view circle for grazing quality i.e. cells with EVI values greater than the threshold of 111 and cell locations are loaded into the grazer's short-term memory, which then governs the grazers foraging pattern. Data is lacking on preferred EVI thresholds of species generally. Therefore the choice of EVI threshold represented an EVI value that was well represented across the current EVI scenario and was within a range of preferred values identified for N. American ungulates – used as a proxy measure (Merkle et al, 2016). Merkle et al (2016) used the Normalised Difference Vegetation Index (NDVI), which were approximated to EVI values, using EVI = 0.67 x NDVI (Kawamura et al, 2005b).

Move

```
If not using memory
    continue in same direction with deviation of +/- $15^0$
else
If using memory
    continue to target destination (grazing patch or waterhole)
```

To replicate the fact that grazers may not have perfect spatial memory or may not maintain a straight course when moving, each movement could deviate up to +/- 15^0 (the actual angle is selected from a Gaussian distribution) from the previous heading.

Forage

```
Calculate most efficient direct grazing path based on distance to each cell within
a patch, avoiding turns > $60^o$
    then update energy level
    then update grazing memory record
```

The short-term memory process calculates the route within a patch to incorporate all the selected cells, sorted by distance, selecting the nearest pixels first. When feeding, grazers generally continue along the same heading and avoid making sharp turns and seldom deviate by more than 60^0 (Allen & Hoekstra, 1992; Ward & Saltz, 1994). Therefore, the angle between pixels (along the "grazing path") is calculated; if after grazing at A the grazer would have to turn by more than 60^0 to face B, B is deleted from the short-term memory.

After foraging an area, the number of suitable pixels within the area and the area's location are loaded into the grazer's long-term grazing memory. The current day is also loaded into the grazing memory, as grazers do not forage at a previously grazed area for a minimum of 9 days as these areas will be depleted. After grazing, the grazers energy level is increased based on the EVI values of the grazed pixels, using the formula described in Box 1.

This increase represents the energy gained by the agent during a 48 minute period, as within each one-hour foraging bout, 12 minutes (20%) are allocated for non-feeding behaviour (movement within the grazing patch or vigilance). Despite the high level of research on movement between foraging patches (i.e. searching behaviour), there is very little research on movement within foraging patches (typically movements of a few metres or less) on which to base the 20% value.

Giles et al (2020) reported that 5.5% of foraging time by domesticated horses and ponies was subject to interruptions (due to movements, vigilance or displacement). However, most of the feeding took place at hay feeding stations (Giles et al, 2020), therefore when at a feeding station, the amount of (local) movement was minimal. In addition, for domesticated animals the level of vigilance is likely lower than for wild animals (for example, the mean value for vigilance alone, recorded for the target spaces during my fieldwork was 6%). Consequently, the value of 5.5% was considered too low for this study. Laca (1998) recorded the amount of time cattle spent moving between feeder locations (placed 5 m apart) and the time spent at the feeders. Cattle spent approximately 27% of the time moving.

Output

Write output data to text file (see Appendix - Fig 4).

On completion of a run, output data is written to a text file for statistical analysis.

Additional information regarding species comparisons

The following provides key information relating to the interspecific comparisons within the Results sections of Chapters 2, 3 and 4. In terms of daily energy expenditure - the Field Metabolic Rate (FMR; Hulbert, 2014) - numerous variations have been suggested for equating mass with FMR (reviewed by Riek, 2008 and Hudson et al, 2013). Riek (2008) suggested the equation:

$$\text{FMR (J)} = 6.68 \pm 1.21(\text{body weight in g})^{0.67 \pm 0.03}$$

Applying the lower, central and upper values, a 200 kg wildebeest would have the following FMR values (MJ/day): 13.51; 23.79; 40.53 respectively.

Given the variability of both calculated FMR values and FMR estimates (Hudson et al, 2013), the bottom of the range of values (shown below) was used as an arbitrary value for comparison between species throughout this thesis.

$$\text{FMR (J)} = 5.47(\text{body weight in g})^{0.64}$$

2.3.4 GIS data processing

Satellite data at 10 m resolution were obtained from the Sentinel 2 mission (European Space Agency; http://sentinel-pds.s3-website.eu-central-1.amazonaws.com) for Mokala for 26/3/2018, 15/4/2018 and 5/5/2018, representing the period of fieldwork. Hereafter the three datasets are referred to as March, April and May. The EVI levels increased across these months indicating increased levels of vegetation productivity. Data were converted to EVI within ArcGIS 10.6.1 using the formula:

$$EVI = 2.5\frac{N - R}{N + 2.4R + 1}$$

where N = near-infrared light (band 8) and R = red light (band 4) (Jiang et al., 2008). Rather than using NDVI, EVI was chosen as it is less sensitive to both attenuation, resulting from the atmosphere and aerosols, and inaccuracy resulting from soil reflectance (Rocha & Shaver, 2009; Jiang et al., 2008).

For the climate change scenarios, EVI values were converted to the -1/+1 scale, then reduced by 30% or 60% and rescaled to a 0-200 scale. Within Java, a pixel is represented as a 4 byte (32-bit) integer comprising 3 colour components: Red, Green, Blue and a data component - Alpha - which contained the EVI/waterhole/border values. Since each component is limited to 8 bits, EVI was rescaled to 0-200 as it could not be represented as a decimal (i.e. on a -1/+1 scale), since Java and ArcGIS require at least 32 bits to represent a decimal. However, subsequent model refinement meant that GIS representation of the waterholes and park fence were not required, although the park fence vector served to define the park within the model GUI.

Waterholes, EVI and the border were combined into a single GIS layer, using the Composite Bands function within ArcGIS v10.6, with the Projected Coordinate System: WGS 1984, UTM Zone 35S. The GIS layer was exported as a PNG file which was accessed by the model.

2.3.5 Statistical rationale for comparing behaviour and social organisation

As simulations produce a complete dataset (instead of a sample taken from a larger population), parametric/non-parametric tests were not appropriate since they are designed for drawing inferences about a population based on a sample. Instead, randomisation tests were devised to determine whether or not factor levels (e.g. different behavioural types) had a stronger influence on the response variable (energy levels) than random expectation, with probability $p < 0.05$. The assignment of the factor levels (e.g. exploratory or non-exploratory) to each response variable was randomised 5000 times.

The p value represents the proportion of randomised values (e.g. the range of median energy levels) - that equal or are greater than the actual range of median values from the simulation. The range of sample medians around the total median represents the effect size. If less than 5% of the randomised datasets had an effect size as large as the observed dataset's effect size, the null hypothesis (of no difference in median response due to the predictor variable) was rejected.

The range of median energy levels was used as a measure of the effect size specifically because it would include outliers (extreme values) - assessing the full range of possible behaviour is a key aspect of this study. The range of all obtained values (rather than the range of *median values*) may have been more representative of the full range of behaviour but since the response variable was the energy level, in many cases the full range would have extended down to 0 MJ - this was considered to be less informative.

Three parameters for the response variable (energy levels) were used in the analysis: the standard median (i.e. for 100% of the data); the median of data < 1st decile (the lowest 10% of data) - also referred to hereafter as the 'least successful grazers', and the median of data > 9th decile (the highest 10% of data) - also referred to as the 'most successful grazers'. The addition of the least and most successful grazers' energy levels as response parameters facilitate comparisons across a broad range of behaviour and is more informative than just focusing on the group median. For example, differences in energy levels between groups varied across parameters (e.g. the most successful grazers in group A have higher energy levels than group B, but that pattern is reversed among the least successful grazers).

Although a significance threshold of 0.05 was used for statistical tests, Edgeworth (1885) originally referred to a significant difference as being simply "indicative of the working of a law other than chance, or merely accidental". Furthermore, recent criticisms assert that a p-value is not evidence regarding a model or hypothesis and it should be irrelevant when deciding which results to present (Wasserstein & Lazar, 2016; Wasserstein et al, 2019). Therefore decisions on which results to highlight were based on visual inspection of plots, consideration of the effect size, p value and the context. In some cases, results that are *interesting* but not statistically significant or with small or negligible effect size are described in depth.

Individual grazers within groups were considered separate data points for the following reasons: grazers were not directed to join specific groups, if “social” grazers encountered groups they would join groups, but even then, some of these grazers were prevented from joining during an initial time period. It was not possible to treat these dynamic groups as a single data point: a group could persist for 30 days, but group size could vary over the simulation period as other grazers joined. Furthermore, group members differed: i.e. leaders v followers, and timid grazers (occupying group margins) and bold grazers (occupying central locations within groups).

2.4 Results

When comparing grazers acquired and required energy levels, the FMR range values are species specific, therefore these comparisons are described in the interspecific analysis - Section 2.4.4. Note that within the boxplots, the blue lines indicate the median of data < 1st decile (the least successful grazers), the red lines indicate the median of data > 9th decile (the most successful grazers).

2.4.1 Model responsiveness to different climate change scenarios

Grazers’ energy levels declined significantly across the scenarios, which was expected, but there was a much larger decline from EVI-30% to EVI-60% than from current EVI to EVI-30% (Fig 2.1, Table 2.1). A wide range of energy values were evident for both current and EVI-30% scenarios, whilst the range of energy values was reduced for the EVI-60% scenario.

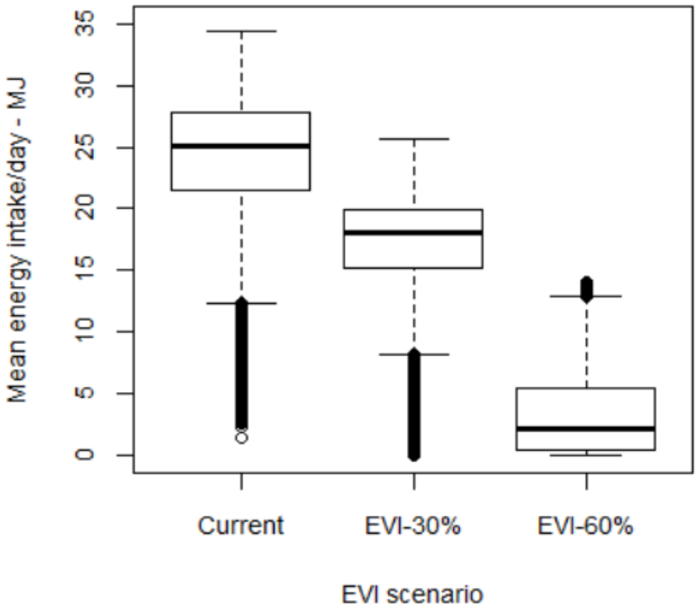

Fig 2.1. Differences in energy levels for all grazers across the three EVI scenarios. Note the additional parameters (median of data < 1st decile and median of data > 9th decile) are not present as the figure provides an indication of the general levels of all grazers within the EVI scenarios.

Table 2.1 Randomisation test results for the effect of EVI scenario on energy levels.

Proportion of randomized ranges ≥ actual range (actual range MJ)		
< 1st decile	= median	> 9th decile
0.0 (17.81)	0.0 (22.90)	0.0 (21.38)

2.4.1.1 EVI scenarios by month

Energy levels differed by month for each of the EVI scenarios (Table 2.2). For each scenario, energy levels increased each month from March to May (Fig 2.2). Under all scenarios, the rate of increase in energy levels declined across months for the most successful grazers (Fig 2.2); this was also the case for the least successful grazers under Current EVI. The rate of increase for grazers at the at median level reduced across months for the current and EVI-30% scenarios but increased under EVI-60%. Under EVI-30%, there was a marked increase in energy levels (of 15.53 MJ) across month for the least successful grazers (Table 2.2).

Table 2.2 Randomisation test results for the effect of differences in EVI levels by month on energy levels.

EVI scenario	Proportion of randomized ranges ≥ actual range (actual range MJ)		
	< 1st decile	= median	> 9th decile
Current	0.0 (8.67)	0.0 (7.19)	0.0 (6.40)
-30%	0.0 (15.53)	0.0 (5.45)	0.0 (4.04)
-60%	NA*	0.0 (4.80)	0.0 (6.24)

*Test result not applicable as 1st decile for March = 0.

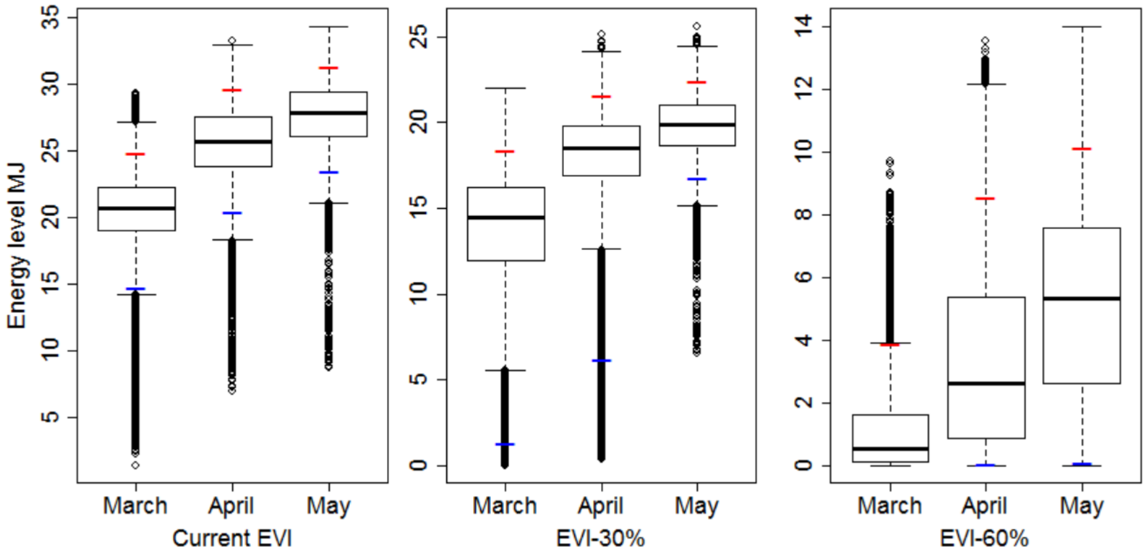

Fig 2.2. Energy levels achieved by all grazers by month for the three EVI scenarios. Note different scales.

2.4.2 Capturing differences between exploratory and non-exploratory behaviour of agents

For all scenarios, grazers energy levels were affected by their exploratory behaviour, although differences between the behavioural types reduced across the EVI scenarios, as levels of vegetation productivity decreased (Table 2.3). Among the least successful grazers, results were not significant under EVI-30% and EVI-60% (Table 2.3). Exploratory grazers generally acquired the higher energy levels under Current and EVI-30% scenarios. This pattern was reversed under EVI-60%, as non-exploratory behaviour resulted in higher energy levels. Note however the variation within the non-exploratory group under EVI-30%: among the most successful grazers and those at the median level, exploratory grazers had higher energy levels but among the least successful grazers, non-exploratory grazers acquired higher energy levels (Fig 2.3). By definition this section excludes the "none" memory type (as the exploratory or non-exploratory behaviour is dictated by memory); all followers were also excluded, since herd movements (and therefore foraging success) are dictated by leaders, but results could be confounded as followers can have a different memory distance, which would affect the results.

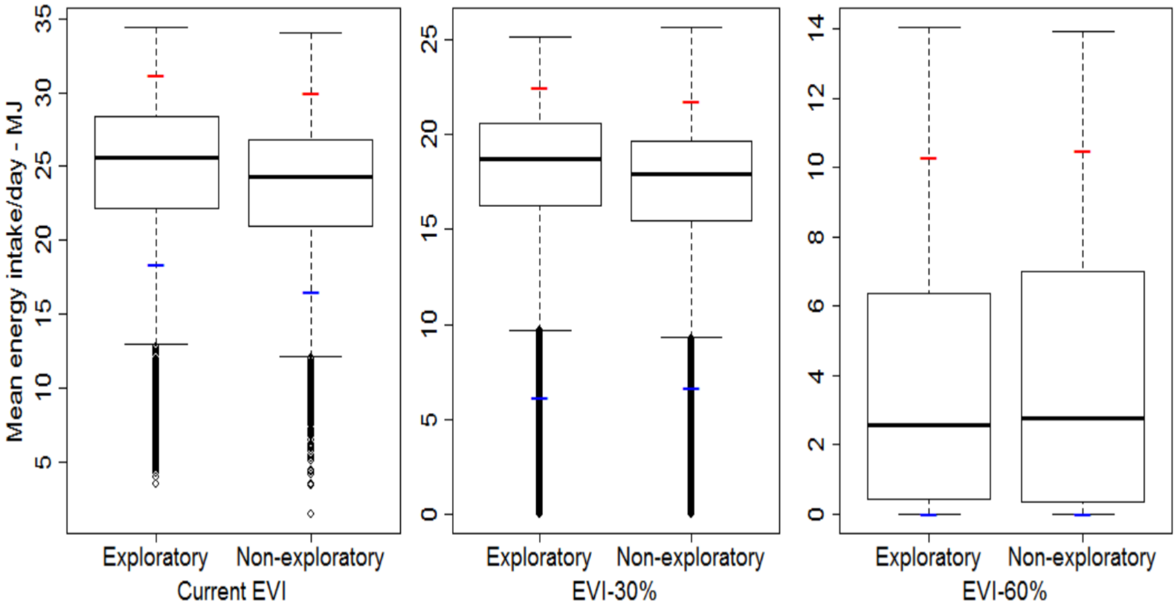

Fig 2.3. Comparison of the different energy levels for grazers across the EVI scenarios memory distances are in cell size (1 cell = 10m). Note different scales.

Table 2.3 Randomisation test results for the effect of exploratory behaviour on energy levels.

EVI scenario	Proportion of randomized ranges ≥ actual range (actual range MJ)		
	< 1st decile	= median	> 9th decile
Current	0.0 (1.79)	0.0 (1.33)	0.0 (1.17)
-30%	0.14 (0.54)	0.0 (0.79)	0.0 (0.75)
-60%	1.0 (0.0)	0.0 (0.23)	0.0 (0.18)

2.4.3 Model responsiveness to differences in agents' cognitive ability

Differences in energy levels were evident between memory classes under the Current EVI scenario although the actual differences (MJ) were marginal (Table 2.4). Under EVI-30%, memory-based foraging (i.e. all memory types except type = 'none') did not differ from random foraging in terms of energy levels for the most successful grazers and those at the median level (Fig 2.4, Table 2.4). Random foraging did result in notably lower energy levels for the least successful grazers under EVI-30% however (Fig 2.4). Similarly, grazers who foraged randomly under EVI-60% also acquired markedly lower energy levels than grazers using memory (Fig 2.4). For both EVI-30% and EVI-60%, energy levels were similar among the memory-based grazers.

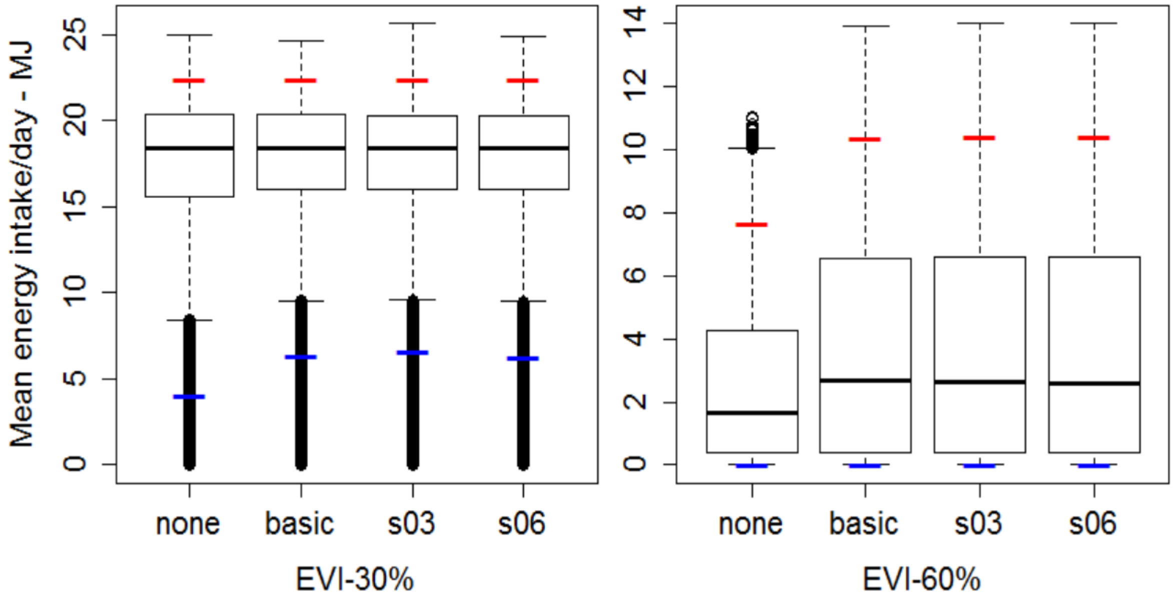

Fig 2.4. Differences in energy levels for the different memory classes under EVI-30% and EVI-60% climate change scenarios.

Table 2.4 Randomisation test results for the effect of memory type on energy levels.

EVI scenario	Proportion of randomized ranges ≥ actual range (actual range MJ)		
	< 1st decile	= median	> 9th decile
Current	0.0 (0.37)	0.03 (0.21)	0.0 (0.18)
-30%	0.0 (2.58)	0.96 (0.03)	0.32 (0.05)
-60%	1.0 (0.0)	0.0 (1.01)	0.0 (2.78)

2.4.4 Inter-specific comparisons

Under the current EVI scenario all grazers (excluding the outliers) across all species acquired energy levels in excess of the required (FMR) energy levels (Fig 2.5). The FMR levels were below the median energy levels of the least successful grazers, therefore more than 90% of the population exceeded their required energy levels. Note that although results are not shown for EVI-30%, the FMR levels were below the 25th percentile for all species under this intermediate scenario, therefore more than 75% of the population exceeded their required energy levels. In contrast, under EVI-60% a much smaller proportion of the populations met or exceeded their required energy levels (Fig 2.5). For blue wildebeest the only grazers exceeding the FMR levels were outliers, while among each of the other species the FMR was higher than the median levels of the most successful grazers. Therefore more than 90% of the population did not meet their required energy levels.

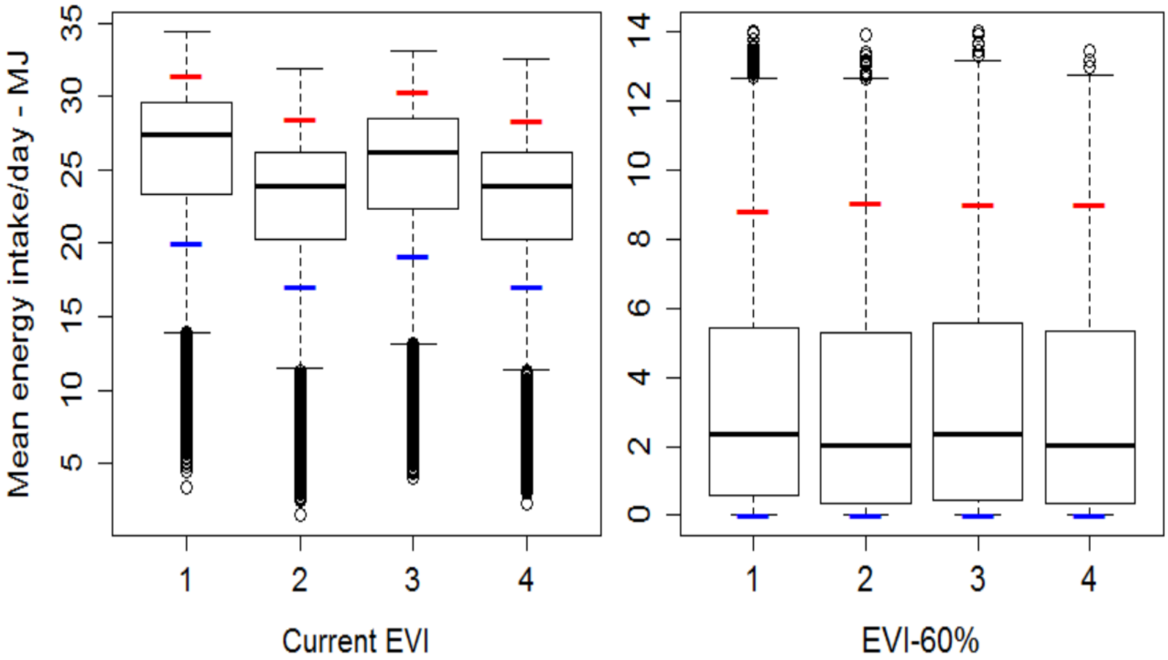

Fig 2.5. Inter-Specific differences in acquired energy levels under Current EVI and EVI-60%. Species with FMR values (MJ/day) in brackets: 1 - blue wildebeest (13.51); 2 - black wildebeest (10.25); 3 - hartebeest (12.63); 4 - tsessebe (9.74).

Energy levels differed between the species across all three scenarios although differences were marginal under EVI-60% (Table 2.5). A consistent pattern was evident under Current EVI (Fig 2.5) and EVI-30%, of blue wildebeest having the highest energy levels, then hartebeest, with black wildebeest and tsessebe having the lowest (and similar) energy levels. For EVI-60%, differences in energy levels between all species were greatly reduced compared with the other EVI scenarios (Fig 2.5). For all scenarios the range of values was similar across the four species (e.g. the IQR and the range between the least successful grazers and most successful grazers).

Table 2.5. Randomisation tests results comparing the effect of species on grazers' energy levels.

EVI scenario	Proportion of randomized ranges ≥ actual range (actual range MJ)		
	< 1st decile	= median	> 9th decile
Current	0.0 (2.92)	0.0 (3.51)	0.0 (3.00)
-30%	0.0 (2.10)	0.0 (2.24)	0.0 (2.04)
-60%	1.0 (0.0)	0.0 (0.31)	0.0 (0.20)

2.4.5 Capturing the effect of social organisation on individual energy intake

Typically there was a hierarchy under current and EVI-30% scenarios, with leaders having higher energy levels than followers, who had higher energy levels than lone grazers, (Fig 2.6). Under EVI-60%, there was a pronounced change to the hierarchy with lone grazers acquiring higher energy levels than followers (the difference was 1.42 MJ, Table 2.6) among the most successful grazers (Fig 2.6). At the median level energy levels between lone grazers and followers did not differ (Table 2.6).

These results highlight the variation within groups. For example, among the most successful grazers, leaders had higher energy levels than followers (Fig 2.6, EVI-30%), but the least successful followers had higher energy levels than the least successful leaders. There was a trend of decreasing differences between groups' median energy levels across the EVI scenarios, particularly between lone grazers and followers (Fig 2.6).

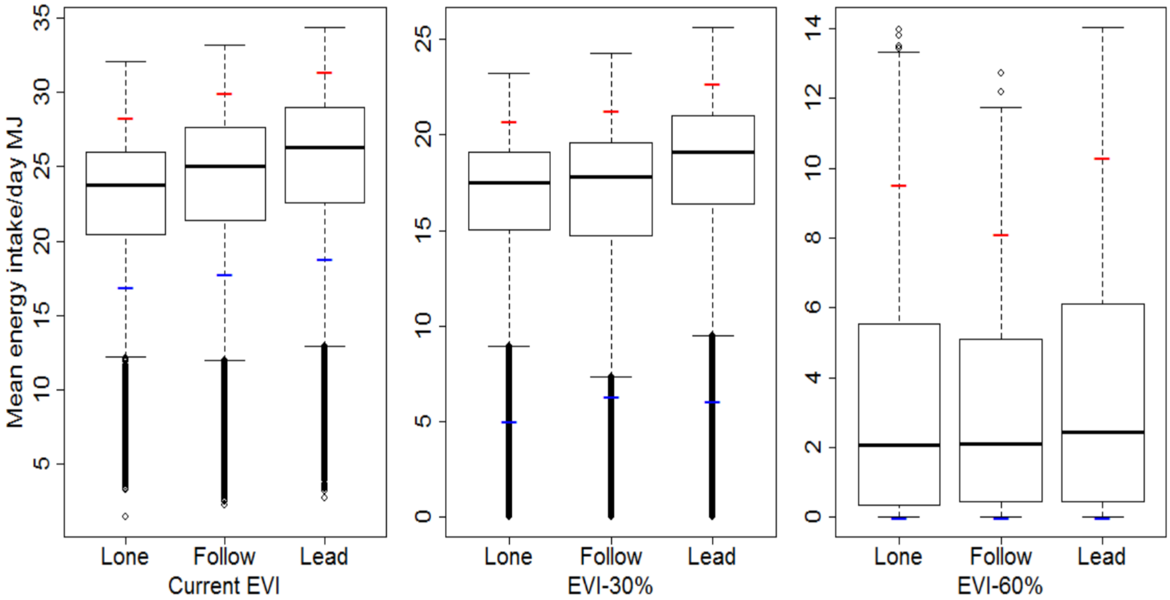

Fig 2.6. Comparison of the difference in energy levels between lone grazers, herd leaders and followers as energy levels declined across the EVI scenarios. Note different scales.

Table 2.6. Randomisation tests results comparing the effect of social organisation (lone grazers v herd followers) on acquired energy levels.

EVI scenario	Proportion of randomized ranges ≥ actual range (actual range MJ)		
	< 1st decile	= median	> 9th decile
Current	0.0 (0.85)	0.0 (1.30)	0.0 (1.66)
-30%	0.0 (1.31)	0.0 (0.29)	0.0 (0.53)
-60%	1.0 (0.0)	0.32 (0.04)	0.0 (1.42)

Note: Fig 2.6 displays all three social groups for reference. Given the exploratory aspect of this chapter, randomisation tests were only carried out on the key relationship of interest – between lone grazers and herd followers. Chapters 3 and 4 incorporate randomisation tests on all relationship combinations and explain them in greater depth.

2.4.6 Lone grazers: antisocial v social

The sociability of lone grazers affected their acquired energy levels, with actual differences (in MJ) varying widely (Table 2.7). Antisocial lone grazers generally achieved higher energy levels than social lone grazers (Fig 2.7). Note however the variation within the social group under the Current EVI and EVI-30% scenarios: for grazers at the median level and especially the least successful grazers, social lone grazers acquired lower energy levels than antisocial lone grazers, but this pattern was reversed among the most successful grazers scenarios (Fig 2.7). This variation was particularly pronounced under the Current scenario: among the least successful grazers, antisocial grazers energy levels were 9.14 MJ higher than social grazers, but among the most successful grazers, social grazers energy levels were 1.13 MJ higher than antisocial grazers (Table 2.7).

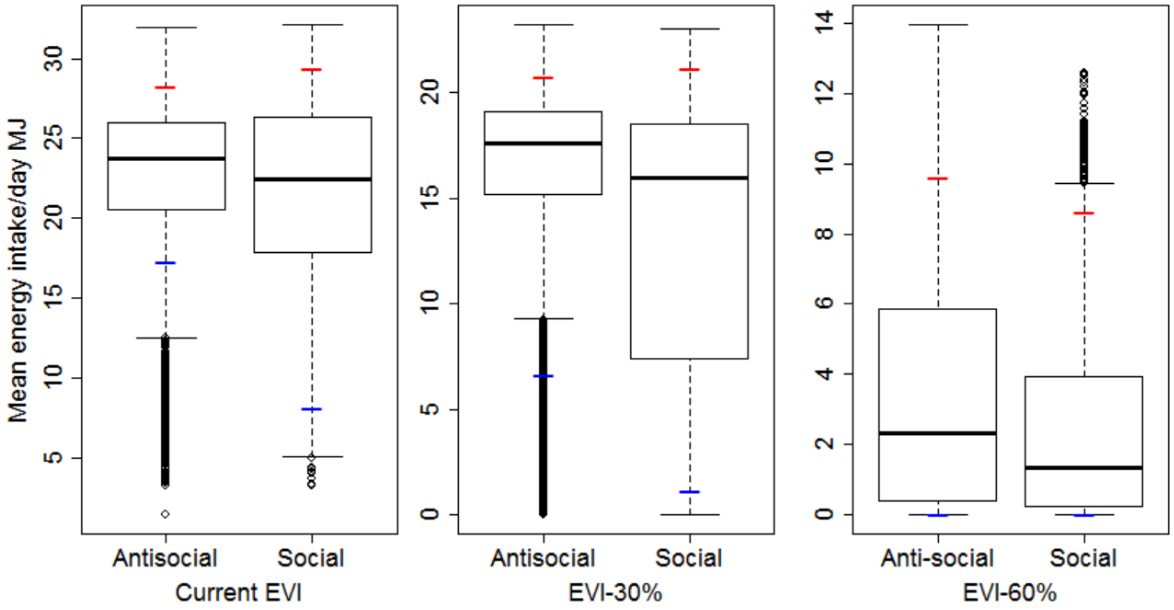

Fig 2.7. Comparison of the difference in energy levels between antisocial and social lone grazers , across the EVI scenarios. Note different scales.

Table 2.7 Randomisation test results for the effect of sociability among lone grazers on energy levels.

EVI scenario	Proportion of randomized ranges ≥ actual range (actual range MJ)		
	< 1st decile	= median	> 9th decile
Current	0.0 (9.14)	0.0 (1.31)	0.0 (1.13)
-30%	0.0 (5.51)	0.0 (1.65)	0.0 (0.42)
-60%	1.0 (0.0)	0.0 (0.97)	0.0 (1.00)

2.5 Validating that MARSC produces sensible results regarding the adaptive capacity of antelope populations to climate change

Variation in behaviour across a range of traits and social organisation resulted in variation in energy levels as expected. The model was sensitive to EVI levels, variation in exploratory behaviour and cognitive ability, social organisation (in terms of herd hierarchy and herds v lone grazers) and species, and also interactions between these variables.

Whilst there was limited difference in energy levels between cognitive classes within EVI scenarios, which was unexpected, this result was consistent with the findings of Merkle et al (2016). The model highlighted the increasing difference between cognitive ability (i.e. random v memory-based foraging) as resource levels declined across the EVI scenarios.

Emergent properties highlighted by MARSC are reasonable, although in some cases they were unexpected (i.e. comparisons between lone grazers and herd followers - Section 2.4.5 and social and antisocial lone grazers - Section 2.4.6), which promoted further consideration and on reflection they are rational (see Section 2.6).

The model was assessed and found to produce sensible results with some interesting emergent properties. Therefore, I concluded that MARSC is ready to be used to simulate the impact of different management scenarios, aimed at mitigating the impact of climate change on the target populations (Chapters 3 and 4).

2.5.1 Testing of the model

MARSC was initially developed with no restrictions on the distribution of the four species during the simulation. However, the fact that black wildebeest avoid the central area of Mokala (pers. obs., pers. comm., see Section 2.3.2) (Fig 2.9) required testing to determine how this restriction on their range affected simulation results. The other three species do not restrict their range (pers. obs., pers. comm.). Nevertheless, amending MARSC to incorporate the restricted range of the black wildebeest resulted in no difference in energy levels under the current EVI scenario, between the original (unrestricted) black wildebeest population and the restricted black wildebeest population (Fig 2.8; Table 2.8). The run size was 720 (240 runs for each of the three months, 120 runs per distribution, each comprising 75 agents - black wildebeest only, totalling 54000 grazer records).

Table 2.8 Randomisation test results for the effect of different distributions on black wildebeest energy levels for the current EVI scenario

Proportion of randomized ranges ≥ actual range (actual range MJ)		
< 1st decile	= median	> 9th decile
0.0 (1.34)	0.0 (0.27)	0.02 (0.07)

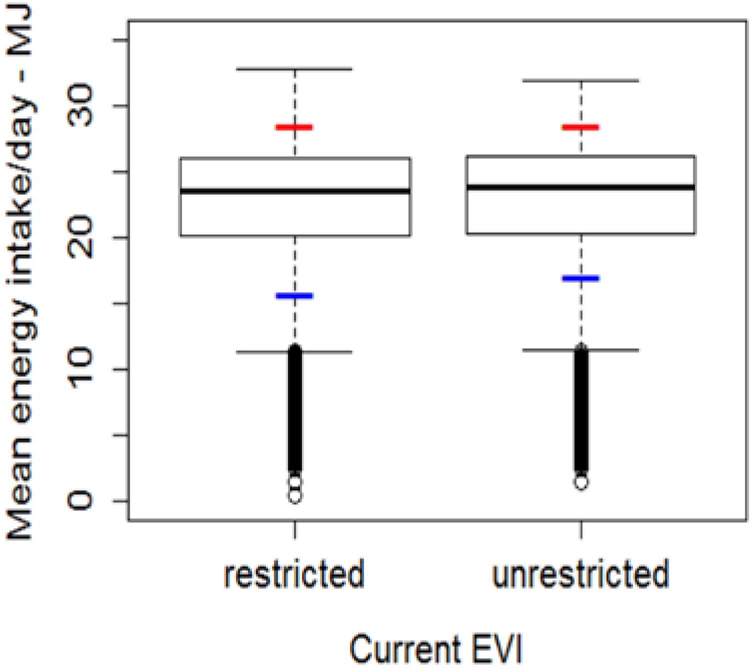

Fig 2.8. Comparison of the effect of black wildebeest distributions on energy levels for Current EVI, for all three months. The location of restricted areas are shown in Fig 2.9 below.

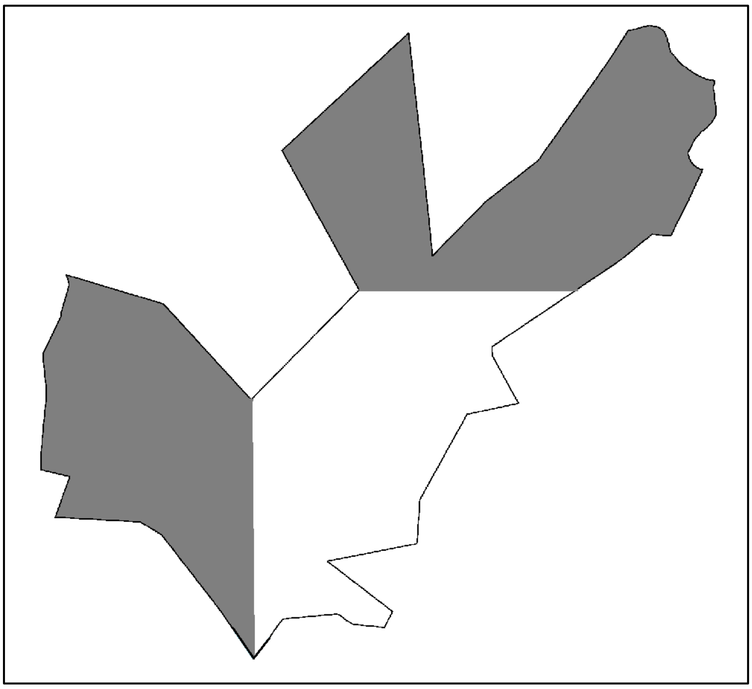

Fig 2.9. Map showing distribution of black wildebeest restricted to the north and west of Mokala (grey areas)

Data from MARSC, in terms of the percentage of time agents spent moving and foraging (Fig 2.10 and Fig 2.11: Current EVI plots) were compared with alternative sources (Table 2.9), including my field observations from 2018 (listed in Table 2.9 as "pers. obs."). Note that within MARSC, "Resting" was set as a constant value of 45.8% across all species (11 hrs/day - compare with Table 2.9) for all species and scenarios. This is broadly in agreement with the resting values shown in Table 2.9 (though admittedly it did differ in the case of hartebeest). The choice of a constant value across all species represents a compromise between ecological reality and software considerations.

Generally there was broad agreement between the MARSC values and the other sources. Although some results from MARSC vary from the sources in Table 2.9 - in particular the time spent foraging in Fig 2.11 - most of the sources were restricted to diurnal monitoring, whereas MARSC simulated a 24 hour cycle. Figures 2.10 and 2.11 also compare the current and EVI-60% scenarios, highlighting the contrast in behaviour as conditions decline. i.e. more time is spent moving and less time foraging as resources decline under EVI-60%.

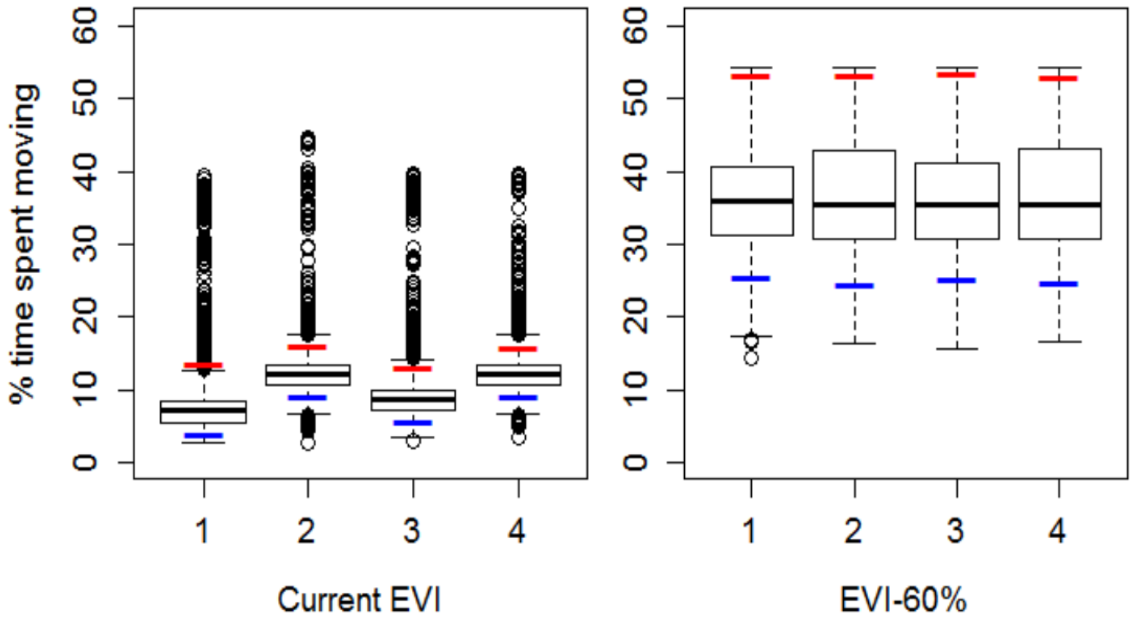

Fig 2.10. Proportion of time spent moving by species within MARSC. Note the contrast between the Current EVI scenario and the EVI-60% scenario. 1 - blue wildebeest; 2 - black wildebeest; 3 - hartebeest; 4 - tsessebe. The moving percentage included time spent going to and from water.

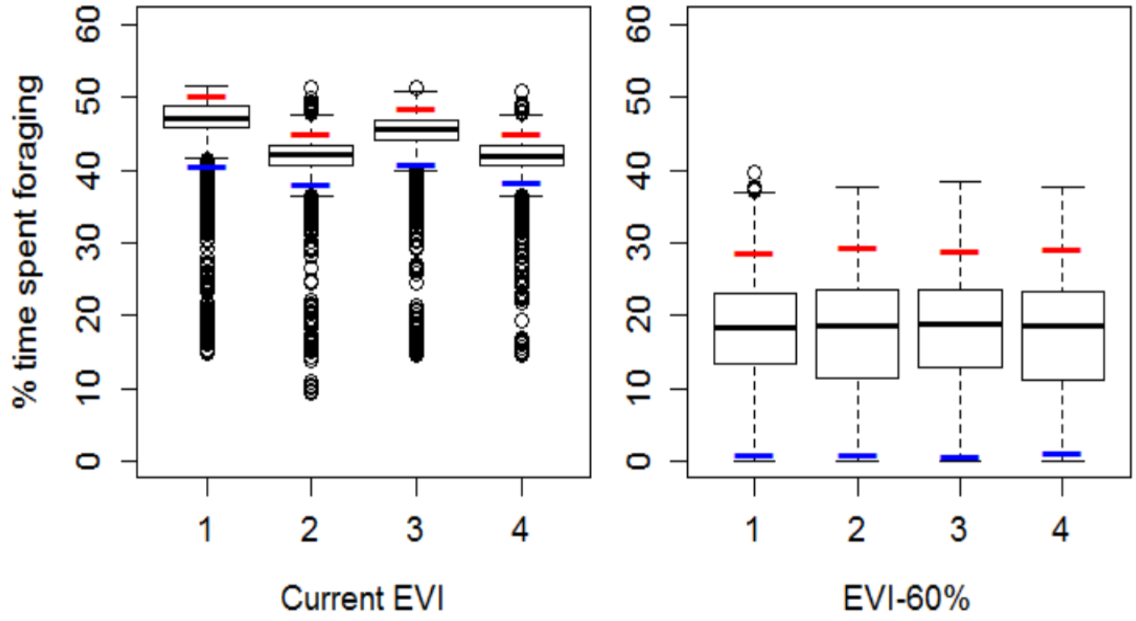

Fig 2.11. Proportion of time spent foraging by species within MARSC. The figure also highlights the reduced time spent foraging under EVI-60%, compared with the Current EVI scenario. 1 - blue wildebeest; 2 - black wildebeest; 3 - hartebeest; 4 - tsessebe.

Table 2.9 Activity budgets reported for the focal species from different sources. Note that most of the observations were limited to diurnal monitoring. Additional notes: **a** - my field observations (in 2018) included a high percentage of "not visible" classifications when monitoring individual's behaviour, these were: Blue wildebeest - 29.1%; Black wildebeest - 7.6%; Hartebeest - 25.1%; Topi -28.2%; **b** – the Rest value comprises lying and standing.

Activity	Species	% of time by activity	Reference	Notes
Move	Blue wildebeest	12.0	Berry, 1980	24 hour monitoring.
		11.1	Knight, 1991	Diurnal monitoring. Mean for Cold-Dry, Hot-Dry and Hot-Wet seasons
		7.0	Helm, 2006	Diurnal monitoring.
		5.8	pers. obs.[a]	Diurnal monitoring.
	Black wildebeest	3.0	Helm, 2006	Diurnal monitoring.
		8.8	pers. obs. [a]	Diurnal monitoring.
	Hartebeest	15.8	Tolcha & Shibru, 2020	Diurnal monitoring. Mean for Wet and Dry seasons
		4.6	pers. obs. [a]	Diurnal monitoring.
	Topi	6.6	Duncan, 1975	24 hour monitoring. Mean of Apr, May, Sep and Nov.
		12.7	pers. obs. [a]	Diurnal monitoring.
Forage	Blue wildebeest	33.0	Berry, 1980	24 hour monitoring.
		42.2	Knight, 1991	Diurnal monitoring. Mean for Cold-Dry, Hot-Dry and Hot-Wet seasons
		45.0	Helm, 2006	Diurnal monitoring.
		38.0	pers. obs. [a]	Diurnal monitoring.
	Black wildebeest	35.0	Helm, 2006	Diurnal monitoring.
		30.1	pers. obs. [a]	Diurnal monitoring.
	Hartebeest	33.0	Tolcha & Shibru, 2020	Diurnal monitoring. Mean for Wet and Dry seasons
		32.2	pers. obs. [a]	Diurnal monitoring.
	Topi	37.6	Duncan, 1975	24 hour monitoring. Mean for Apr, May, Sep and Nov.
		30.7	pers. obs. [a]	Diurnal monitoring.
Rest	Blue wildebeest	53.0	Berry, 1980	24 hour monitoring.
		44.6	Knight, 1991	Diurnal monitoring. Mean for Cold-Dry, Hot-Dry and Hot-Wet seasons
		46.0	Helm, 2006 [b]	Diurnal monitoring.
	Black wildebeest	60.0	Helm, 2006 [b]	Diurnal monitoring.
	Hartebeest	24.4	Tolcha & Shibru, 2020	Diurnal monitoring. Mean for Wet and Dry seasons.
	Topi	55.9	Duncan, 1975 [b]	24 hr monitoring. Mean of Apr, May, Sep and Nov.

2.5.2 Sensitivity Analysis

A sensitivity analysis of the EVI/energy input conversion value was produced by keeping all other parameters constant and varying the parameter of interest (Hamby, 1994), in this case the energy conversion value was altered by +/- 10% and +/- 30% to assess the effect on agents' acquired energy levels (Table 2.10, Fig 2.12).

Model predictions of agents' energy levels were sensitive to the EVI/energy intake conversion factor (Table 2.10). There was a high correlation between the energy conversion factor and the agents' energy levels (Fig 2.12); this correlation applied to all data (i.e. not just the medians), across all five energy conversion factors scenarios (-30% to + 30%, including the standard factor used in MARSC) for the Current EVI scenario, for May only (Spearman rank correlation rs = 0.903; p < 0.001). The analysis was restricted to May only, as that month resulted in the highest energy levels and should therefore highlight the greatest differences between conversion factors. Furthermore, this was also a compromise between obtaining sufficient data within a limited time: each month resulted in 180,000 records, if March and April were included, the data set would comprise 540,000 records but would also require a longer run time.

Table 2.10 Sensitivity Analysis of agents' energy levels to variations in the conversion rate from EVI to energy intake.

Change in energy conversion factor relative to the standard MARSC runs	Percentage change in energy levels relative to the standard MARSC runs		
	< 1st decile	= median	> 9th decile
-30%	-30.1%	-30.1%	-30.0%
-10%	-10.0%	-10.1%	-10.0%
+10%	+9.8%	+10%	+9.9%
+30%	+30.3%	+29.9%	+30.0%

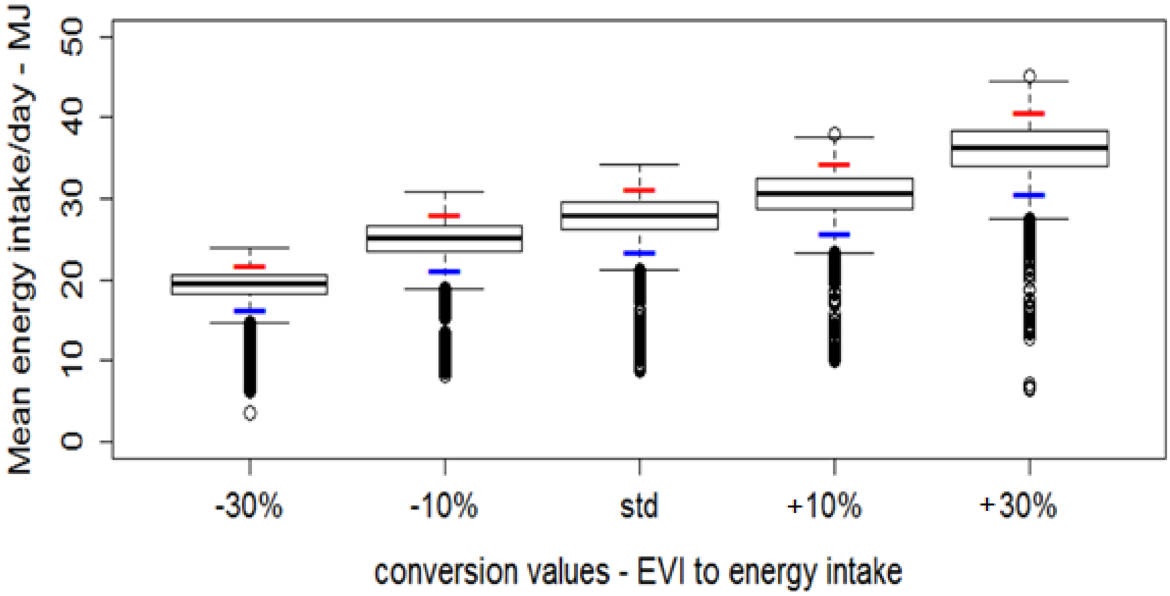

Fig 2.12. Sensitivity of predicted energy levels to changes in the EVI/energy intake conversion factor, relative to the standard conversion used within MARSC, for the Current EVI scenario, for May only.

A potential issue within MARSC is that the EVI value of any grazed pixel is reinstated in the next cycle (i.e. each hour). In reality, after grazing, a pixel may reduce to 0 and take several days to return to the original EVI value, making it unavailable to other agents during this time. However, to assess every pixel within the landscape on a daily basis, to determine if it was due to have its original EVI value reinstated, would have been very costly in terms of computer memory and run time. Furthermore, the increase in EVI value would not suddenly occur on one specific day - this would be a gradual process. To incorporate this process would be even more costly for runtime and computer memory.

Aspects of both MARSC and the species may mitigate the potential impact of the “instant regrowth” issue. There is niche separation between the species, determined by vegetation growth stage (though this is not incorporated within MARSC), with wildebeest, topi and hartebeest preferring early, intermediate and late-stage growth respectively (Murray & Brown, 1993; Estes, 2014; see also the species descriptions in the Appendix). Therefore, in reality there could be some facilitation between the species, as grazing by topi and hartebeest results in fresh growth preferred by wildebeest. However, there is no facilitation within the species or from wildebeest for topi and hartebeest. Grazers using memory-based foraging avoid recently grazed patches (see Section 2.3.3 - Submodels), although they may later return to a patch to find that it has been grazed by conspecifics, which obviously also applies to any patch that a random forager may approach.

As an approximate test of the impact of the “immediate” regrowth within MARSC, simulations were run covering periods of nine days with immediate regrowth and without immediate regrowth (i.e. the pixel value remains at zero for the nine days). The period of nine days was used as that is the length of time memory-based grazers avoid a previously grazed area, as it will be depleted (see Section 2.3.3 - Forage). Simulations were run for the month of May for two climate scenarios: current EVI and EVI-60%. In each case simulations were carried out for one species (blue wildebeest, comprising 75 agents) in order to assess the impact of intraspecific competition, and for all four species (300 agents). Each simulation comprised a total of 60 runs (30 with regrowth, 30 without regrowth).

Based on a visual inspection of the plots (see Appendix Figs 5 and 6), immediate regrowth of grazed pixels did not affect the results within MARSC. The lack of effect of immediate regrowth is likely influenced by the fact that none of the park’s other herbivores are incorporated within MARSC.

2.6 Discussion

The key finding of this chapter, is the wide range of energy levels acquired by grazers who exhibited wide behavioural variation. Although the variation in energy generally reduced as resources declined under future scenarios.

This key finding reinforces two points: firstly, it is important to assess the full range of behavioural variation (i.e. the full range of personalities) that exists for a target population, rather than just the mean or median. Identifying the full range of behavioural variation is particularly important in relation to climate change (Hetem et al, 2014; Fuller et al, 2016; Rabaiotti & Woodroffe, 2019); behavioural variation provides the opportunity for individuals to acclimate to the effects of climate change

(Beever et al, 2017). Second, by working at the level of the individual and simulating how the individual interacts with its biotic and abiotic environment, ABMs are well suited for investigating complex systems: in this case, antelope species within Mokala National Park, under current and predicted future scenarios. ABMs facilitate the identification of emergent properties and unexpected, apparently counterintuitive results, promoting further reflection on the system.

The inclusion of the least and most successful grazers’ energy levels as response parameters (in addition to the median) allowed comparisons across a broad range of behaviour and revealed subtle aspects in relation to behaviour and social organisation which would not have been identified by focusing only on the group median.

2.6.1 EVI scenarios

Whilst it was expected that energy levels would be lower for the future EVI scenarios, the size of the reduction for EVI-60% was surprising and suggests a threshold between EVI-30% and EVI-60% which threatens at worst, localised extinction, or at least a serious decline in population for these species. The existence of such a threshold resonates with the findings of Urban (2015), who predicts one in six species will be threatened by a post-industrial temperature increase of 4.3° C.

The differences in the rate of increase in energy levels between months and between the least and most successful grazers are relevant for management interventions. For example, under EVI-30% the increased energy levels of the least successful grazers across months demonstrates adaptive capacity as EVI levels increased i.e. grazers responded to increased vegetation productivity. This did not happen under EVI-60%, instead increased energy levels were evident for the most successful grazers and those at the median level. This suggests the time for interventions would be at or before EVI-30% levels are reached, as it can benefit all animals in a population (but it would assist the least successful behavioural types the most), allowing behavioural variation to persist. By the time levels are at EVI-60%, interventions may be ineffective for the least successful grazers, resulting in reduced behavioural variation, which may inhibit species' capacity to mitigate further environmental change (Beever et al, 2017).

One method by which the species may mitigate the low-energy levels acquired under the EVI-60% scenario is through use of forage reservoirs (Riginos, 2015), in this case foraging among the rocky hillsides present within the southern half of the park. Rocky habitats provide a cooler, sheltered, microclimate which is a more stable environment than ambient conditions and allow species to persist under (supposedly) unsuitable conditions (Varner & Dearing, 2014). The fact that the target species do forage among the park's rocky outcrops (pers. obs.), particularly during the dry season (Johann de Klerk, Manager, Mokala National Park - pers. comm.) is a further demonstration of how behavioural plasticity allows individuals to mitigate the negative impact of harsh environmental conditions.

2.6.2 Exploratory v non-exploratory grazers

The results suggest an interaction between exploratory behaviour and the level of resources. Exploratory grazers increased their chances of finding spatially dispersed resources and so acquired higher energy levels than non-exploratory conspecifics, as suggested by Schuster et al. (2017) and Schirmer et al. (2019). However, this only applied to the current and EVI-30% scenarios. As resources reduced under the EVI-60% scenario, non-exploratory behaviour resulted in the higher energy levels. This is an emergent property of MARSC, i.e. it was not a direct result of the programming code. In effect, under EVI-60% as resources decline, exploratory grazers spend time and energy foraging across a wide area, but foraging trips are often unsuccessful. This finding is, to some extent, in agreement with the assertion that exploratory behaviour is maladaptive in changing environments (Coppens et al., 2010), although this applied only to the worst-case change of environment to EVI-60%, not the change from current conditions to EVI-30%.

Under EVI-60% it is better to remain in familiar territory rather than explore new locations. This is logical - familiarity with their home range should promote more efficient foraging, as the grazer will know the location of resource-rich patches to utilise, as well as barren areas to avoid. In other words, less exploratory grazers are more responsive to their environment (Coppens et al., 2010; Mazza et al, 2018). However, this is relative, under harsh conditions grazers should remain in a (relatively) resource-rich location, but in a location that has insufficient resources, grazers may as well explore other locations.

2.6.3 Memory type

Key findings in relation to memory type were the similarity in energy levels between memory-based foraging groups for both future climate scenarios, and the similarity in energy levels between random foraging and memory-based foraging under EVI-30%. In contrast, memory-based foraging resulted in higher energy levels under EVI-60%, since random foraging is less likely to locate foraging areas.

The similarity in energy levels achieved between the three memory-based foraging groups was unexpected; as the level of resources declined, it was expected that grazers using the smart06 memory threshold (the most selective, see Section 2.3.3 – Spatial memory) would obtain higher energy levels than the other groups. However, because the smart06 strategy is more selective, at any given location a smart06 grazer will likely have less choice among memory records. Therefore, the grazer may have to travel further to graze, which incurs higher energy and time costs, assuming the grazer has memory records that meet the 06 threshold, if it does not, the grazer will spend more time foraging randomly. This suggests that as resources decline, it is worth travelling to any known (or expected) areas of available forage.

Note that similar energy levels among different levels of memory-based foraging grazers was evident in a memory-based foraging model developed by Merkle et al (2016), from which they concluded a degree of random movement was of benefit to foraging that is primarily memory driven, in agreement with the view of Boyer & Walsh (2010). Similarly, Falcón-Cortés et al (2021) reported a mixture of memory-based foraging and random foraging among elk.

Use of memory may be an advantage or disadvantage under climate change. Memory use promotes more efficient foraging (Laca, 1998) which allows grazers to obtain sufficient energy intake in less time than random foraging - this will reduce the time grazers are exposed to deleterious extremes (i.e. elevated temperatures) (Hall & Chalfoun, 2018). Less time spent moving and more time spent foraging were key determinants of whether musk ox survived winter (Chimienti et al, 2020). Alternatively, memory use may facilitate an ecological trap (Schlaepfer et al, 2002) if the resource is no longer available. In which case, exploration of new areas would be better than reliance on memory. Management interventions such as habitat management (see Chapter 3) could reduce the likelihood of ecological traps by ensuring foraging areas retain high levels of productivity.

2.6.4 Social organisation of the target populations

As expected, herd members generally acquired higher energy levels than lone grazers (McNaughton 1984). This reflects reality - in a given amount of time a group of individuals can sample a larger area than one individual. Herd members can sense grazing patches but unlike a lone individual they can also regularly rely on social information, i.e. the presence of many herd members at a patch indicates to other herd members the location of good grazing. Likewise, the herd may comprise a gradient in sensing ability and so individuals with lower abilities can benefit from those with higher abilities; a lone grazer cannot.

Within herds, leaders generally gaining higher energy levels than followers makes sense: herds move to the leaders' preferred areas, and leaders feed in the best grazing patches; those on the periphery potentially feed in poorer quality patches and are constantly accumulating memory of 'poor' grazing areas. The findings that leaders acquired higher energy levels than followers and lone grazers, and that in some situations lone grazers acquired higher energy levels than followers, was also evident in the model developed by Patin et al (2019). Empirical evidence of lone individuals being more successful in foraging than group members is reported by Gompper (1996).

The higher energy levels for antisocial lone grazers compared with social lone grazers was unexpected and is an emergent property of MARSC, but in agreement with Nawroth et al. (2017) who found that less sociable goats performed better at relocating food patches. Although herd membership offers advantages such as scrounging and anti-predator benefits, there are also disadvantages which do not affect lone grazers. Principally, lone grazers do not need to monitor the behaviour of fellow herd members, which may allow them more time to focus on foraging.

The only difference between these two groups within MARSC is that antisocial grazers actively avoid conspecifics. The expectation was that there would be an opportunity cost for antisocial lone grazers, as time and energy are spent moving away from other grazers rather than towards a resource. However, the additional movement may allow antisocial grazers to discover more grazing patches - i.e. they develop a more detailed spatial knowledge of their local habitat.

2.6.5 Interspecific comparison

The results suggest that if vegetation levels decline to EVI-60%, the majority of the antelope populations may die. Although the EVI-60% scenario is an arbitrary level equating to twice the maximum deviation from the long-term mean of vegetation productivity for Mokala (Smit & Simms, 2015). Therefore that level may not be reached. Regardless, the results suggest the presence of a threshold between EVI-30% and EVI-60% beyond which a much greater proportion of the population will not survive.

The results for the current EVI scenario highlight the benefits of the reduced water requirement for blue wildebeest and hartebeest, in terms of energy levels. The higher energy levels for blue wildebeest and hartebeest are an emergent property of the model. Reduced water dependence allows grazers access to ungrazed (or lightly grazed) areas that have low densities of waterholes, as they are avoided by more water-dependent species (Cain et al, 2012; Estes, 2014; Valls-Fox et al, 2018).

The similarity in energy values between species for EVI-60% (Fig 2.5) suggests that reduced water dependence is of little benefit for foraging when EVI values decline below a certain threshold - the threshold being somewhere between EVI-30% (when blue wildebeest and hartebeest still achieved higher energy levels than their congeners) and EVI-60%.

Cain et al (2012) suggest that whilst reduced reliance on water allows a species to forage further away from waterholes, this entails an increased cost in time and energy when making longer return trips to water sources. However, the ability to forage further from water allows blue wildebeest and hartebeest to discover additional waterholes (particularly in PAs which provide artificial waterholes) in addition to more grazing patches, as they increase their spatial knowledge of their local habitat. This is similar to the higher energy levels of the antisocial lone grazers – Section 2.4.6. Knowing the locations of more waterholes may mean their journeys to water are shorter than black wildebeest and tsessebe. The ability of blue wildebeest and hartebeest to range further from water may facilitate coexistence of all four species.

In summary, MARSC simulated how a wide range of behavioural variation results in a wide range of energy levels (that were within sensible limits), relevant to survival and indicative of the potential adaptive capacity among the populations (Beever et al, 2017). MARSC met expectations that the simulation of this complex ecological system would produce emergent properties, which in some cases were counter-intuitive, which promoted additional lines of analysis of the system - in line with complex systems philosophy.

Based on the assessment of MARSC, the model serves its purpose and is ready to simulate the effect of the different management interventions which are the basis for Chapters 3 and 4. The results and emergent properties highlighted by MARSC in this chapter provide a foundation for the assessment of the effectiveness of habitat management (Chapter 3) and park expansion (Chapter 4).

Chapter 3 Modelling the effects of habitat management on antelope populations under climate change

3.1 Abstract

A key issue for herbivore conservation is the negative impact of climate change on vegetation productivity. Habitat management offers the potential to mitigate this impact of climate change. The objective of this study is to simulate the effect of three different habitat management schemes on a community of antelope species within a South African national park, under two projected climate change scenarios (an intermediate and a worst-case scenario). The schemes comprised different numbers of 500 m x 500 m managed patches of vegetation at different locations within the park. Comparisons of the schemes were based on animals' energy levels within the populations using three parameters (median, high and low energy levels) and whether the schemes selected for specific behaviour or social organisations. Use of three parameters for energy levels revealed variation within factor levels that would not be evident from a single parameter such as the median. Acquired energy levels were broadly similar under the three schemes. Habitat management resulted in higher energy levels compared with no habitat management under the worst-case climate change scenario, but not under the intermediate scenario. However, selection pressures for specific behaviour and social organisation were evident, which may result in reduced behavioural variation and changes to social cohesion among the population under climate change.

3.2 Introduction

This chapter begins with a brief introduction on the potential of habitat management for conservation to mitigate the impact of climate change and explains the importance of this issue. Subsequent sections present simulation results to compare the effectiveness of three different management schemes and also compare the effectiveness of the management schemes with no habitat management. Finally, key findings are discussed, and the merits and demerits of habitat management discussed.

As global temperatures increase under climate change, the frequency and intensity of extreme weather events - such as droughts and heatwaves – will also increase (IPCC, 2021). This in turn has a negative impact on ecosystems, e.g. the 2014-2016 drought in South Africa resulted in reduced grass production, which resulted in herbivore die-offs (Swemmer et al, 2018).

Possible approaches to mitigate this problem are habitat management or habitat restoration. Since the latter involves restoring habitat after it has been degraded, intuitively it seems the better approach would be habitat management, i.e. prevention is better than cure (Possingham et al., 2015). Furthermore, habitat restoration has a poor track record of increasing biodiversity and target species' fitness (Hale & Swearer, 2017; Hale et al., 2020). A possible explanation for this could be the mismatch between human and animal perception of habitat (Hale & Swearer, 2017). Lawton et al (2010) suggested that investment in habitat management was an "absolute priority", and without effective habitat management, most other conservation interventions will fail. The need to mitigate the impact of climate change on habitat is reinforced by the fact that more than 30% of large terrestrial herbivores (mass >= 100 kg) are threatened by habitat loss and the remaining habitat is generally less productive (Ripple et al, 2015).

Whilst much research has focussed on assisting or accommodating species' range shifts in response to climate change, research on assisting species' adaptive capacity *in situ* (e.g. through habitat management) is limited (Greenwood et al., 2016; Pearce-Higgins et al., 2019). This is surprising because a mainstay of conservation is the static fenced protected area, which prevents range shifts beyond its boundary (Monzon et al, 2011). In any event, where species do shift their range, knowledge of *in situ* conservation is required at the new location, otherwise the risk is that all that is *really* happening is the extirpation event is shifted.

There is an urgent need for further research into how *in situ* management can mitigate the vulnerability of populations to climate change impacts (Pearce-Higgins et al.,2019). Furthermore, habitat management is fundamental to maintaining grass cover, in order to counter bush encroachment in savannas (Soto-Shoender et al., 2018). This is relevant as bush encroachment is a potential threat to Mokala's existing habitat heterogeneity (Mokala National Park, 2017) and therefore also to the target species. Consequently, it seems likely that some form of habitat management is required within Mokala.

Habitat management has had successful conservation outcomes for species (Lawton et al, 2010), e.g. in the case of Eld's Deer *Cervus eldii* (Zhang et al, 2019), the silver-spotted skipper butterfly *Hesperia comma* (Lawson et al (2014) and the steppe marmot *Marmota bobak* (Savchenko & Ronkin, 2018). Similarly, habitat management contributed to increased engineering effects of the California ground squirrel *Otospermophilus beecheyi* (an ecosystem engineer), which in turn served to restore degraded habitat to levels suitable for the western burrowing owl Athene *cunicularia hypugaea* (McCullough Hennessy et al, 2016).

Various examples underline the importance of habitat to species conservation. Habitat quality - in terms of abundance, mineral content and digestibility - is correlated with density, reproduction rates, population growth rates and male-biased gender ratios among Cape mountain zebra *Equus zebra zebra* populations (Lea et al, 2016). Lea et al (2016) point out that the Cape mountain zebra, like many species, has in effect, 'refugee' populations, which are restricted to protected areas that comprise suboptimal habitat. The conservation of populations (or entire species) within suboptimal, unsuitable habitat is difficult and ineffective (Lea et al, 2016), and also therefore an inefficient use of limited funds.

A sudden decline in habitat quality was cited as a possible reason for the deaths of 28 out of 30 black lechwe *Kobus leche smithemani* translocated within Zambia (Nyambe et al, 2017). Habitat loss is a key factor in the continued reduced population size of the most endangered antelope, the hirola *Beatragus hunteri* - which can be considered a refugee species, i.e. the entire species is restricted to suboptimal habitat (Ali et al, 2017), and contributed to reduced body size and mass among mouflon *Ovis gmelini musimon* (Garel et al., 2007).

The importance of habitat management increases with our changing environment and it is suggested some species in some areas may require management indefinitely (Osborne & Seddon, 2012). Whilst irrigation may be required, patches of higher quality vegetation created or maintained through management may become self-sustaining, i.e. the habitat is maintained by the grazers (which could theoretically be possible within Mokala). The Serengeti has a number of hotspots - temporally and spatially stable patches with high concentrations of resident herbivore populations (Estes, 2014). These hotspots are characterised by higher mineral concentrations (e.g. sodium, phosphorous and magnesium) in the soil and more importantly, higher leaf concentrations of nitrogen, sodium and magnesium concentrations than surrounding areas (McNaughton, 1988; Anderson et al., 2010). The mineral differences are not due to physical or geological attributes (McNaughton, 1988). These hotspots may originate from ancient disused cattle enclosures - cattle’s urine and faeces originally enriched the soil and these patches have since been similarly maintained and fertilised by wild herbivores (Reid, 2012; Estes, 2014).

Habitat management could also become self-sustaining within Mokala, due to the niche separation among the target species: wildebeest prefer young fresh leaves, tsessebe are intermediate in their preference, while hartebeest favour green leaves among late growth stages (Murray & Brown, 1993; Estes, 2014). Therefore, patches could be initially grazed by wildebeest, but then abandoned if overgrazed, allowing grass to grow (assuming the wildebeest do not return) which then attracts topi, which could again lead to subsequent abandonment due to overgrazing, allowing grass to grow (assuming the topi do not return) to be replaced by hartebeest. Alternatively, some managed areas could be temporarily fenced off to ensure different growth stages to suit the different species.

Although the threats to species from habitat loss and climate change have received much attention, the interaction between these factors has received less attention, yet it also represents a major threat (Mantyka-Pringle et al.,2012; Segan et al., 2016). For savanna/grassland biomes, increasing temperatures - as predicted for Mokala (Mokala National Park, 2017) - are likely to increase the negative impact of habitat loss or fragmentation on species (Mantyka-Pringle et al.,2012; Segan et al., 2016).

The main benefit of habitat management is maintenance of population levels by ensuring a constant food supply as resources decline, thereby allowing populations to persist (Lea et al, 2016). For example, habitat management resulted in a 15% increase in fawn survival rates and an 8% increase in body fat in adult females among mule deer *Odocoileus hemionus* over winter, compared with unmanaged locations, although this did not translate into higher densities as the authors had expected (Bergman et al 2014a, 2014b, 2015). Management can also prevent ecological traps (Schlaepfer et al, 2002) - grazers' returning to maintained patches will still find good quality grazing.

Habitat management offers additional benefits for conservation. For example it represents a cheaper, more responsive and straightforward option compared with alternatives such as habitat restoration (Possingham et al., 2015), or the gazetting of new PAs which may be fraught with challenges from politicians and local communities (Pringle, 2017).

Habitat management could also complement park expansion - which is another option to mitigate the impact of climate change (discussed in Chapter 4). For example, managed patches that are relatively close to the boundary between the existing park and proposed expansion areas, could encourage colonisation of the expansion areas, i.e. acting as stepping-stones.

The aim of this study is to simulate how habitat management impacts on the adaptive capacity of antelope populations to mitigate the effect of climate change. A fundamental advantage of running a computer simulation is that various different habitat management schemes can be compared under different future climate scenarios, which would not be practical in the real world, due to the costs and timescales involved. The study compares the effectiveness of three different levels of habitat management on a community of antelope populations within Mokala National Park, South Africa, under different climate change scenarios (an intermediate and a worst-case scenario) using an agent-based model. The species are blue wildebeest *Connochaetes taurinus*, black wildebeest *Connochaetes gnou*, tsessebe (also known as topi) *Damaliscus lunatus* and red hartebeest *Alcelaphus buselaphus.*

There are three key objectives of the study. First, to compare the habitat management schemes, based on grazers' energy levels under the two climate change scenarios. Energy levels provide an indication of the effects of habitat management on population persistence. Second, to assess and compare how behavioural variation and social organisation contribute to the capacity of the antelope populations to adapt to climate change within the habitat management schemes. Third, to evaluate whether habitat management selects for specific behaviour or social organisation within the populations (the social organisation comprises herd leaders and followers, and lone grazers).

Objectives two and three were also based on grazers' energy levels. Determining the benefits of habitat management in terms of grazers' energy levels is important, but consideration is also needed of whether habitat management selects for specific behaviour or social group, effectively reducing behavioural variation or affecting the social cohesion of the populations. Reduction in behavioural variation within populations would reduce the adaptive capacity in mitigating climate change impacts (Beever et al (2017). The results facilitate identification of the most efficient management scheme, and also highlight potential disadvantages resulting from reduced behavioural variation or changes in social structure within the populations.

Regardless of what form they take, conservation interventions need to be tested to determine their effectiveness (Akçakaya et al., 2014; Greenwood et al, 2016). The purpose of the simulation was to test the potential effectiveness of different management interventions under future scenarios, which would not be practical *in situ*, i.e. the research is exploratory in nature - there was no ground truthing.

3.3 Methods

The simulation used the MARSC model validated in Chapter 2 but with an amended landscape, therefore the following sections describe the habitat management schemes, the statistical analysis and include just a brief overview of the model.

3.3.1 The model

Simulations were run using the MARSC model with the landscape modified to incorporate three alternative habitat management schemes within Mokala National Park. Chapter 2 (Section 2.3.3) provides a full description of the model and the representation of the landscape. MARSC simulates grazers moving across the Mokala landscape, developing a spatial memory of resource locations of grazing patches and waterholes. The population comprises lone individuals and herds who respond to environmental and internal physiological cues and to conspecifics.

The total run size was 2160 runs (648,000 grazer records), with 1080 runs for each of the climate change scenarios. Each climate change scenario comprised 360 runs for each of the three habitat management schemes. The choice of run size was a balance between obtaining meaningful data and time constraints. Each run comprised 300 agents (75 agents per species) and simulated their behaviour over 30 days. For each run, the agents are initially located randomly and assigned random headings. At the start of each run agents have no knowledge of the landscape.

3.3.2 Habitat management schemes

Vegetation productivity levels within Mokala were indicated by the EVI value of each pixel (see section 2.3.4). Three different levels of habitat management were simulated, referred to as Minimum, Maximum and LowEVI. Each level incorporated patches of 500m x 500m maintained at an EVI value of at least 112 (or pre-existing level if higher) within the park. The patches offer grazers consistent areas of foraging as resources decline across the park. The choice of 112 as the EVI value was based on the upper range of mean recorded NDVI values for the Negev desert in Israel, which is subject to continuous rehabilitation and has dry and wet seasons (Dall'Olmo & Karnieli, 2002), therefore it was assumed to represent a reasonable proxy measure. The NDVI values were multiplied by 0.67 to convert to EVI (Kawamura et al., 2005b). The number of patches for the three levels were: Minimum - 8; Maximum - 32; Low EVI - 17. The distribution of these patches is shown in Figs 3.1 – 3.3.

Fig 3.1. Location of managed patches for the Low EVI habitat management scheme

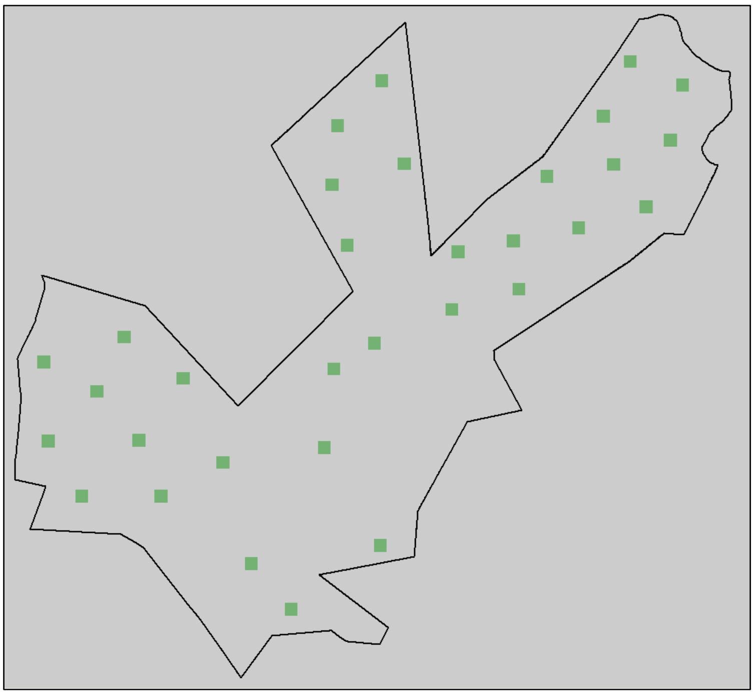

Fig 3.2. Location of managed patches for the Maximum habitat management scheme

Fig 3.3. Location of managed patches for the Minimum habitat management scheme

The locations of managed patches were at or near waterholes (to facilitate irrigation of the patches) and to distribute patches relatively evenly across the park for the Maximum and Minimum management schemes. In the case of the Low EVI habitat management scheme, patches were located in areas of low productivity (low EVI values).

Initially there were no managed patches in the park's central region, partly due to the presence of a seasonal river and the surrounding area normally has high EVI values, but also due to the assumption that the area's rocky terrain is unsuitable for management. However, expert advice (Johann de Klerk, Manager, Mokala National Park) suggested locating some patches in this region as it is used by the target species when resources are lacking elsewhere in the park. The distribution of patches within the three levels were deemed reasonable by Johann de Klerk, Manager, Mokala National Park (pers. comm.).

3.3.3 Statistical analysis

Randomisation tests were performed to assess if the factor levels (the different behavioural types and social groups) affected the response variable (grazers' energy levels), based on a threshold of $p < 0.05$. The factor levels were randomised 5000 times. Three parameters for the response variable were used in the analysis: the standard median (i.e. 100% of the data); the median of data < 1st decile (the lowest 10% of data) - also referred to as the least successful grazers, and the median of data > 9th decile (the highest 10% of data) - also referred to as the most successful grazers. The energy levels of the least and most successful grazers were included as response parameters to facilitate comparison of groups across a wide range of behaviour - a key objective of this study. Chapter 2 (Section 2.3.5) describes the statistical methods in full.

3.4 Results

Note that within the boxplots, the blue lines indicate the median of data < 1st decile (the least successful grazers)., the red lines indicate the median of data > 9th decile (the most successful grazers). The results in relation to memory use were not particularly informative and so are not described in this chapter.

3.4.1 Model responsiveness to different habitat management scenarios

The type of habitat management schemes influenced grazers' energy levels in all cases, although generally the difference in MJ between management schemes was small (< 0.5 MJ) for both EVI scenarios, with the exception of the least successful grazers under EVI-30% (Table 3.1). The least successful grazers gained the highest energy levels with the Minimum habitat management scheme (Fig 3.4), which was unexpected.

Grazers in the maximum habitat management scheme acquired higher median energy levels compared with the other schemes under EVI-60% (Fig 3.5), while the lowest median energy levels were acquired under Minimum habitat management as expected, although for the most successful grazers the difference between schemes was minimal (Table 3.1).

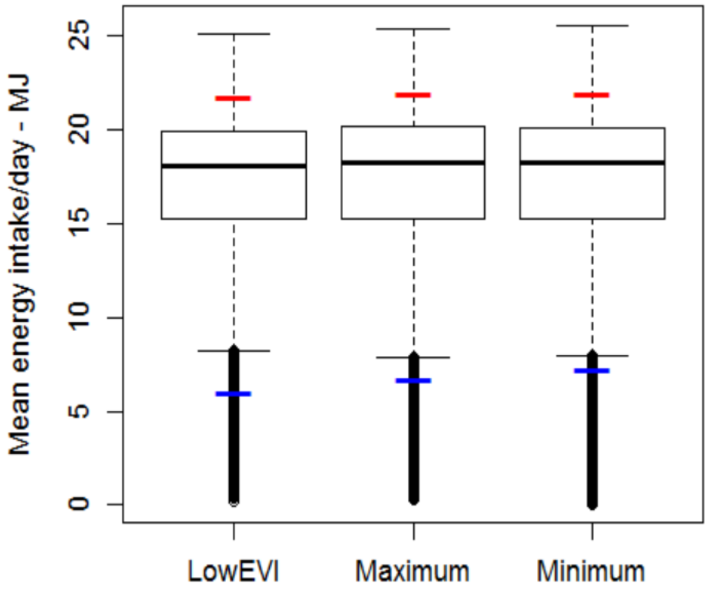

Fig 3.4. Differences in energy levels for all grazers across the three habitat management scenarios, under the EVI-30% scenario.

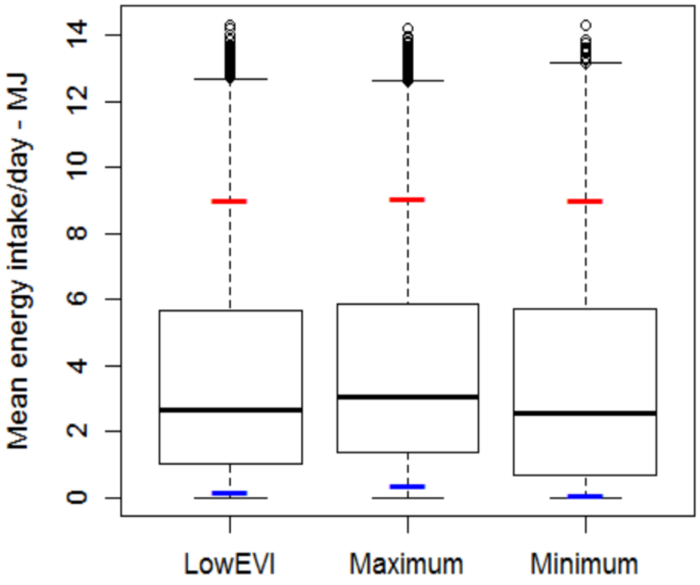

Fig 3.5 Differences in energy levels for all grazers across the three habitat management scenarios, under the EVI-60% scenario.

Table 3.1. Randomisation test results highlight the influence of the type of habitat management on grazers' energy levels.

EVI scenario	Proportion of randomized ranges ≥ actual range (actual range MJ)		
	< 1st decile	= median	> 9th decile
-30%	< 0.001 (1.21)	< 0.001 (0.19)	< 0.001 (0.19)
-60%	< 0.001 (0.31)	< 0.001 (0.48)	0.04 (0.05)

3.4.2 Capturing differences between exploratory and non-exploratory behaviour of agents

Generally the level of exploratory behaviour affected the energy levels acquired by grazers (Table 3.2) for both EVI-30% and EVI-60% scenarios, though the difference in energy levels (MJ) was greater for the former. Under the Minimum habitat management scheme for EVI-30%, the results suggest the least successful grazers' energy levels were not affected by the level of exploratory behaviour (Table 3.2). Nonetheless, the actual difference (0.4 MJ/day) could represent a significant difference for grazers in the two groups in terms of fitness and survival. Note that this section follows the same convention as Section 2.4.2 - grazers with memory type "none" and followers were excluded.

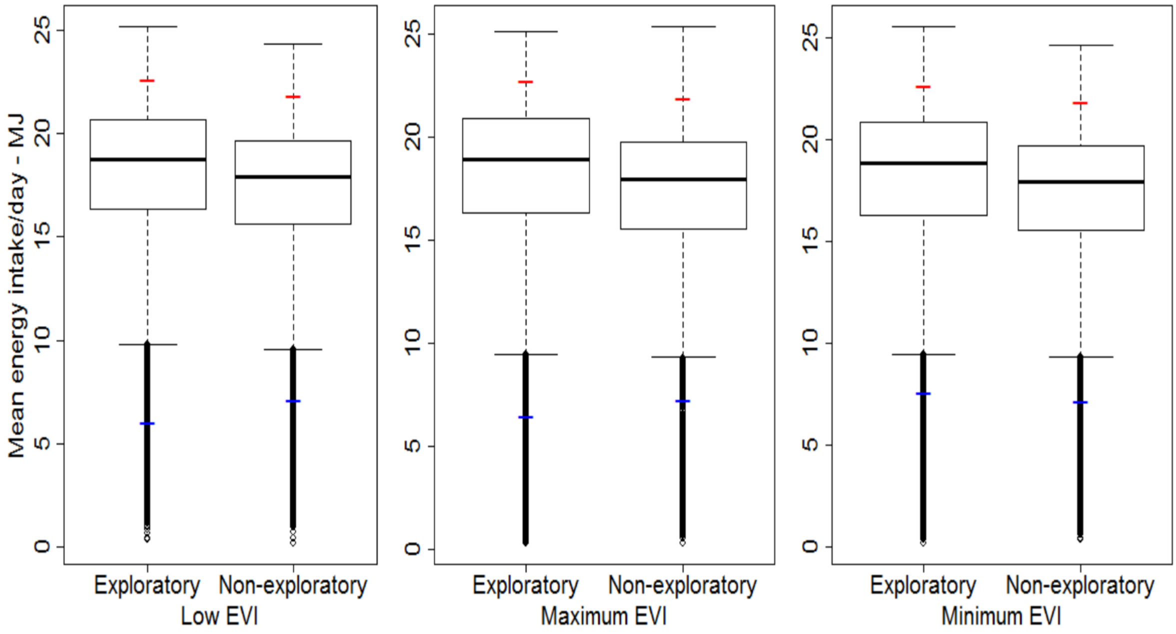

Fig 3.6. Comparison of the different energy levels for exploratory and non-exploratory grazers under EVI-30%, across the habitat management scenarios.

Energy levels were broadly similar across the management schemes under EVI-30% (Fig 3.6) but among the least successful grazers levels were notably higher for exploratory grazers under Minimum habitat management. Under EVI-30%, among the most successful grazers and those at the median level, exploratory behaviour resulted in higher energy levels than non-exploratory behaviour for all habitat management schemes (Fig 3.6). The situation was reversed for the least successful grazers for the Low EVI and Maximum habitat schemes, with the exploratory grazers achieving lower energy levels.

Table 3.2 Randomisation test results for the effect of exploratory behaviour on energy levels.

EVI scenario	**Habitat mgmt scheme**	Proportion of randomized ranges ≥ actual range (actual range MJ)		
		< 1st decile	= median	> 9th decile
-30%	Low EVI	0.001 (1.03)	< 0.001 (0.84)	< 0.001 (0.76)
-30%	Max	0.02 (0.84)	< 0.001 (0.93)	< 0.001 (0.80)
-30%	Min	0.07 (0.4)	< 0.001 (0.87)	< 0.001 (0.85)
-60%	Low EVI	< 0.001 (0.02)	< 0.001 (0.47)	< 0.001 (0.20)
-60%	Max	< 0.001 (0.05)	< 0.001 (0.73)	< 0.001 (0.37)
-60%	Min	0.009 (0.05)	< 0.001 (0.48)	< 0.001 (0.30)

For EVI-60%, grazers obtained higher energy levels under Maximum habitat management and in other respects results were the opposite of the EVI-30% results: non-exploratory grazers achieved higher energy levels (although generally the difference was less than 0.5 MJ) among the median and the most successful grazers (Fig 3.7, Table 3.2).

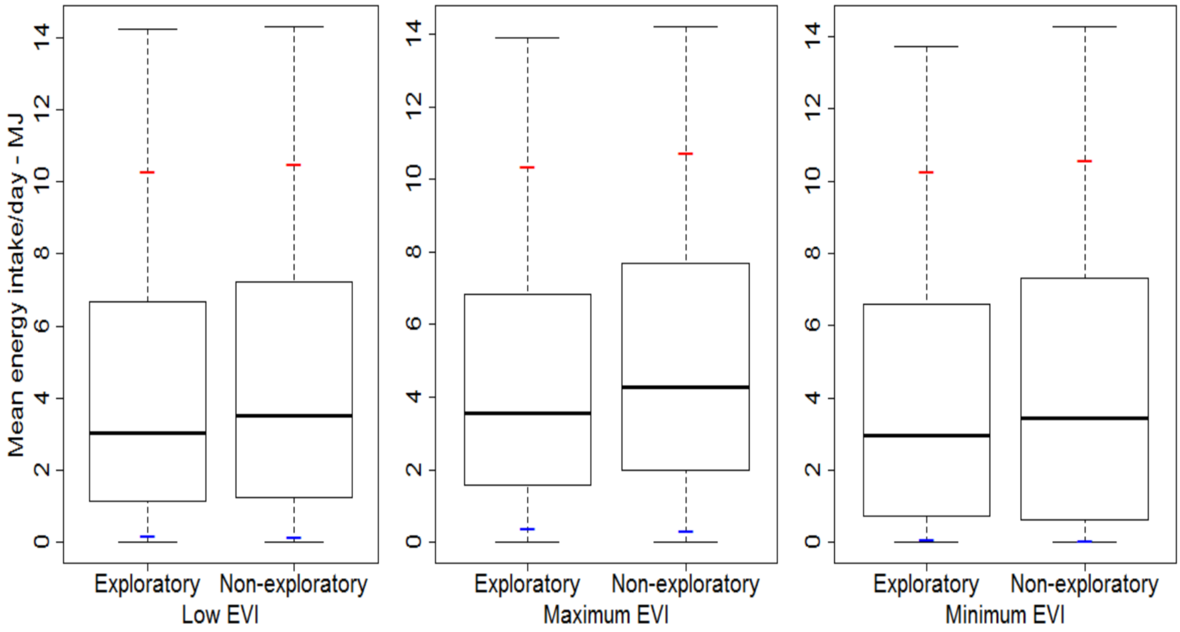

Fig 3.7. Comparison of the different energy levels for exploratory and non-exploratory grazers across the habitat management schemes, under EVI-60%.

3.4.3 Capturing the effect of social organisation on individual energy intake

3.4.3.1 Differences under the EVI-30% scenario

Social organisation influenced energy levels for most of the grazers (Table 3.3) under EVI-30% but was less influential among the least successful grazers. Generally, leaders acquired higher energy levels than followers and lone grazers (Figs 3.8 and 3.9). Followers also acquired higher energy levels than lone grazers, although a direct comparison is not shown (but comparisons can be drawn between follower values in Fig 3.8 and lone grazer values in Fig 3.9). Among the least successful grazers, social organisation did not affect energy levels under the Low EVI habitat management scheme, likewise, leaders and lone grazers did not differ under the Maximum management scheme, and followers and leaders did not differ under the Minimum management scheme (Table 3.3).

Energy levels of the different social groups were similar across the three habitat management schemes among grazers achieving median or the highest energy levels (Figs 3.8 and 3.9). In contrast, energy levels among the least successful grazers were more variable across the management schemes. Energy levels for the least successful grazers were highest under Minimum habitat management for leaders and followers. Surprisingly, among these less successful grazers, leaders' energy levels were slightly lower than followers for the Low EVI (although not statistically significant) and Maximum habitat management schemes (Fig 3.8).

Table 3.3. Randomisation test results for the effect of social group on energy levels - EVI-30%.

Habitat mgmt scheme	**Social pairings**	Proportion of randomized ranges ≥ actual range (actual range MJ)		
		< 1st decile	< 1st decile	< 1st decile
Low EVI	Follower/Leader	0.13 (0.28)	< 0.001 (1.28)	< 0.001 (1.42)
Low EVI	Lone/Leader	0.82 (0.04)	< 0.001 (1.58)	< 0.001 (1.92)
Low EVI	Lone/Follower	0.11 (0.32)	< 0.001 (0.30)	< 0.001 (0.50)
Max	Follower/Leader	0.047 (0.37)	< 0.001 (1.26)	< 0.001 (1.39)
Max	Lone/Leader	0.52 (0.19)	< 0.001 (1.66)	< 0.001 (1.97)
Max	Lone/Follower	0.01 (0.56)	< 0.001 (0.41)	< 0.001 (0.58)
Min	Follower/Leader	0.64 (0.06)	< 0.001 (1.23)	< 0.001 (1.36)
Min	Lone/Leader	< 0.001 (1.13)	< 0.001 (1.67)	< 0.001 (2.02)
Min	Lone/Follower	< 0.001 (1.19)	< 0.001 (0.44)	< 0.001 (0.65)

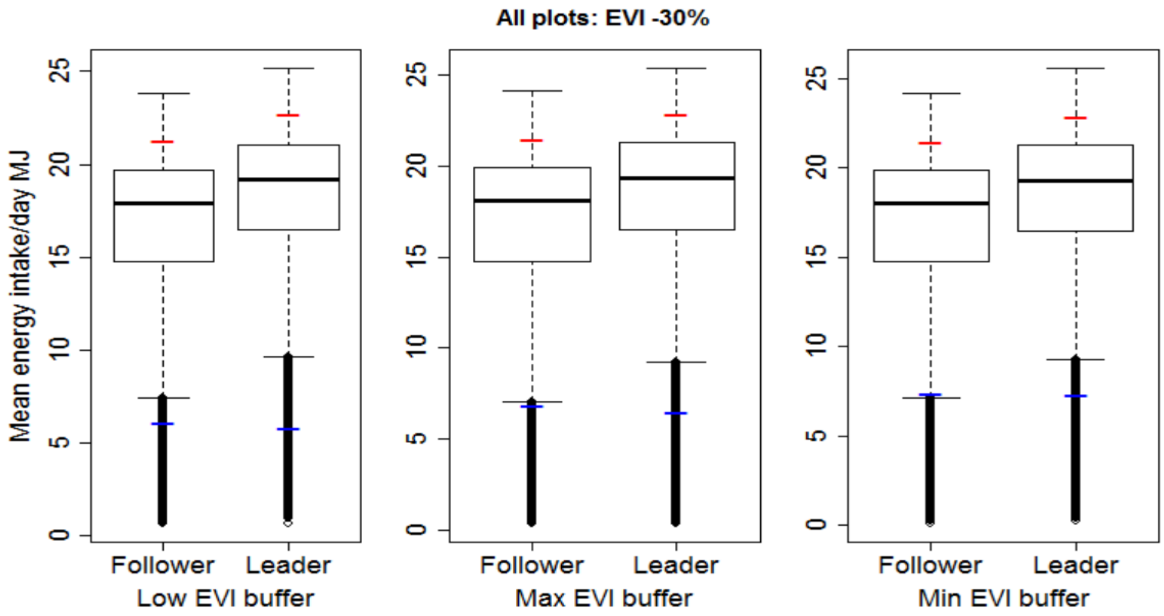

Fig 3.8. Differences in energy levels between followers and leaders across the three habitat management scenarios, for the EVI-30% scenario.

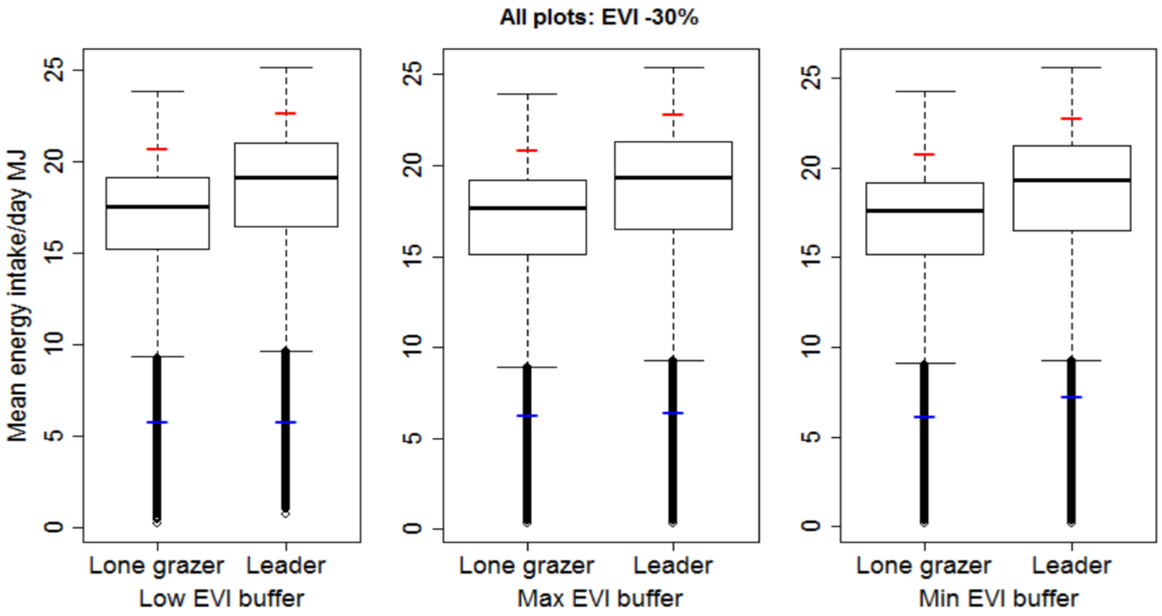

Fig 3.9. Differences in energy levels between lone grazers and leaders across the three habitat management scenarios, for the EVI-30% scenario. The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile.

3.4.3.2 Differences under the EVI-60% scenario

As expected, leaders had higher energy levels than followers, for all habitat management schemes, energy levels of leaders were more than 2 MJ higher than followers' energy levels (Fig 3.10, Table 3.4). Although leaders achieved higher energy levels than lone grazers, across all habitat management schemes the difference was less than 0.9 MJ; noticeably less than for EVI-30%. However, leaders' energy levels were only marginally higher than lone grazers at the median level under the Maximum habitat management scheme (Fig 3.11, Table 3.4). Under EVI-60%, the most surprising finding was that among the most successful grazers, lone grazers acquired higher energy levels than followers for all habitat management schemes (Fig 3.12), this was also the case at the median level for the Maximum habitat management scheme.

Social organisation influenced all grazers' energy levels, with two exceptions: energy levels of the least successful followers and leaders did not differ under the Low EVI and Minimum habitat management scenarios (Table 3.4). Note however that for the least successful grazers, actual differences in energy levels between social groups were very small - the largest difference was 0.1 MJ.

Table 3.4 Randomisation test results for the effect of social group on energy levels - EVI-60%

Habitat mgmt scheme	**Social pairings**	Proportion of randomized ranges ≥ actual range (actual range MJ)		
		< 1st decile	= median	> 9th decile
Low EVI	Follower/Leader	0.19 (0.002)	< 0.001 (0.48)	< 0.001 (2.07)
Low EVI	Lone/Leader	< 0.001 (0.04)	< 0.001 (0.40)	< 0.001 (0.78)
Low EVI	Lone/Follower	< 0.001 (0.04)	< 0.001 (0.08)	< 0.001 (1.29)
Max	Follower/Leader	< 0.001 (0.1)	< 0.001 (0.58)	< 0.001 (2.18)
Max	Lone/Leader	< 0.001 (0.08)	< 0.001 (0.18)	< 0.001 (0.72)
Max	Lone/Follower	< 0.001 (0.1)	< 0.001 (0.40)	< 0.001 (1.46)
Min	Follower/Leader	1.0 (0.0)	< 0.001 (0.45)	< 0.001 (2.15)
Min	Lone/Leader	< 0.001 (0.05)	< 0.001 (0.56)	< 0.001 (0.86)
Min	Lone/Follower	< 0.001 (0.05)	0.01 (0.11)	< 0.001 (1.28)

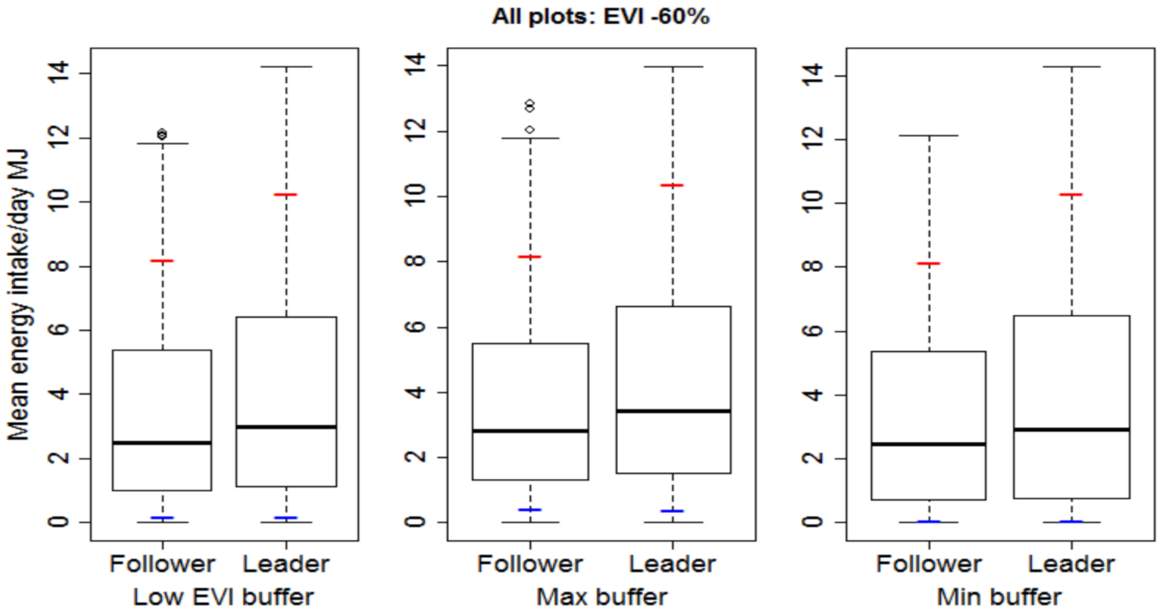

Fig 3.10. Differences in energy levels between followers and leaders across the three habitat management scenarios, for the EVI-60% scenario. The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile.

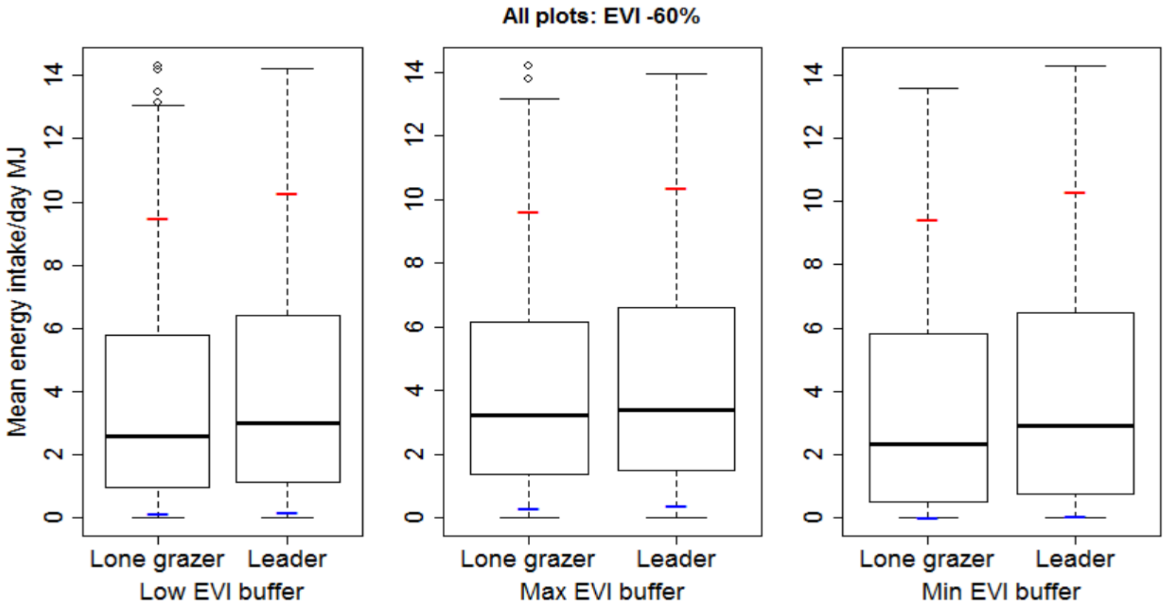

Fig 3.11. Differences in energy levels between lone grazers and leaders across the three habitat management scenarios, for the EVI-60% scenario. The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile.

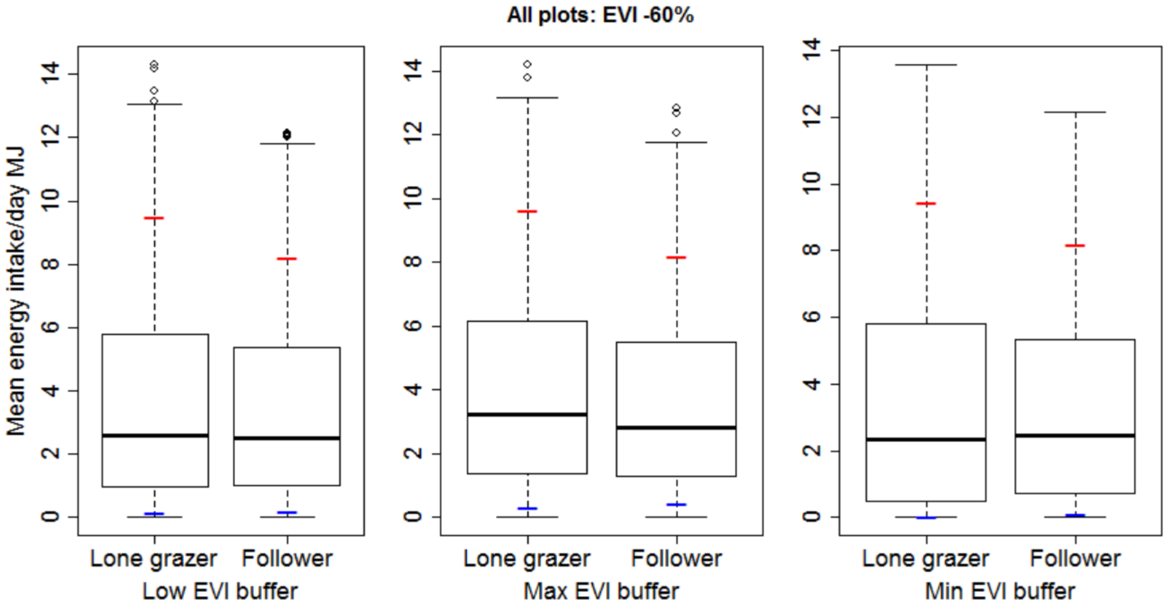

Fig 3.12. Differences in energy levels between lone grazers and followers across the three habitat management scenarios, for the EVI-60% scenario. The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile.

3.4.4 Lone grazers: antisocial v social behaviour

Sociability influenced grazers' energy levels across all habitat management schemes (Table 3.5). The greatest differences between groups were among the least successful grazers, for the Minimum habitat management scheme the difference was 5.17 MJ (Table 3.5). Median energy levels for social grazers were noticeably higher for the Maximum habitat management scheme compared with the other schemes (Fig 3.13). Variation within groups was evident. For example, antisocial grazers acquired higher energy levels than social grazers for all habitat management scenarios for the median and particularly the least successful grazers (Fig 3.13). However, the most successful social lone grazers had higher energy levels than the most successful antisocial grazers.

The IQR for antisocial grazers was smaller, compared with social lone grazers (Fig 3.13). In particular, the 25th percentile for social grazers was much lower than for antisocial grazers. Similarly the range between the least successful and most successful grazers was smaller for antisocial grazers (Fig 3.13).

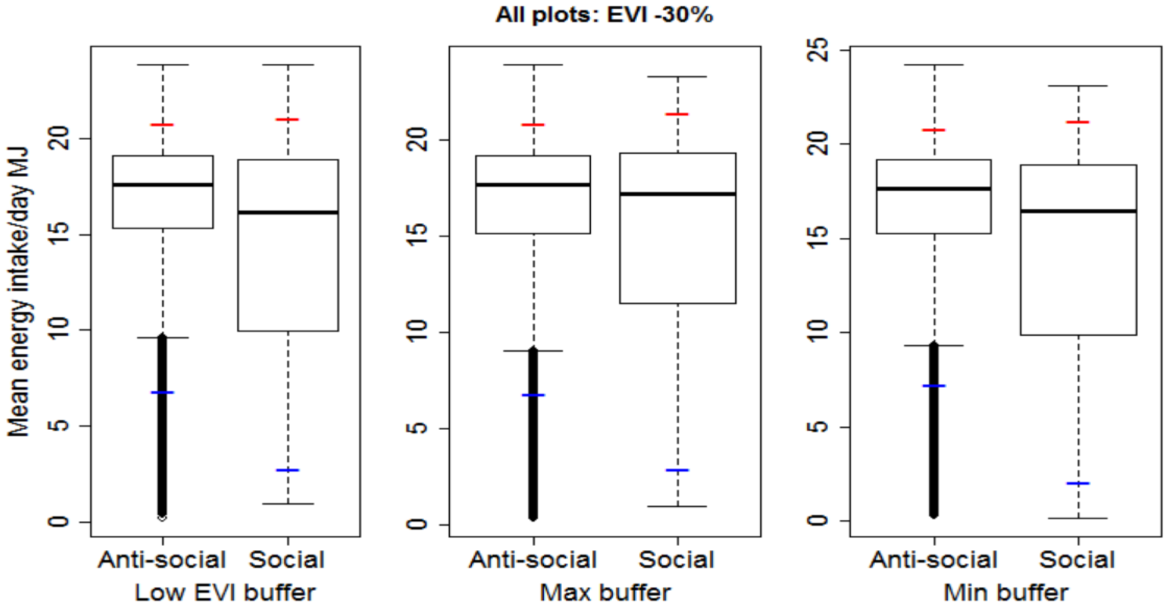

Fig 3.13. Comparison of the difference in energy levels between antisocial and social lone grazers, across the habitat management scenarios. The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile.

Under the worst-case scenario (EVI-60%), antisocial lone grazers achieved higher energy levels than social lone grazers for all habitat management schemes (Fig 3.14). As with EVI-30%, energy levels for social grazers were highest under the Maximum habitat management scheme. In contrast with EVI-30%, antisocial grazers exhibited a greater range of energy levels than social grazers, particularly the IQR for the Low EVI and Minimum habitat management schemes (Fig 3.14).

Table 3.5 Randomisation test results for the effect of sociability among lone grazers on energy levels.

EVI scenario	**Habitat mgmt scheme**	Proportion of randomized ranges ≥ actual range (actual range MJ)		
		< 1st decile	= median	> 9th decile
-30%	Low EVI	< 0.001 (4.09 MJ)	< 0.001 (1.48 MJ)	< 0.001 (0.28 MJ)
-30%	Max	< 0.001 (3.88 MJ)	< 0.001 (0.48 MJ)	< 0.001 (0.58 MJ)
-30%	Min	< 0.001 (5.17 MJ)	< 0.001 (1.19 MJ)	< 0.001 (0.45 MJ)
-60%	Low EVI	< 0.001 (0.14 MJ)	< 0.001 (1.16 MJ)	< 0.001 (1.16 MJ)
-60%	Max	0.001 (0.05 MJ)	0.01 (0.29 MJ)	< 0.001 (0.52 MJ)
-60%	Min	0.001 (0.05 MJ)	< 0.001 (1.38 MJ)	< 0.001 (1.31 MJ)

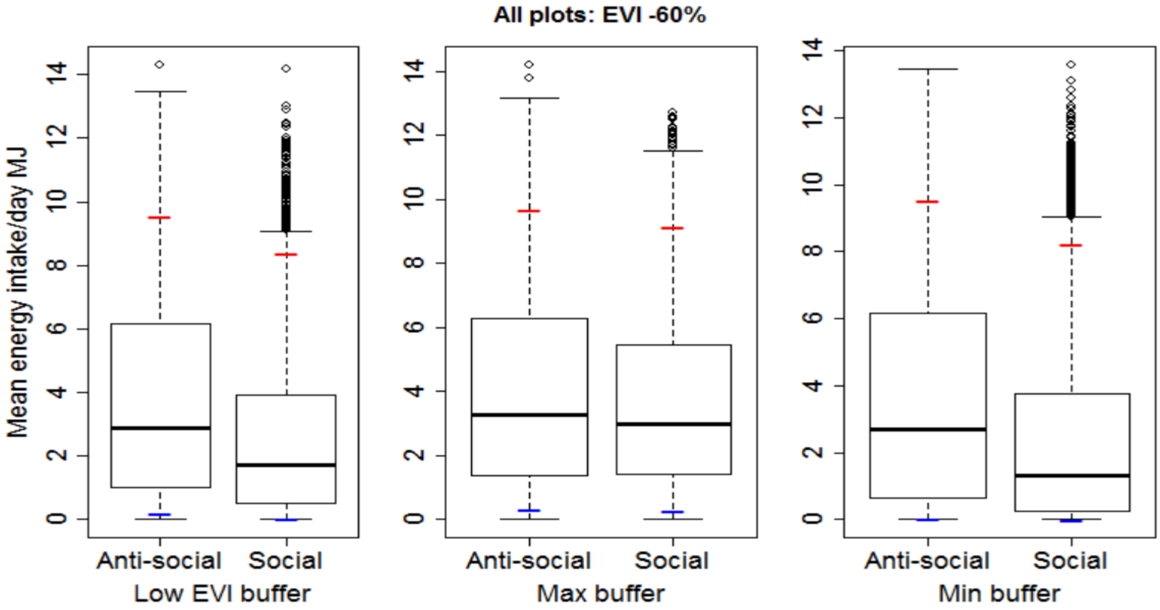

Fig 3.14. Comparison of the difference in energy levels between antisocial and social lone grazers, across the EVI scenarios. The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile.

3.4.5 Inter-specific comparisons

The most interesting result was that under EVI-60% most grazers failed to acquire their required energy levels, in the case of blue wildebeest only a limited number of outliers equalled or exceeded the required levels (Fig 3.16). In contrast, the majority of grazers for all species exceeded their required energy levels under EVI-30% (Fig 3.15). The required (FMR) levels were between the 25th percentile and the median level of the least successful grazers (Fig 3.15), i.e. more than 75% of grazers exceeded their required energy levels. Note that for comparisons of acquired and required energy levels, the bottom of the range of FMR values was used (see Section 2.3.3).

Energy levels were influenced by grazers' species in most, but not all, cases (Table 3.6). Actual differences in MJ were much higher under EVI-30% across all habitat management schemes - at the median level they exceeded 2 MJ (Table 3.6). Under EVI-30% a pattern emerged of blue wildebeest achieving highest energy levels with hartebeest having slightly lower energy levels, and tsessebe and black wildebeest both achieving similar but lower energy levels (Fig 3.15 - median and the most successful grazers). This pattern was less pronounced for the least successful grazers for the Low

EVI and Minimum habitat management schemes. Median energy levels were broadly similar for Maximum and Minimum habitat management, with levels slightly lower for the LowEVI management scheme (3.15). Energy levels of the least successful grazers were lower under the Low EVI management scheme for all species.

Results for EVI-60% were the reverse of EVI-30% on two counts: first, differences in energy levels between species were much lower than for EVI-30% (Table 3.6, Fig 3.16). Second, energy levels were notably higher under the Maximum management scheme for grazers at the median energy level (Fig 3.16). Differences in the median values between species for the Low EVI and Maximum habitat management schemes were not statistically significant (Table 3.6).

Table 3.6 Randomisation test results for the effect of species on energy levels.

EVI scenario	**Habitat mgmt scheme**	Proportion of randomized ranges ≥ actual range (actual range MJ)		
		< 1st decile	= median	> 9th decile
-30%	Low EVI	< 0.001 (1.47 MJ)	< 0.001 (2.21 MJ)	< 0.001 (2.01 MJ)
-30%	Max	< 0.001 (1.87 MJ)	< 0.001 (2.08 MJ)	< 0.001 (1.64 MJ)
-30%	Min	< 0.001 (0.74 MJ)	< 0.001 (2.08 MJ)	< 0.001 (1.65 MJ)
-60%	Low EVI	< 0.001 (0.15 MJ)	0.36 (0.07 MJ)	< 0.001 (0.29 MJ)
-60%	Max	< 0.001 (0.05 MJ)	0.05 (0.10 MJ)	< 0.001 (0.20 MJ)
-60%	Min	< 0.001 (0.05 MJ)	0.03 (0.13 MJ)	< 0.001 (0.32 MJ)

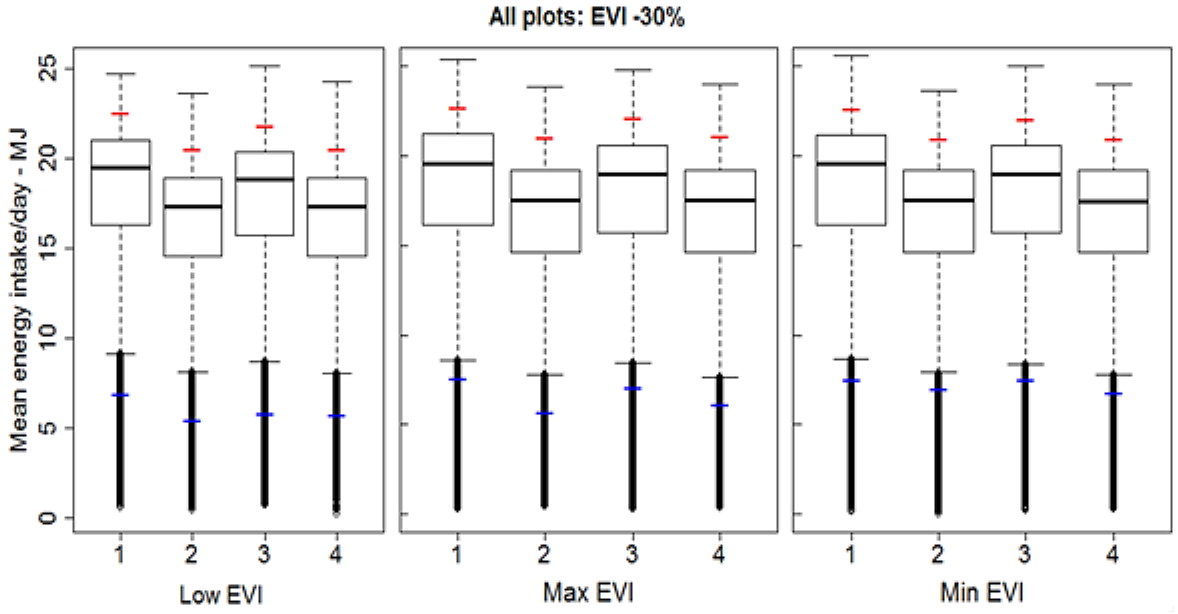

Fig 3.15. Inter-Specific differences in acquired energy levels across the different habitat management schemes for EVI-30%. Species with FMR values (MJ/day) in brackets: 1 - blue wildebeest (13.51); 2 - black wildebeest (10.25); 3 - hartebeest (12.63); 4 - tsessebe (9.74).

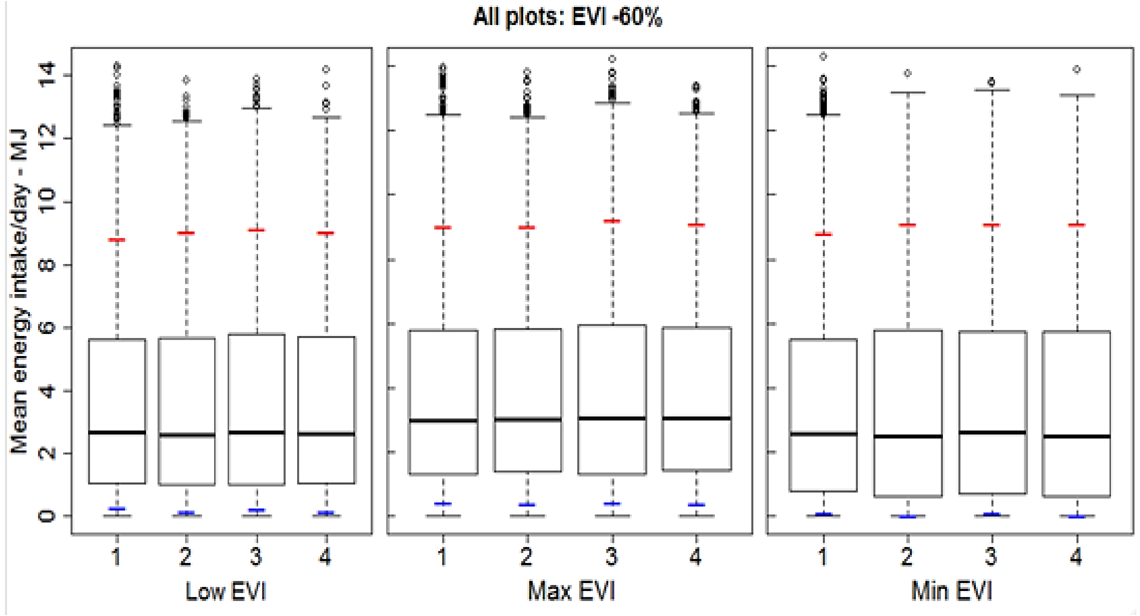

Fig 3.16. Inter-Specific differences in acquired energy levels across the different habitat management schemes for EVI-60%. Species with FMR values (MJ/day) in brackets: 1 - blue wildebeest (13.51); 2 - black wildebeest (10.25); 3 - hartebeest (12.63); 4 - tsessebe (9.74). Blue lines indicate the median of data < 1st decile, red lines indicate the median of data > 9th decile. The Y-axis scale is the same across the plots.

3.5 Discussion

3.5.1 The impact of different habitat management schemes

Generally there were only minimal differences between habitat management schemes in terms of acquired energy levels. Whilst these differences were small, two key points need to be considered which frame this Discussion. First, assuming blue wildebeest can survive on stored body fat for perhaps one month (Rysava et al, 2016) and that this ability is broadly applicable to the other three target species also (given the paucity of data in this area), then small increases in energy levels are assumed to be important in allowing more individuals to survive until conditions improve. Small differences in energy levels are important when animals function at close to their limit, e.g. the migratory Serengeti wildebeest are at starvation level much of the time but survive by mobilising fat reserves when needed from bone marrow (Grant Hopcraft – pers. comm.). This Discussion proceeds on the assumption that small differences in energy levels do matter to individuals.

Second, the purpose of the simulation was to explore possibilities. For example, the higher median energy levels for the Maximum habitat scheme under EVI60% suggest that different levels and/or configurations of habitat management can produce higher energy gains for grazers. Further simulations could assess if different configurations of habitat management produce greater differences. Increased numbers of patches and targeting of poor quality areas should yield higher energy gains for grazers (Bergman et al., 2014a). This demonstrates a key benefit of simulation, comparing a number of alternative habitat management schemes would not be possible in the real world. The simulations also suggest increased management *is* needed given the low or extremely low (or zero!) energy levels for all but the most successful grazers under EVI-60%. The findings add to the research on conserving species *in situ* through the potential of their adaptive capacity, which has received little attention thus far (Greenwood et al., 2016; Pearce-Higgins et al.,2019).

3.5.2 Exploratory and non-exploratory behaviour

The finding that both groups achieved higher energy levels with the Maximum habitat management scheme under EVI-60%, compared with the other Management schemes and no habitat management is logical. With the highest number of managed patches, Maximum habitat management increases the likelihood of exploratory grazers locating these patches and of non-exploratory grazers having these patches within their home range. The pattern of exploratory behaviour resulting in higher energy levels under EVI-30%, but lower levels for EVI-60% is consistent with the results for the no habitat management simulation (Chapter 2). This suggests the presence of a threshold between the two EVI scenarios which affects behaviour and foraging success.

The higher energy levels for non-exploratory grazers under EVI-60% agrees with the findings of Hefty & Stewart (2019) and supports the view that this behaviour results in more thorough, efficient search behaviour (Sulikowski, 2017). The reduced energy levels of the exploratory grazers support the view that the behaviour of exploratory grazers is maladaptive in changing environments (Coppens et al., 2010). This is an example of an emergent property, i.e. the difference in energy levels was not a direct result of the programming code.

The deleterious impact of the lower energy levels of exploratory grazers under EVI-60% may be compounded by their higher energy requirements compared with less exploratory individuals (Careau et al., 2008) as they experience a higher deficit between energy intake and energy requirements. Despite these findings which favour non-exploratory grazers as habitat changes and declines, future environmental stochasticity (e.g. drought or extreme weather events) may represent a selection for exploratory behaviour if the home ranges of non-exploratory grazers offer only poor quality forage.

3.5.3 The effect of social organisation on agents energy levels

That leaders were more successful in terms of energy intake than followers and lone grazers, but lone grazers were also more successful than followers in some situations, is in agreement with the finding of Patin et al. (2019). Within MARSC, leaders benefit from being decision-makers - they decide when to move and where to move, i.e. they select resource rich patches that they are familiar with. Within the model developed by Patin et al (2019), followers were less vigilant than leaders as they needed to spend more time foraging since they had no control over when to move to more resource rich patches. The finding that followers can be more disadvantaged than leaders or lone grazers raises the possibility of future generations of these gregarious antelope species becoming mostly solitary, or at least suggests possible disruption to the social organisation of gregarious species.

Other foraging simulations also found that solitary individuals' food intake rate was higher than group members (e.g. Beecham and Farnsworth, 1998; Beauchamp & Ruxton, 2005). An interesting finding of Beauchamp & Ruxton (2005) was that when a limited amount of role reversal was included (solitary foragers join groups or group members become solitary foragers) an initial population comprising only group foragers could be invaded and replaced by individual foragers. The solitary foragers would then dominate, with only sporadic, short-lived outbreaks of group foragers.

The finding that among the least successful grazers, leaders acquired slightly lower energy levels than followers under EVI-30% for the Low EVI and Maximum habitat management schemes is puzzling, especially as their energy levels were between 5 - 7 MJ. It is not surprising that all of the least successful grazers achieve very low energy levels (typically close to zero) under the worst-case scenario (EVI-60%), regardless of traits. The *median* energy levels for leaders were clearly higher than followers under EVI-60% across all schemes (2 - 4 MJ), but they were much lower than the median levels for the least successful grazers under EVI-30%. So this anomalous finding for EVI-30% was not due to particularly low energy values.

3.5.4 Lone grazers: antisocial v social

The provision of more managed patches under Maximum habitat management offers two potential benefits. First, the increased energy levels of social lone grazers increase the likelihood of maintaining stable social organisation within the populations. In other words, otherwise low energy levels among many social lone grazers may promote increased numbers of antisocial individuals, eventually leading to the extirpation of herds within the populations. This reflects the finding of Beauchamp & Ruxton (2005) that populations can switch from only containing herds to only lone individuals, a prospect that may occur more readily given the flexible nature of the target species' social organisation (Estes, 1992). Second, grazing conspecifics at managed patches may attract social lone grazers which, apart from the benefit of foraging on this better quality grazing, increases the likelihood that they join existing herds or form new herds at these patches.

3.5.5 Interspecific differences in acquired energy levels

The pattern of blue wildebeest and hartebeest gaining the highest energy levels under EVI-30%, regardless of habitat management scheme, suggests an advantage to being less water dependent, which allows further exploration increasing the likelihood of finding more grazing patches. Nonetheless, the lower energy levels of black wildebeest and tsessebe may be offset by two factors: first, if their smaller size correlates with reduced energy requirements; second, the higher surface area-to-mass ratio of these smaller species is advantageous in allowing heat dissipation to the environment (Hetem et al, 2014), this may facilitate longer foraging/grazing bouts compared with the larger species. These two points would apply equally to the EVI-60% scenario, where energy levels between species were broadly similar, meaning that blue wildebeest and hartebeest may then be disadvantaged under this worst-case scenario.

The higher energy levels (albeit the difference was small) of all the species under Maximum habitat management for EVI-60% suggests that increased numbers of managed patches result in higher energy gains for the species. These higher energy levels also demonstrate an advantage of habitat management, compared with no habitat management, that was not evident under EVI-30%.

There are two main positive conclusions from simulating the effect of habitat management. First, habitat management resulted in higher energy levels for grazers than no management (Chapter 2). Second, with a few exceptions, the general similarity in energy levels across the management schemes was unexpected but suggests none of the schemes were particularly deficient (within the confines of the model), i.e. no scheme represented a particularly poor approach.

Further simulations with increasing numbers of patches would assist management assessment on the cost/benefit of increased levels of habitat management. If managed patches benefit from increased mineral and nutrient content from grazers' urine and faeces to form self-sustaining hotspots (Reid, 2012; Estes, 2014), grazers' energy levels may be higher under both EVI scenarios than suggested by MARSC. Including estimates of higher EVI levels at hotspots would be considered in any refined version of MARSC.

Chapter 4 Modelling the effectiveness of different expansion configurations of a protected area for species conservation under climate change.

4.1 Abstract

A key issue for conservation is that the static nature of protected areas prevents resident animal populations tracking climate change over large distances. However, expansion of protected areas may offer some mitigation against climate change by increasing the level of resources available to animals. Further understanding is needed of the effects of protected area expansion on species' capacities to respond to climate change. What costs accompany the benefits, such as selection pressures for certain behaviours, leading to reduced behavioural variation? The objective of this study is to assess the effectiveness of different expansion configurations of a South African national park, under different climate change scenarios (an intermediate and a worst-case scenario) using an agent-based model. A key component of the study is the extent to which behavioural variation contributes to the capacity of four antelope species to adapt to climate change within the park configurations. Alternative park configurations resulted in different energy levels among the agents and there were selection pressures for specific behavioural types and social groups. Three parameters for grazer energy levels (median, high and low) were used to compare park configurations, as opposed to one measure of central tendency. This broader assessment revealed variation within factor levels. For example, among animals with high and median energy levels, herd leaders had higher energy levels than followers, but among animals with low energy levels, followers had higher energy levels than leaders. This study demonstrates the benefit of simulations to compare the impact of different park expansion configurations. The results suggest climate change may disrupt the social structure of these populations, for example by selecting for lone animals or selecting against herd leaders. The selection pressures exerted by climate change may vary at local spatial scales and with the level of climate change, but more importantly with the foraging success of individuals.

4.2 Introduction

This chapter begins with a brief introduction on advantages and disadvantages of park expansion and introduces an example of expansion of a specific PA, which is the subject of this study. Subsequent sections present the results and discussion in relation to the effectiveness of two different park expansion configurations.

A key issue for conservation is that given the dynamic impact of climate change and the likely dynamic response of species, the static nature of PAs prevents resident animal populations from tracking climate change over large distances (Monzon et al, 2011). Static fenced PAs may therefore be unable to conserve their current or future ecological communities (Monzon et al, 2011). Gazetting new PAs would likely be politically controversial, opposed by affected local communities and involve higher costs (Pringle, 2017). Expansion of PAs avoids these issues, but still offers mitigation against climate change by increasing the level of available resources and allowing local populations to move to more favourable locations within a PA (Thomas & Gillingham, 2015).

Given the legal status of existing parks, expansion may require less time and legislation than the creation of a new PA (Pringle, 2017). Existing parks have material assets in place, along with administrative infrastructure (Pringle, 2017), and benefit from management familiarity with the landscape, local communities and other interested parties.

Park expansion represents an economic benefit as operating costs (per unit area) reduce with increasing size (Balmford et al., 2003; Von Maltitz et al., 2006). Park expansion offers advantages over alternative options such as the use of corridors between reserves, translocations and conservation outside of reserves (i.e. buffers) (Von Maltitz et al., 2006). For example, expansions allow ecological processes to persist and intact habitats are maintained, along with a high proportion of biodiversity (Von Maltitz et al., 2006). Expansion of national parks ensures state control over the reconfigured reserve, and reserves represent the most secure approach for conservation, particularly under climate change (Von Maltitz et al., 2006).

In addition to benefits from park expansion, there may be costs or unexpected consequences, such as selection pressures on social organisation or for certain behaviour among faunal populations, leading to reduced behavioural variation. For example, elephants responded differently to the expansion in 2004 of Phinda Reserve in South Africa (Druce et al.,2008). Initially the new area was avoided, but within one month older, recently introduced males moved into the new area, but family groups and younger, resident bulls took from five to eight months to enter the new area and, unlike the older bulls, only entered at night (Druce et al.,2008). Thus, initially the park expansion selected for older bulls, and even after one year most groups and individuals only incorporated small sections of the new area into their home ranges (Druce et al., 2008). In contrast, Pandraud et al (2020) reported rapid colonisation by elephants of an additional expansion of Phinda Reserve in 2017. The difference in the colonisation of the two expansion areas is likely explained by differences in habitat quality and the fact that elephants were regularly in close proximity to the fence that was removed in 2017 (Pandraud et al, 2020). Similarly, woylie *Bettongia peniciallata* promptly colonised the expansion zone of a reserve in western Australia, significantly increasing their home range and the level of home range overlap (Jones, 2018).

Gorongosa National Park experienced catastrophic declines in large herbivore numbers during the Mozambique Civil War, but those populations have been recovering since 2004 (Stalmans et al., 2019). Therefore the park serves as a proxy for how populations and communities may evolve in new areas. Waterbuck *Kobus ellipsiprymnus* represented just 4% of biomass of nine selected species in the park pre-war, but increased to more than 74% of biomass in 2018 and are now the dominant species, replacing buffalo *Syncerus caffer* in that role (Stalmans et al., 2019).

Although assessments of park configurations exist, research on the effect of PA expansion on the behaviour and social organisation of populations is limited (Von Maltitz et al, 2006; Druce et al., 2008; Jones, 2018). However, the above examples illustrate the importance of assessing the impact of park expansion on behaviour and demographics, to identify those areas for expansion with the best chance of meeting conservation aims. Lack of research prior to expansion could result in expansion zones that are avoided or only used by some animals, leading to fragmentation of the population.

Given the threat posed by climate change and the limited funding typically available for conservation (Di Minin and Toivonen, 2015), it is important that park authorities are aware of the impact and effectiveness of PA expansion when planning such interventions. Simulating the responses of populations and communities under predicted future scenarios can inform conservation strategy. Simulations also allow for testing for unexpected results from proposed management interventions - of particular use when planning climate change mitigations (Miller & Morisette, 2014).

The aim of this study is to investigate how, and to what extent, expansion of a protected area may allow a community of antelope species to respond to different climate change scenarios. The study compares the effectiveness of two different expansion configurations of Mokala National Park, South Africa, under different climate change scenarios (an intermediate and a worst-case scenario) using an agent-based model to simulate the behaviour of four populations of antelope species. The species are blue wildebeest *Connochaetes taurinus*, black wildebeest *Connochaetes gnou*, tsessebe (also known as topi) *Damaliscus lunatus* and red hartebeest *Alcelaphus buselaphus.*

The aim of this study comprises three key objectives. First, to compare the park configurations with respect to grazers' energy levels under climate change, as an indication of the configurations' effects on population persistence. Second, to compare how the antelope populations respond and adapt to the park configurations under climate change. Third, to determine if the park configurations select for specific behaviour and social organisation of the populations, which comprises herd leaders and followers, and lone grazers. Objectives two and three were also based on grazers' energy levels. Comparing the different park configurations using grazers' energy levels is a key objective, but it is also important to determine if the configurations select for specific behaviour or social group, which may impact on the populations future adaptive capacities to mitigate climate change effects (Beever et al, 2017).

The simulations were designed to compare different park configurations under climate change scenarios, which would not be possible *in situ*, i.e. this was an exploratory study - there was no ground truthing.

4.3 Methods

The model is a variant of the MARSC model refined to incorporate two different expanded configurations of Mokala National Park. Therefore, the following model description details only a brief overview of the model and changes to the original model that were made to deliver the objective of this study, in additional to detailing the two park configurations and statistical analysis. Chapter 2 (Section 2.3.3) provides a full description of the model and the representation of the landscape.

4.3.1 The model

The model simulated variation in behaviour, social organisation and interactions with conspecifics within a community of antelope species within Mokala, to investigate how this variation contributes to the adaptive capacity of the populations. As agents moved across the Mokala landscape, they developed a spatial memory of resource locations (grazing patches and waterholes) and responded to environmental and internal physiological cues and to conspecifics. Agents differed in their level of exploratory behaviour and social group (lone grazers, herd leaders and followers).

The total run size was 1440 runs (432,000 grazer records), with 720 runs for each of the two park configurations. Each configuration comprised two EVI scenarios (EVI-30% and EVI-60%), each of 360 runs. The choice of run size was a balance between obtaining meaningful data and time constraints. Each run comprised 300 agents (divided equally between the four species) and simulated their behaviour over 30 days. For each run, initially the 300 agents are randomly located within each park configuration and have random headings and all agents have no knowledge of the landscape. Agents' energy levels were used to compare variation in behaviour, cognitive ability and social organisation, and the effect of different environmental scenarios and differences between the species.

4.3.2 Park configurations

The two park configurations (Figs 4.1 and 4.2) were created in ArcGIS Desktop v 10.6.1 and incorporated within the MARSC model. For each configuration, the expansion zone was approximately 5500 hectares. The expansion zone of park configuration 1 has 16 existing waterholes, whereas park configuration 2 has seven existing waterholes within the expansion zone. Locations of the waterholes were provided by SANParks and verified using Google Earth (https://www.google.com). Park configuration 1 has the lower vegetation productivity of the two configurations (compare Figs 4.1 and 4.2), although it is the expansion priority for the park authorities (Mokala National Park, 2017). Park configuration 2 is also an option for expansion (Johann de Klerk, Manager, Mokala National Park - pers. comm.). Park configuration 1 is in part favoured by park authorities as it addresses to some extent the "park's rather inefficient shape" (Mokala National Park, 2017), by removing the concave boundary in the north-western section

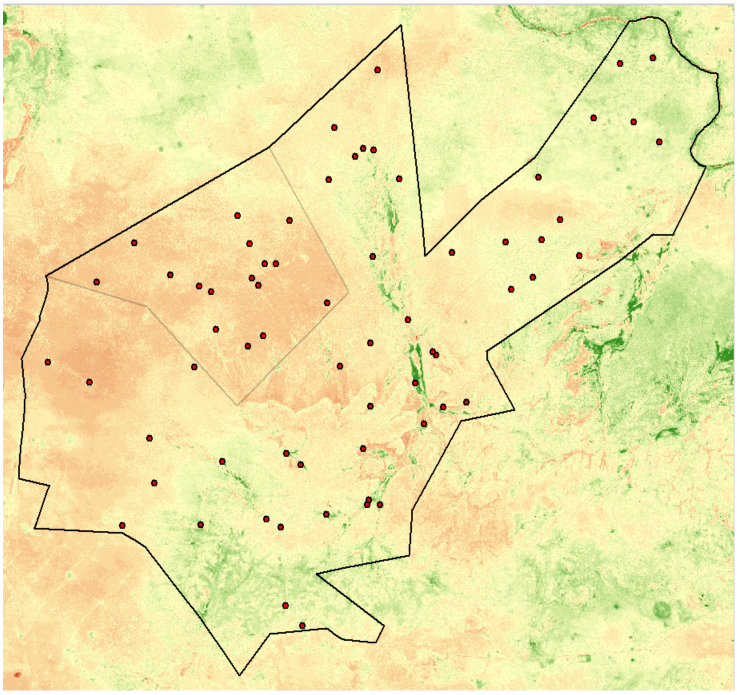

Fig 4.1. Park configuration 1, depicting the worst-case climate scenario – March, EVI-60%. Waterhole locations are shown in red, the current border is shown in grey, highlighting the expansion zone.

of the park (Fig 4.1). Vegetation productivity levels were indicated by the EVI value of each pixel (see section 2.3.4).

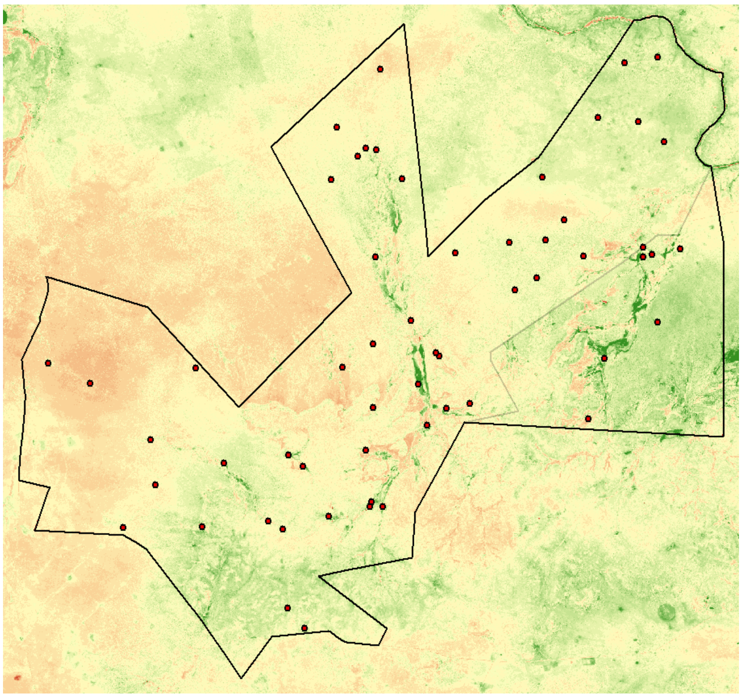

Fig 4.2. Park configuration 2, depicting the worst-case climate scenario March, EVI-60%. Waterhole locations are shown in red, the current border is shown in grey, highlighting the expansion zone. Note the contrast in vegetation productivity (green) within the expansion zone with that of the park configuration 1 expansion zone above (Fig 4.1).

4.3.3 Statistical analysis

Randomisation tests assessed if the factor levels (comprising the different behavioural groups and social groups) influenced the response variable (grazers' energy levels), using a threshold of $p < 0.05$. For each test the factor levels were randomised 5000 times. Since a key point of the study was to compare groups across a broad range of behaviour, three parameters were used for the response variable in the analysis. The standard median (i.e. 100% of the data); the median of data < 1st decile (the lowest 10% of data) - also referred to as the least successful grazers, and the median of data > 9th decile (the highest 10% of data) - also referred to as the most successful grazers. Chapter 2 (Section 2.3.5) describes the statistical methods in full.

4.4 Results

Note that the results in relation to memory use were not particularly informative and so are not described in this chapter.

4.4.1 Comparison of grazers energy levels for different park configurations

The different park configurations affected grazers’ energy levels for both EVI-30% and EVI-60% (Table 4.1). Grazers acquired higher energy levels within park configuration 2 under EVI-30%, in particular the least successful grazers energy levels were notably higher compared with park configuration 1 (Fig 4.3; Table 4.1). Higher energy levels were also obtained by grazers within park configuration 2 under EVI-60%, the largest difference was at the median level (Fig 4.4). Under EVI-60%, park configuration 2 represented a modest improvement in grazers’ median energy levels over the habitat management schemes (see Chapter 3), whereas energy levels in park configuration 1 were lower.

Table 4.1. Randomisation test results for the effect of park configuration on energy levels

EVI scenario	Proportion of randomized ranges ≥ actual range (actual range MJ)		
	< 1st decile	= median	> 9th decile
-30%	0.0 (4.26)	0.0 (0.93)	0.0 (0.49)
-60%	NA*	0.0 (1.95)	0.0 (0.98)

*Test result not applicable as 1st decile = 0.

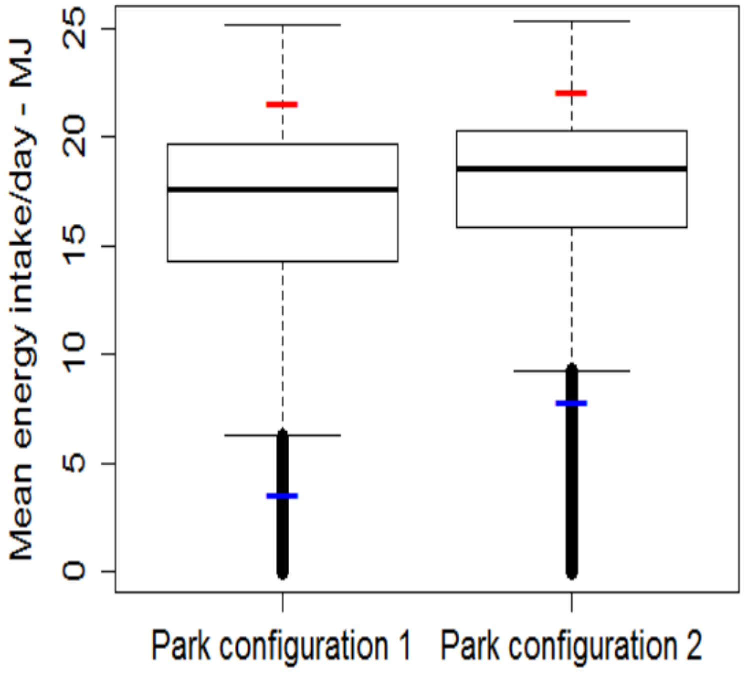

Fig 4.3. Comparison of grazers' energy levels between the two configurations of Mokala, under EVI-30%. The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile.

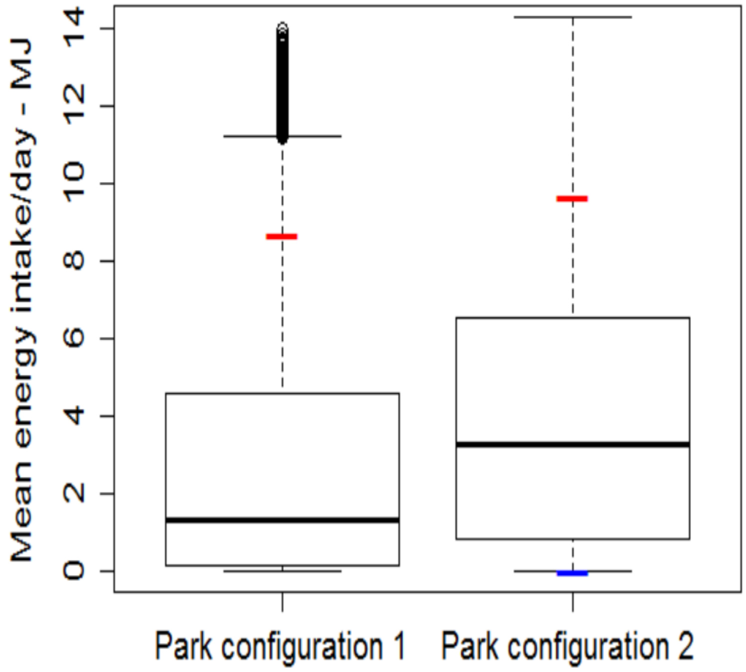

Fig 4.4. Reduced energy levels of grazers for both park configurations under EVI-60%. Note: the value for the median of data < 1st decile for Zone 1 is not applicable as 1st decile = 0. The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile.

4.4.2 Capturing the effect of social organisation on individual energy intake

Social class affected grazers' energy intake in most cases for both park configurations and both EVI scenarios (Table 4.2). However, the key point of interest is that in several cases the influence of social class varied within the class. For example, consider leaders and followers within park configuration 2 under EVI-30% (fig 4.5). Among the most successful grazers and grazers at the median level, herd leaders had higher energy levels than followers, but among the least successful grazers, followers' energy levels were higher than leaders - which was unexpected.

Similarly, for both park configurations under EVI-30%, variation within social classes was evident between followers and lone grazers (Fig 4.6). Followers had higher energy levels than lone grazers among the most and least successful grazers, but their energy levels did not differ at the median level for park configuration 1 (Table 4.2). For park configuration 2, followers had distinctly higher energy levels than lone grazers among the least successful grazers (Fig 4.6). This difference was reduced at the medium level and among the most successful grazers, lone grazers had higher energy levels (albeit the difference was minimal). Lone grazers acquired lower energy levels than followers for both park configurations under EVI-60% at the medium level but among the most successful grazers, lone grazers had markedly higher energy levels than followers (Fig 4.7).

Herd members and lone grazers acquired higher energy levels in park configuration 2 under the intermediate (EVI-30%) and worst-case (EVI-60%) climate scenarios (Figs 4.5 - 4.7). The highest differences between park configurations were among the least successful grazers under EVI-30% and at the medium level under EVI-60%.

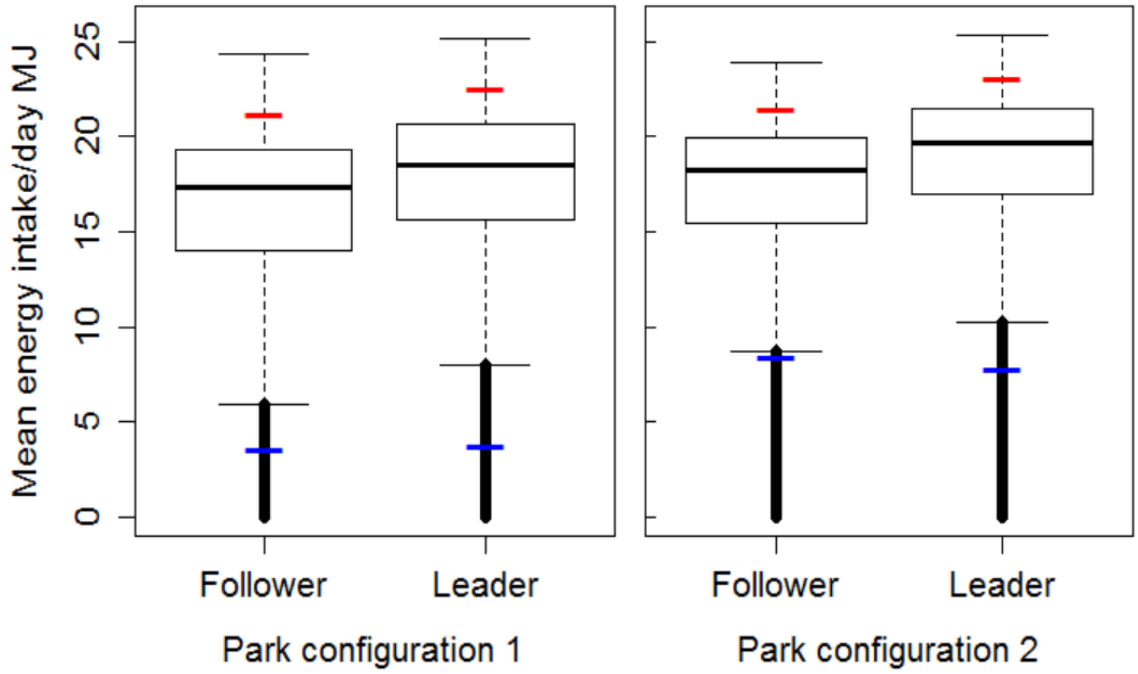

Fig 4.5. Differences in energy levels between herd leaders and followers for the two park configurations under EVI-30%. The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile.

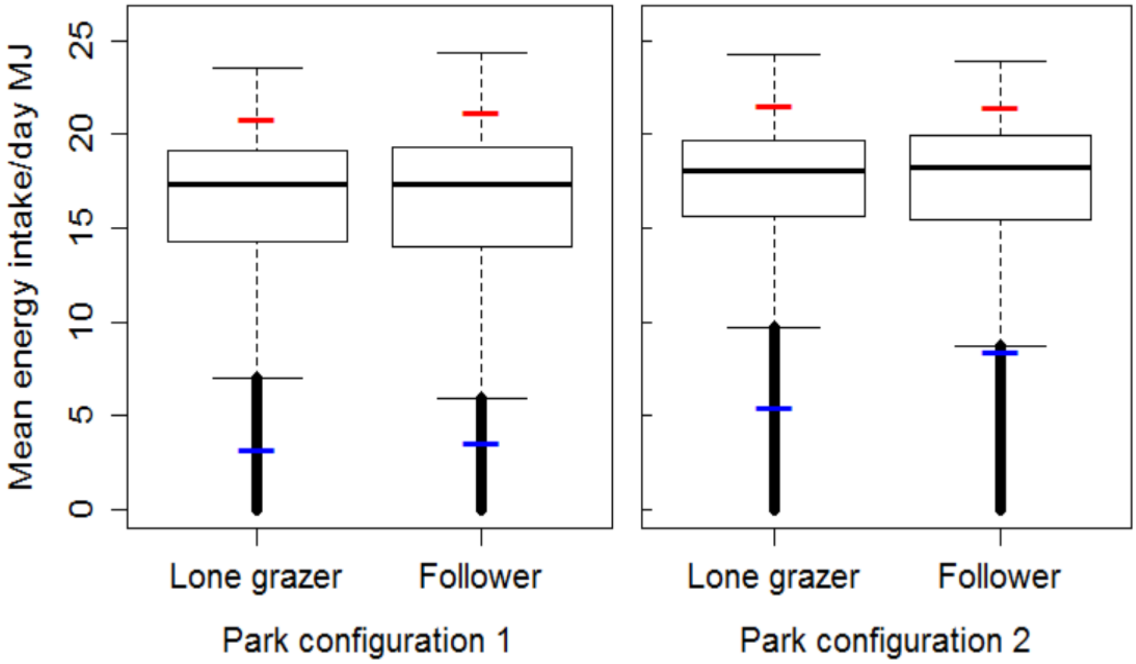

Fig 4.6. Differences in energy levels between lone grazers and followers for the two different park configurations under EVI-30% The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile.

Table 4.2 Randomisation test results for the effect of social group on energy levels

EVI scenario	Park config.	Social pairings	Proportion of randomized ranges ≥ actual range (actual range MJ)		
			< 1st decile	= median	> 9th decile
-30%	1	Follower/Leader	0.02 (0.14)	0.0 (1.17)	0.0 (1.39)
-30%	1	Lone/Leader	0.0 (0.55)	0.0 (1.18)	0.0 (1.77)
-30%	1	Lone/Follower	0.0 (0.41)	0.82 (0.01)	0.0 (0.37)
-30%	2	Follower/Leader	0.0 (0.60)	0.0 (1.43)	0.0 (1.63)
-30%	2	Lone/Leader	0.0 (2.33)	0.0 (1.61)	0.0 (1.56)
-30%	2	Lone/Follower	0.0 (2.93)	0.0 (0.18)	0.0 (0.07)
-60%	1	Follower/Leader	NA*	0.0 (0.17)	0.0 (2.04)
-60%	1	Lone/Leader	NA*	0.0 (0.33)	0.0 (0.68)
-60%	1	Lone/Follower	NA*	0.0 (0.16)	0.0 (1.37)
-60%	2	Follower/Leader	1.0 (0.0)	0.0 (0.47)	0.0 (2.17)
-60%	2	Lone/Leader	1.0 (0.0)	0.0 (0.68)	0.0 (0.80)
-60%	2	Lone/Follower	1.0 (0.0)	0.0 (0.21)	0.0 (1.40)

*Test result not applicable as 1st decile = 0.

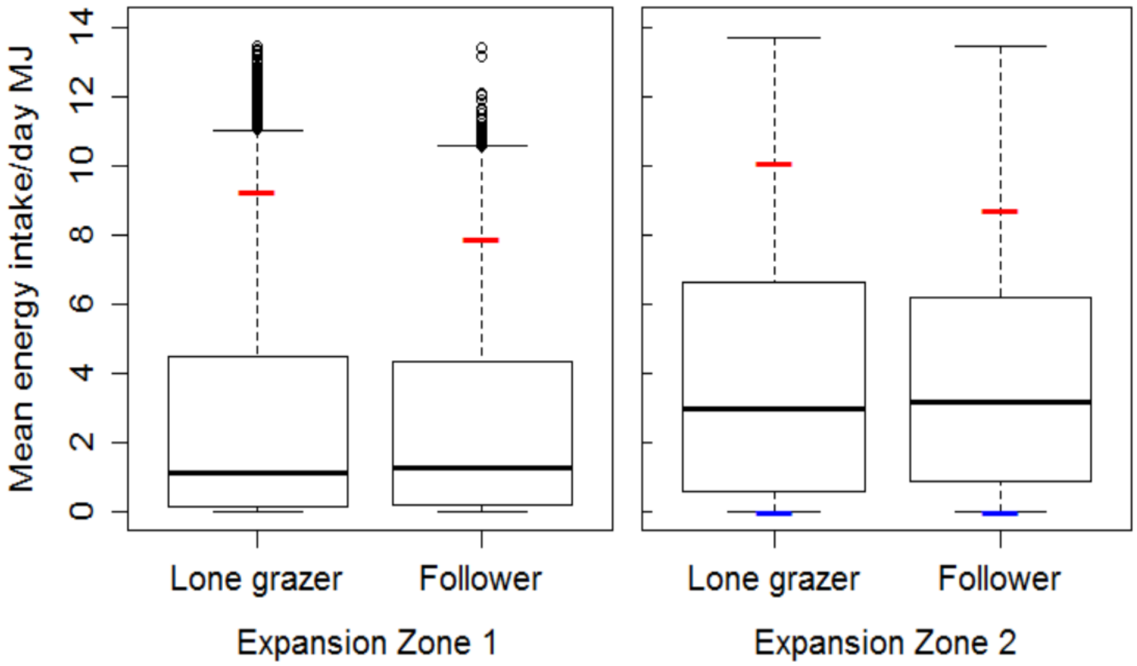

Fig 4.7. Differences in energy levels between lone grazers and followers for the two different park configurations under EVI-60%. Note: values for median of data < 1st decile are not shown for Zone 1 as 1st decile = 0 for both groups. The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile.

4.4.3 Lone grazers: antisocial v social behaviour

The sociability of lone grazers affected their energy levels, with three exceptions (Table 4.3). Antisocial lone grazers attained higher energy levels than social lone grazers for both climate change scenarios and both park configurations, and park configuration 2 yielded higher energy levels than park configuration 1 (Fig 4.8 and 4.9). The difference between the groups was most noticeable for the least successful grazers in park configuration 2 under EVI-30% (Fig 4.8, Table 4.3).

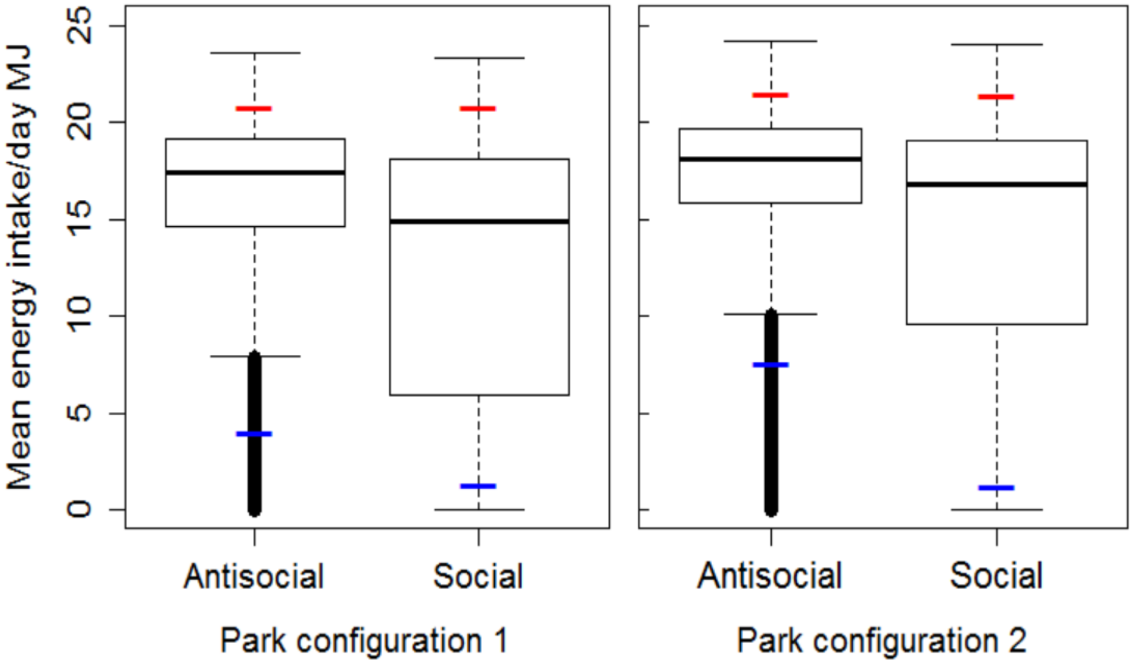

Fig 4.8. Differences in energy levels between antisocial and social lone grazers within the two different park configurations under EVI-30%. Note: values for median of data < 1st decile are not shown for Zone 1 as 1st decile = 0 for both groups. The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile.

Table 4.3 Randomisation test results for the effect of sociability among lone grazers on energy levels.

EVI scenario	Park configuration	Proportion of randomized ranges ≥ actual range (actual range MJ)		
		< 1st decile	= median	> 9th decile
-30%	1	0.0 (2.64)	0.0 (2.57)	0.86 (0.02)
-30%	2	0.0 (6.30)	0.0 (1.34)	0.08 (0.15)
-60%	1	NA*	0.0 (0.69)	0.0 (1.13)
-60%	2	1.0 (0.0)	0.0 (2.0)	0.004 (0.20)

*Test result not applicable as 1st decile = 0.

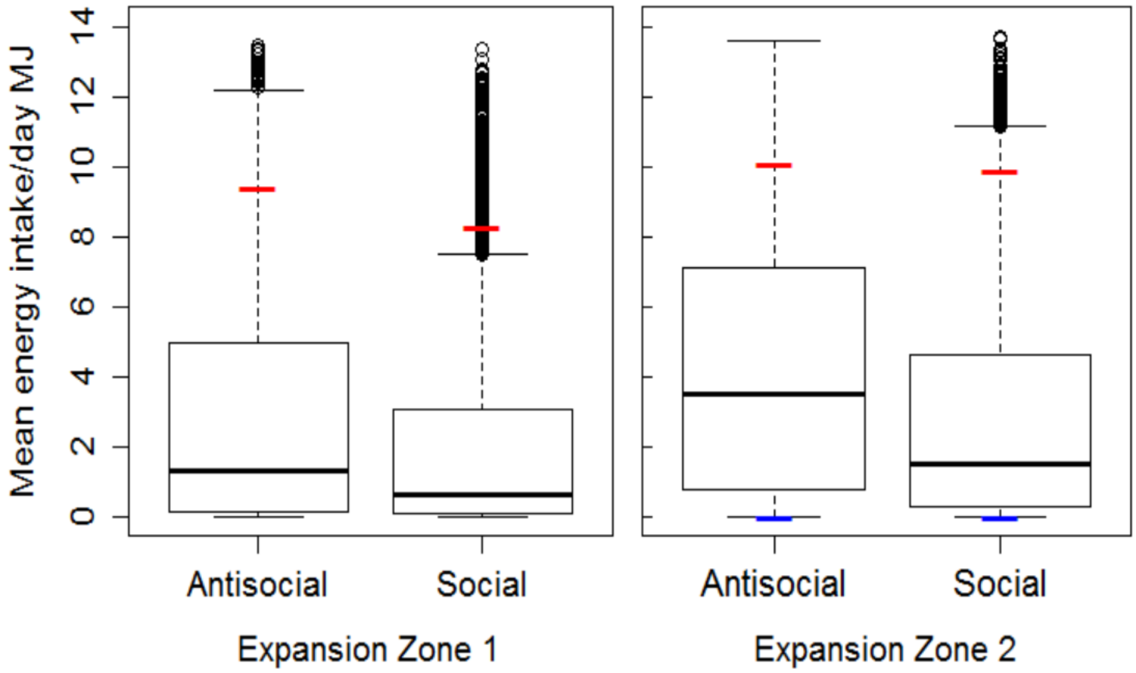

Fig 4.9. Differences in energy levels between antisocial and social lone grazers within the two different park configurations under EVI-60% . Note: values for median of data < 1st decile are not shown for Zone 1 as 1st decile = 0 for both groups. The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile.

4.4.4 Capturing differences between exploratory and non-exploratory behaviour of agents

Grazers exploratory behaviour influenced their energy intake in most cases, although all differences were less than 1 MJ (Table 4.4). For the most successful grazers and those at the median level, exploratory behaviour resulted in higher energy levels than non-exploratory behaviour for both park configurations under EVI-30% (Fig 4.10). This is consistent with the results from Chapters 2 and 3. Energy levels were lower for park configuration 1 under EVI-30%, particularly for the least successful grazers (Fig 4.10). Differences in energy levels between park configurations were evident under EVI-60%, with grazers having higher energy levels in park configuration 2, notably at the median level (Fig 4.11).

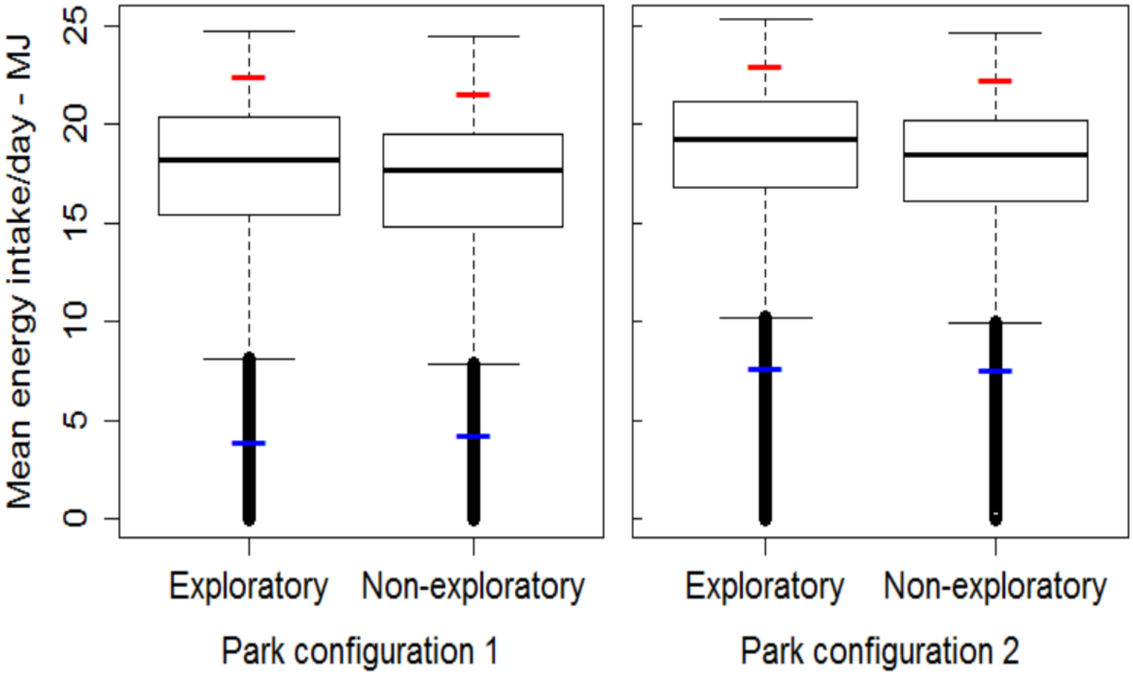

Fig 4.10. Comparison of exploratory and non-exploratory grazers' energy levels acquired within the different park configurations under EVI-30%. The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile.

Table 4.4. Randomisation test results for the effect of exploratory behaviour on energy levels

EVI scenario	Park configuration	Proportion of randomized ranges ≥ actual range (actual range MJ)		
		< 1st decile	= median	> 9th decile
-30%	1	0.01 (0.34)	0.0 (0.57)	0.0 (0.87)
-30%	2	0.61 (0.15)	0.0 (0.85)	0.0 (0.68)
-60%	1	NA*	0.82 (0.01)	0.0 (0.33)
-60%	2	1.0 (0.0)	0.0 (0.43)	0.0 (0.25)

*Test result not applicable as 1st decile = 0.

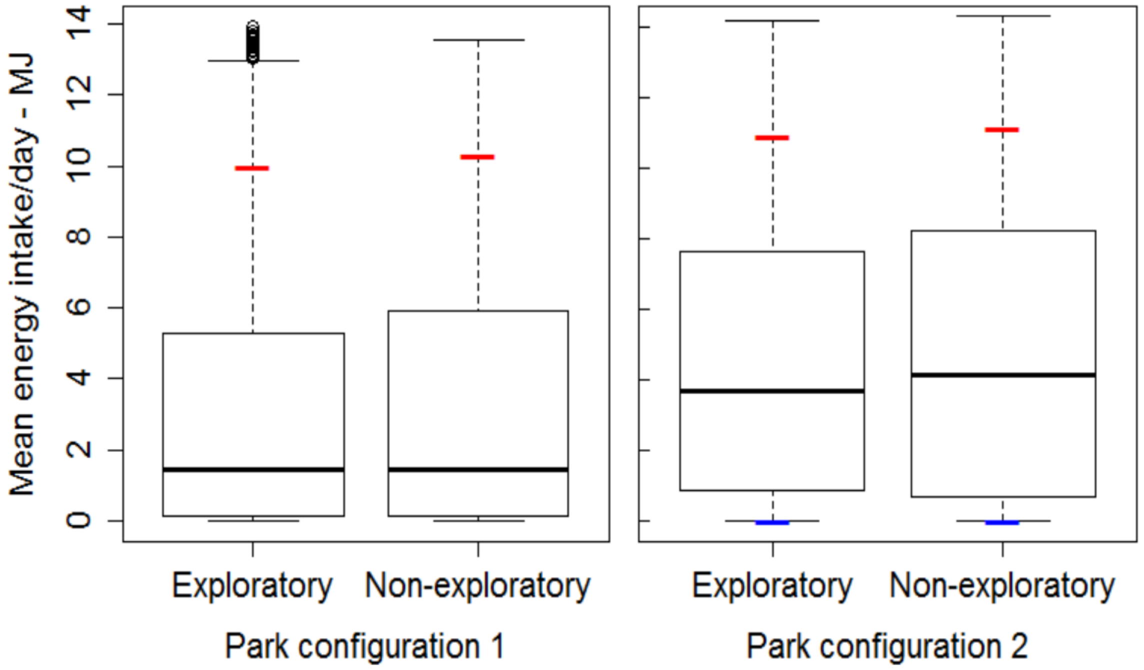

Fig 4.11. Comparison of exploratory and non-exploratory grazers' energy levels acquired within the different park configurations under EVI-60%. Note: values for median of data < 1st decile are not shown for Zone 1 as 1st decile = 0 in these cases. The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile.

4.4.5 Inter-specific comparisons

The most important result under EVI-30% was that for both configurations, the majority of grazers (more than 75%) within each population exceeded their required energy level (the FMR, Fig 4.12). In all cases the FMR was between the 25th percentile and the median of the least successful grazers. Note that when comparing the acquired and required energy levels, the bottom of the range of FMR values was used (see Section 2.3.3). Energy levels followed the pattern of blue wildebeest having the highest levels, then hartebeest, then black wildebeest and tsessebe had the lowest but similar energy levels. Grazers' energy levels were notably higher for park configuration 2 compared with park configuration 1, particularly the least successful grazers (Fig 4.12). The species differed in acquired energy levels, especially under EVI-30% (Table 4.5).

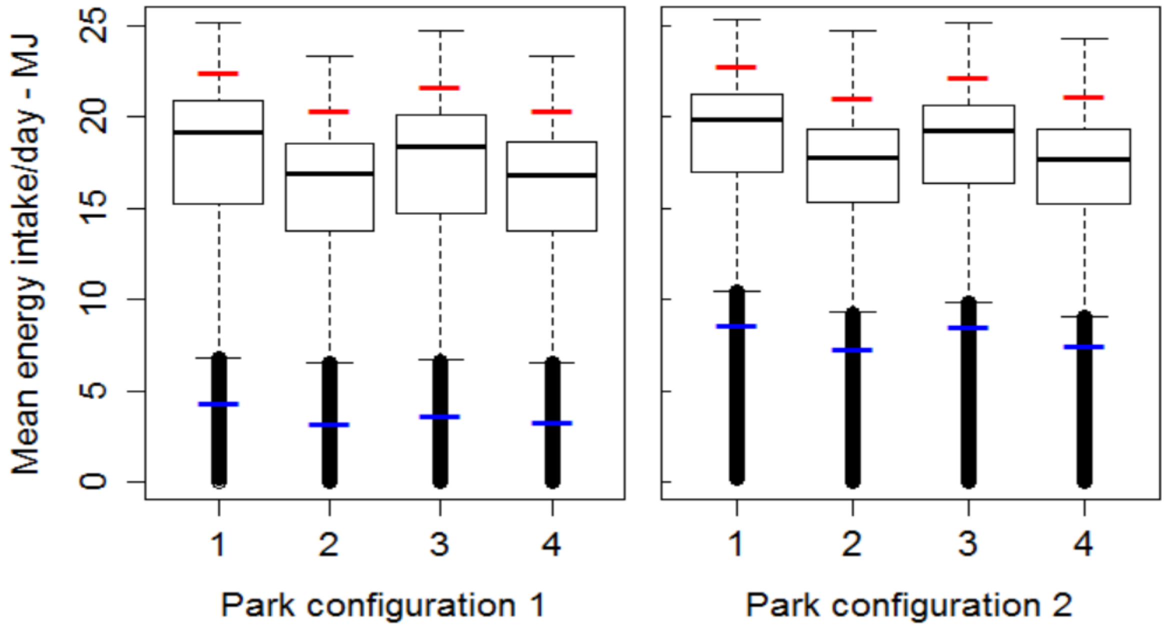

Fig 4.12. Comparison of energy levels by species between the different park configurations under EVI-30%. Note the higher energy levels of the least successful grazers for the Zone 2 configuration. The blue lines indicate the median of data < 1st decile, the red lines indicate the median of data > 9th decile. Species with FMR values (MJ/day) in brackets: 1 - blue wildebeest (13.51); 2 - black wildebeest (10.25); 3 - hartebeest (12.63); 4 - tsessebe (9.74).

Table 4.5 Randomisation test results for the effect of species on energy levels

EVI scenario	Park configuration	Proportion of randomized ranges ≥ actual range (actual range MJ)		
		< 1st decile	= median	> 9th decile
-30%	1	0.0 (1.09)	0.0 (2.31)	0.0 (2.07)
-30%	2	0.0 (1.25)	0.0 (2.16)	0.0 (1.73)
-60%	1	NA	0.0 (0.26)	0.0 (0.30)
-60%	2	0.0 (0.05)	0.0 (0.23)	0.0 (0.42)

*Test result not applicable as 1st decile = 0 for three of the species.

The situation under EVI-60% was more negative for both configurations, in contrast to EVI-30%. In all cases the required (FMR) levels were above the median of the most successful grazers (i.e. the median of data > 9th decile), in other words less than 10% of grazers achieved the required energy levels (Fig 4.13). In the case of the blue wildebeest, the FMR values were only marginally below the highest energy levels (Fig 4.13). In contrast, for the tsessebe the median energy level of the most successful individuals was 9.71, only 0.03 MJ below the FMR level, for park configuration 2.

Median energy levels were markedly higher for park configuration 2 than for park configuration 1 for all species.

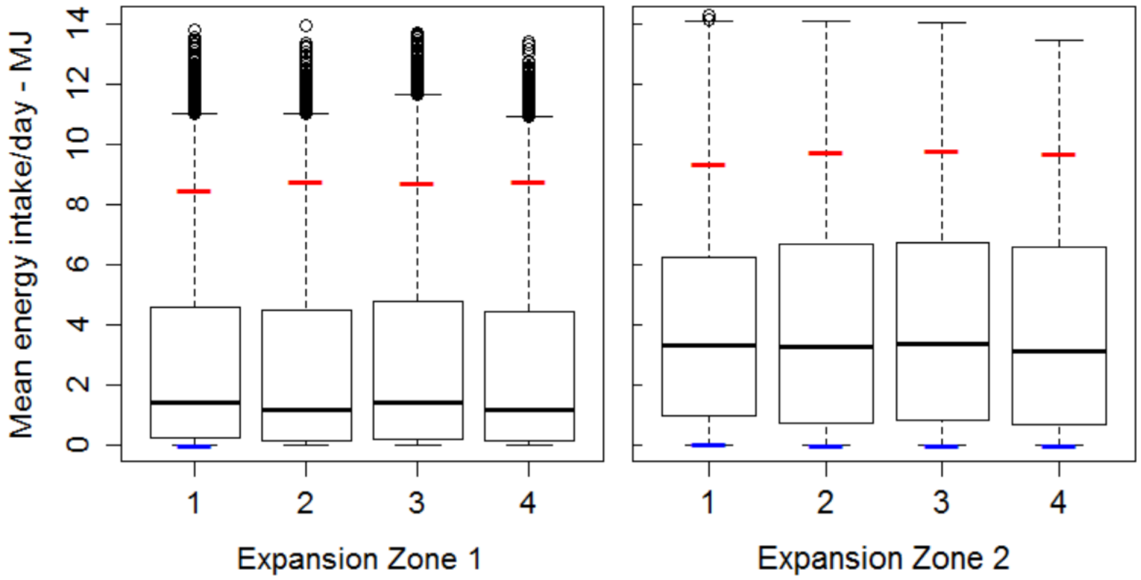

Fig 4.13. Comparison of energy levels by species between the different park expansion configurations under EVI-60%, showing the higher energy levels acquired by grazers for the Zone 2 configuration. Species with FMR values (MJ/day) in brackets: 1 - blue wildebeest (13.51); 2 - black wildebeest (10.25); 3 - hartebeest (12.63); 4 - tsessebe (9.74).

4.5 Discussion

Based on grazers' energy levels, park configuration 2 represents the better option for the persistence of the target populations under climate change. The higher energy levels are consistent with the higher vegetation productivity in the expansion zone of park configuration 2, compared with the park configuration 1 expansion zone (Figs 4.1, 4.2). The gain in grazers' energy levels for park configuration 2 suggests further increases in grazers' energy levels may be possible if (proposed) additional park expansion encompasses other more productive areas (e.g. the areas in the bottom-right, top-left and the V-shaped concave area in the top-right of Fig 4.2)

4.5.1 Comparison of grazers energy levels for different park configurations

Park configuration 2 represents the better option for expansion in terms of higher energy levels for grazers, although park configuration 1 is the authorities' preferred option. Given the lower energy levels of the least successful grazers for park configuration 1 under EVI-30% (Fig 4.3), grazers' energy levels for this configuration under EVI-60% may be lower than indicated by the simulation. If higher numbers of the least successful grazers die from starvation in park configuration 1 than park configuration 2 under EVI-30%, this would reduce behavioural variation among the population. The negative impact of reduced behavioural variation on the adaptive capacity of the population (Beever et al, 2017) would likely cause numbers to decline even further under EVI-60%.

The aim of PA design generally has been to maximise species representation (Strimas-Mackey & Brodie, 2018). This study focussed more on how park expansion may affect population persistence, i.e. the study compared different park configurations with grazers' behaviour under future climate change scenarios to predict the impact on grazers' energy levels. This approach is broadly in line with that advocated by Strimas-Mackey & Brodie (2018) who suggest the focus of conservation planning should be on ensuring species persistence.

The results illustrate the difference in benefits (in terms of grazers' energy levels) from expanding into different areas, and highlight the need for further research into the effects of park expansion (Jones, 2018). Gorongosa National Park (GNP) and Área de Conservación Guanacaste (ACG) represent success stories of park expansion in Mozambique and Costa Rica respectively (Pringle, 2017). The ACG extends 50 km inland from the Pacific Ocean, encompassing both terrestrial and marine biomes; similarly GNP is undergoing further expansion, with a view to extending across 200 km to the Indian Ocean (Pringle, 2017). Expansion allows PAs to better represent the environmental heterogeneity experienced by species across their range, currently this representation is inadequate (Hanson et al., 2020).

Considering the benefits of large-scale expansion, it is worth remembering that this simulation was a binary comparison between two park configurations. The expansion plans for Mokala envisage a more than fourfold increase in size (Mokala National Park, 2017), therefore both expansion zones may be incorporated as the park expands to become a more representative (of environmental heterogeneity) and ecologically coherent protected area.

Given the need for informed, efficient expansion, computer simulations can inform management of the positive and negative impacts of different expansion configurations, whereas actual testing of different configurations is not possible.

4.5.2 The effect of social organisation on agents energy levels

Two key findings were evident regarding the social organisation of the target populations. First, under EVI-30% interesting emergent properties were evident when comparing the energy levels of the least successful lone grazers and followers for park configuration 2 (and to a lesser extent park configuration 1, Fig 4.6) with those of the least successful antisocial and social lone grazers (Fig 4.8, Section 4.4.3). Recall that antisocial grazers actively avoided conspecifics, social lone grazers simply failed to find herds to join. Failing to join a herd represents a large energetic cost for these least successful social lone grazers and most, if not all, of this group will be extirpated. If populations reduce and fragment under climate change, the loss of these potential new herd members represents the loss of new genetic and behavioural variation within populations.

Second, there is selection pressure among the most successful followers to become leaders or lone grazers under EVI-60% within both park configurations, possibly leading to social disruption. Both leaders and lone grazers had higher energy levels than followers. Highlighting the possibility of disruption to social organisation due to changes in ecological pressure is in agreement with Dennehy (2001). As different followers try to become leaders, herds may fragment if other herd members opt to follow different 'leaders', while some followers opt to become lone grazers, leading to smaller herds. Both options lead to reduced behavioural and genetic variation within herds under EVI-60%. Note that although leaders also had higher energy levels than followers under EVI-30% (among the most successful followers and those at the median level), followers energy levels were relatively high, suggesting less selection pressure to become leaders, than under EVI-60%.

Taken together, these points highlight a succession of reduced population sizes and behavioural and genetic variation from the current situation to EVI-30%, at which point the least successful social lone grazers may have been extirpated, to EVI-60%, at which point many of the most successful followers have become lone grazers, potentially leading to further loss of genetic variation and behavioural within the populations.

The relevance of the least successful grazers is worth commenting on since in some instances (e.g. Fig 4.3, park configuration 2) under EVI-30%, their energy levels may be sufficient to prevent starvation (see comments on wildebeest survival in Section 3.5.1), alternatively their extirpation represents a reduction in both population size and behavioural variation.

A common theme within these examples is of reduced behavioural variation which further reduces the adaptive capacity of populations to mitigate the negative effects of climate change (Beever et al, 2017). This reinforces the need for further research on individual energy requirements within species, to allow more accurate assessments of survival rates under climate change scenarios. To my knowledge this is the first study to highlight the effect of PA expansion on the social organisation of gregarious species.

4.5.3 Interspecific differences in acquired energy levels

The key conclusion based on grazers’ energy levels is that for both park configurations under EVI-30%, most individuals within the different populations will survive. In contrast, for both park configurations under EVI-60%, most individuals will die, regardless of the species. Arguably, one positive aspect is that the tsessebe population, which is endangered in South Africa (SA Govt, 2007), fared better than the other species when comparing acquired and required energy levels. The increased energy levels for park configuration 2 demonstrates the advantage of expanding into areas with higher vegetation productivity (EVI) levels.

Although the simulation showed the blue wildebeest population would be greatly reduced under EVI-60%, this species has especially efficient muscle (Curtin et al, 2018), but the MARSC simulation did not incorporate this parameter. Curtin et al (2018) were assessing the thermoregulatory capacity of the species, but the increased efficiency may mean that the energy requirement of blue wildebeest is lower than the level used within MARSC. The FMR values vary widely within species (Hudson et al, 2013) and so are only used as a crude measure for comparison. However, when comparing results of the simulation using FMR, the bottom of the range of FMR values was used (see Section 2.3.3), therefore comments on the numbers of individuals surviving may be too optimistic. If true, this is particularly concerning under EVI-60%, as the predicted survival rates were already very low.

The results suggest the presence of a threshold between EVI-30% and EVI-60%, this resonates with the finding of Urban (2015), who identified a major extinction threshold (at an increase of 4.3° C over pre-industrial levels). This suggests management interventions are required before vegetation productivity declines to EVI-60%.

Although energy levels were higher for blue wildebeest and hartebeest under EVI-30%, their energy requirements were also higher. In other words, no species appears to dominate in either park configuration, based on the energy acquired/required comparison. This finding may be advantageous in that it suggests there is no disruption within the community under EVI-30%. This would be in stark contrast to Gorongosa National Park which is still experiencing a marked change in the faunal community structure which started in 2004 (as the park recovered after the Mozambique Civil War), but which may require intervention to redress the imbalance in species numbers (Stalmans et al., 2019).

Chapter 5 Discussion

This concluding chapter initially reflects on the thesis as a whole (i.e. what have I learned and contributed?) and necessarily returns to the thesis title, which was the driving factor behind the research: "Simulating the consequences of behavioural variation among African antelope populations under a changing climate and different land management scenarios". Subsequently, specific contributions to knowledge resulting from the thesis are highlighted. Limitations and possible future developments and are also discussed prior to the final conclusion.

Throughout this thesis, four key interconnected points are demonstrated:

1. the importance and effect of behavioural variation among populations responding to changes in climate and habitat
2. the utility of ABMs
3. the benefits of taking a complex systems approach to complex issues
4. the benefits of a fine-scale, localised model

1. Behavioural variation

This study demonstrates the contribution behavioural variation makes to animals' adaptive capacities with regard to climate change. Furthermore, the use of additional medians highlighted the variation that was present within the same behavioural type or social group (Chapters 2, 3 and 4), and revealed significant differences between behavioural types, or highlighted effects of conservation interventions, that would be missed by a single metric, in agreement with Bennett (1987). A conservation intervention may have a positive outcome for some animals in a population, but negative for others (as shown in Chapters 3 and 4). This point alone reinforces the importance of considering behavioural variation in conservation interventions and research, particularly with regard to climate change, in agreement with Wolf & Weissing (2012), Moran et al (2016), Beever et al (2017) and Merrick & Koprowski

(2017).

Whist the central measure can be important depending on the research question, it can also be a distraction and focus attention away from the level of variation (Bennett, 1987), which in some instances is the important factor to consider. In other words, the signal obscures the noise. Using just one measure will not adequately record the consequences of behavioural variation and risks failure for conservation interventions, or at least unintended and possibly deleterious consequences.

Regardless of the scenario and behaviour types, energy levels varied widely within the populations. Reducing variation to one central measure risks overlooking numerous important and interesting questions (Bennett, 1987). In particular, considering the worst-case scenario (EVI-60%), why did some agents obtain a daily energy intake of 14 MJ, while for others the intake was 0 MJ (Chapters 2, 3 and 4)? Was this simply due to the original location of the agents, e.g. some agents were located in better quality habitat, consistent with the importance of location suggested by Pandraud et al (2020)? Alternatively, was this due to variation in individual adaptive capacity, and if so, what are the reasons for this variation (i.e. the functional basis) and the consequences? Are there combinations of behavioural traits that lead to high or low adaptive capacity? Do the benefits of better quality habitat have a dampening effect on the future adaptive capacity of individuals? If so, individuals in better quality habitat may be less able to survive the impact of climate change than conspecifics that previously faced more challenging environments. These questions reinforce the view that behavioural variation represents a rich vein for future research, both from an applied conservation perspective (the more pressing issue) and a theoretical perspective.

2. The utility of ABMs

ABMs allow the simulation of a population or community as it is - a collection of individuals, rather than assigning attributes to the whole group (e.g. applying a mean reproduction rate or mean dispersal rate). ABMs are ideal for simulating the consequences of behavioural variation (Revilla et al 2004; Gilroy & Lockwood, 2016;

Bracis & Mueller, 2017; Wood et al, 2021) as they focus on the individual, from which population level dynamics derive (Pauli et al, 2013; Stillman et al, 2015).

An additional benefit is the emergent properties which ABMs can reveal, and which can inform conservation management. Emergent properties were evident in Chapters 2, 3 and 4 and have also been reported by various researchers, e.g. van der Vaart and Verbrugge (2008), Pauli et al (2013), Merkle et al (2016), Patin et al (2019) and Chimienti et al (2020).

A key benefit of emergent properties within ABMs is that they are frequently unforeseen (i.e. they would not have been considered by the researcher), but also any negative consequences are virtual. For example, MARSC predicted a significant decline in energy levels among the least successful grazers for the park authorities' preferred expansion option (Chapter 4). Instead of simulating this proposed expansion, discovering that the actual expansion (had it taken place) had a (real) unforeseen negative impact could result in a reduction in population size and may have a cascade effect. For example, lower energy levels among the least successful grazers could lead to a reduced population size, which leads to a reduction in behavioural variation, resulting in a reduced adaptive capacity within the population.

ABMs allow individuals to modify their behaviour in ways that reflect their personality, but also affect population dynamics, e.g. within MARSC antisocial lone grazers change direction on seeing conspecifics, whereas social lone grazers would join conspecifics, increasing group size.

The benefits resulting from the ability of ABMs to provide a graphical interface should not be underestimated (Cartwright et al, 2016), both for developing and testing the model (in identifying errors or areas for improvement), and for users running the model (to understand how agents and the model itself behave). The graphical interface is particularly effective when considering different input parameters or comparing alternative conservation interventions (see Section 5.3 on the use of agents' trails).

3. A complex systems approach

Typically, populations of animals comprise individuals that exhibit behavioural variation, make decisions (which may be based on imperfect perception and, to put it simply, may be good or bad decisions), interact with each other and their environment (which is heterogeneous and typically subject to modification by climate change), and relationships between these aspects are non-linear (Sih, 2013; Merkle et al, 2015; Ruddell et al., 2016; Ranc et al, 2021). By definition, this is a complex system. This level of complexity was reflected and incorporated within MARSC, in addition to the EVI/energy intake conversion and use of multiple medians in the statistical analysis. This study supports the view that predictions about complex systems require models that incorporate the complexity of the system (Stillman & Goss-Custard, 2010; Sih, 2013), rather than taking a reductionist approach which, by definition, either omits or overgeneralizes aspects of the system, making the robustness of this approach questionable (Ruddell et al., 2016).

Key findings such as the possible social disruption within populations (Chapters 2, 3 and 4), and differential variation in the effect of conservation interventions within factors and levels (Chapters 3 and 4) resulted from the level of complexity incorporated within MARSC. These key findings were emergent properties of the model. Arguably the case for adopting complex systems methodology is supported by the increasing levels of complexity that are being incorporated within other types of models, as discussed in Chapter 1 (such as hybrid SDMs and ENMs, e.g. D'Amen et al, 2013; Bush et al, 2016; Razgour et al, 2019).

Increasing levels of complexity risks making models difficult to understand. However, progress is possible through a measured, heuristic approach, in other words by making small changes to models (which increase their complexity) and assessing their impact on the results obtained.

4. The benefits of a fine-scale, localised model

Key to identifying differences between behavioural types or social groups was the measurement of energy intake, which derived from the fine-scale EVI maps. Compared with a low resolution model (e.g. having a coarse scale of say a 500 x 500 m cell size), by using a 10 x 10 m cell size MARSC was able to incorporate a much greater level of habitat heterogeneity and therefore capture agents' behaviour at a finer scale - especially their foraging, movement and use of spatial memory.

Chapter 4 in particular adds weight to the argument for using fine-scale, localised models when considering conservation interventions. A key point is that the two PA expansion configurations were broadly similar. They both incorporated the existing PA and differed only in the relatively small expansion zones, yet agents' energy levels differed significantly between the configurations. Therefore, MARSC demonstrated that the agents adapted to local conditions, in agreement with Pinter-Wollman et al (2009), Scillitani et al (2012), Savolainen et al. (2013) and Weise et al (2015). This study reinforces the view that fine-scale, area-specific models are more sensitive to the consequences of behavioural variation (Malishev & Kramer-Schadt, 2021) and exhibit greater accuracy (Velazco et al, 2020). The difference in energy gain between the PA configurations resonates with the differential usage of different expansion zones by elephants in Phinda Reserve in South Africa (Druce et al., 2008; Pandraud et al, 2020).

There are other advantages to localised models that are worthy of mention. Compared with broad-scale models, it is easier for a researcher to gain a high level of knowledge of a local area, both from personal experience (fieldwork) and through local expert opinion. My knowledge of Mokala was useful during the development of MARSC and when running simulations (e.g. incorporating the restricted usage of the park by black wildebeest - Chapter 2). There are also logistical and financial benefits from researching a local area, rather than a much wider area.

Based on my findings and the points made in Chapter 1 on broad, coarse-scale models, I would emphasize the importance of fine-scale, localised models for conservation, and argue for a greater use of this approach, and less emphasis on generalised models, which may be inadequate. Developing numerous localised models would be financially costly and time-consuming. Broad-scale, generalised models may seem a reasonable response to the limited funding of conservation. I suggest that rather than accepting the funding situation, the conservation community should make a sustained, concerted effort to ensure decision-makers see that this situation is unacceptable. A reasonable assumption is that inadequate funding likely leads to inadequate results.

5.1 Key contributions to knowledge

Use of Multiple Medians

This thesis demonstrated that multiple medians provide additional useful information when considering behavioural variation, whereas a single median fails to capture the full impact of variation and may be misleading (Bennett, 1987). This was evident in Chapter 3 where exploratory behaviour was beneficial for most grazers but disadvantageous among the least successful grazers. Similarly, Chapter 4 demonstrated the different park configurations had a small effect on most agents' median energy levels, but the difference among the least successful grazers was more pronounced.

Conservation interventions based on a measure of central tendency may have unforeseen results, as the intended benefit may not be equally distributed across the population; for some individuals there may be no benefit. When comparing possible conservation interventions (e.g. options A and B), the option with the higher median (or mean), say option A, may seem the logical choice. Additional medians (or means) may show the majority of individuals thrive under either option, but if less successful individuals have markedly lower fitness under A, then option B may be the best choice.

Converting Vegetation Indices to Energy Intake

Whilst vegetation indices are useful, since they have no units they do not directly translate into animals' energy intake and are limited to comparisons (i.e. area X is more productive than area Y). Conversion from EVI to grazers' energy intake results in a metric which has the same unit as energy budgets. As far as I am aware, this is the first use of such a conversion.

Use of this metric may allow better understanding of how habitat actually affects herbivores, such as determining if a habitat provides sufficient energy to maintain the Field Metabolic Rate of a species. For example, use of this metric highlighted the rapid decline in acquired energy levels between the intermediate and worst-case scenarios, compared with the current and intermediate scenarios (Chapter 2). This metric could also facilitate assessment of whether a habitat provides sufficient energy for lactating females, or predictions of migration routes, based on the energy content of different patches in the landscape. Use of this conversion could increase the accuracy of other approaches such as Population Viability Analysis.

The benefit of spatial memory

The use of spatial memory when foraging was found to vary with the level of resources, with spatial memory becoming more beneficial under the worst-case climate scenario (Chapter 2). In contrast, use of spatial memory was no better than random foraging for most agents under the intermediate climate change scenario. Given the energetic costs involved in memory use and maintenance (Dukas, 1999), the results obtained from the MARSC simulation suggest a degree of flexibility in the application of spatial memory is beneficial. This finding concurs with the findings of Boyer & Walsh (2010) and Falcón-Cortés et al (2021). In other words, if random foraging represents an adequate strategy, animals may as well use it; but as resources decline under climate change, the appropriate adaptation would be to switch to the more efficient memory-based foraging.

Effects of social organisation

The thesis demonstrated the potential for disruption to social organisation within the populations under climate change. There is selection pressure on the most successful followers to become leaders or lone grazers under the worst-case climate scenario, as both leaders and lone grazers had higher energy levels than followers (Chapters 2, 3 and 4). Disruption to social organisation due to changes in ecological pressure has been suggested by Dennehy (2001). Whilst the target species already exhibit variation in social organisation (Estes, 2014), this could still be a cause for concern both locally and on a wider scale. Locally, given the intention to reintroduce large predators to Mokala (Mokala National Park, 2017), lone grazers would likely be more vulnerable to predation. On a wider scale, if this selection pressure appeared among species that exhibited less variation in social organisation, this disruption could result in a decline in population size and genetic variation.

5.2 Future developments

Future enhancements of the model would include the ability to track grazers across the landscape, which would be of benefit for visual assessment. Some preliminary work has been completed in this respect which shows promise, with grazers creating visible trails as they traverse the landscape. This could be beneficial given the planned park expansion, particularly if comparing different expansion configurations of the park. Simulations could be run with agents initially located close to those sections of the original fence which would be removed to enable the expansion. A visual assessment of the trails would be useful in predicting both the extent to which antelope colonise new areas and the timeframe involved. Positioning other agents further away from the fence, would allow a comparison of the role of the proximity of agents to newly created areas in colonisation of the areas (as highlighted by Pandraud et al, 2020). Adding a grid to the landscape would facilitate spatial analysis of the colonisation of these areas (e.g. whether there were differences between species or behavioural types).

Displaying key data during the simulation, e.g. the highest and lowest energy values obtained by individual agents, combined with the ability to pause the model and highlight those agents with the highest or lowest energy levels and their trails, would be useful in identifying behaviour or spatial patterns that are either well adapted or maladapted to the habitat.

Arguably of greater benefit would be the facility to record and output all grazers locations at every time-step with markers to identify the path taken, i.e. to facilitate the direction of travel. This is relatively straight-forward from a programming point of view, but is very costly in terms of processing and run time. This would enable spatial analysis, i.e. comparing distances travelled and spatial utilisation of the park by different individuals, groups, species or behavioural type (in particular, comparing random foraging against memory-based foraging).

Analysis of foraging efficiency would be advantageous and facilitated by recording which memory records of grazing areas were actually used. Although numbers of grazing records were recorded for the three with-memory classes, currently the number of redundant memory records is unknown. Analysis of energy levels, the number of memory records used and distance travelled would offer a useful insight into variation between behavioural types and the social groups.

Of particular benefit is the capacity to highlight agents' response to management interventions such as the provision or relocation of artificial waterholes. The management of Mokala's population of disease-free buffalo has required the removal of other species from part of the park (Mokala National Park, 2017), MARSC could be parameterised to assess the ecological effect of removing or reintroducing species.

The use of machine learning within MARSC would be useful for two reasons. Firstly, to increase the level of behavioural variation within the population. Currently, although there is variation due to the fact that agents are assigned to different groups (e.g. random foraging, basic memory use, smart memory use), individuals within each group share the same set of rules which govern their behaviour. Incorporation of machine learning techniques would mean each individual could potentially develop their own set of rules (DeAngelis & Diaz, 2019). Secondly, this approach would allow individuals to learn from their own experience and make decisions accordingly. For example, within the current MARSC model, each individual searches all of its memory records at every time step during memory-based foraging. However, if individuals have learned about their environment, they may not need to take this approach. Instead, they may simply know from experience that at certain times, specific areas should be avoided due to reduced resource levels at these locations.

5.3 Limitations

Any thesis which includes a model is subject to the limitation that, according to the statistician George Box, “All models are wrong, but some are useful”. It is easy for any modeller to fall into the trap of believing their model is predicting what *will* happen, rather than predicting what *may* happen, based on assumptions incorporated within the model. Other limitations are present within the model, often reflecting a compromise between ecological reality and technical (software) considerations. Some limitations have already been discussed in Chapter 2 (Section 2.5), e.g. the “immediate regrowth” of grazed patches.

Although a preliminary version of the model included elevation data, the final version of MARSC is 2-dimensional - it does not include the park’s topography and therefore does not reflect the cost of movement within the park, e.g. an individual may prefer a longer journey across flat terrain than a short, uphill journey. A future refinement of the model would benefit from elevation data, due to the use of rocky elevations by the target species at times when resources are reduced (pers. obs., pers. comm.).

The model does not reflect behaviour to avoid heat exposure (e.g. seeking shade during the hottest part of the day) or the fact that black wildebeest are more tolerant of heat/direct sunlight than other species. They rarely seek shade, which means they do not expend energy and time moving to sheltered areas (Estes, 1992; Lease et al, 2014). MARSC does not include any other herbivores, yet in reality, the presence of other herbivores has an influence, e.g. they represent competition for grazing. MARSC could be expanded to include other species.

Similarly, the model does not include reproduction or incorporate subsequent generations. These factors could be incorporated within MARSC to simulate the populations demographics over several generations. However, on both these points a balance is needed between incorporating as much detail and information as possible without making the model too complex to understand and maintain.

5.4 Final conclusions

1. Behavioural variation represents the potential within a population to adapt or respond to a situation or event, and as such is fundamental when it comes to animals' ability to mitigate the impacts of climate change.

2. When analysing results (particularly in relation to behavioural variation), I would argue for the use of multiple metrics (e.g. multiple medians) rather than just one - avoid 'the tyranny of the Golden Mean' (Bennett, 1987).

3. Whilst broad, coarse-scale analyses have their place, local conservation interventions are better served by fine-scale, area-specific, local analyses.

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Appendix

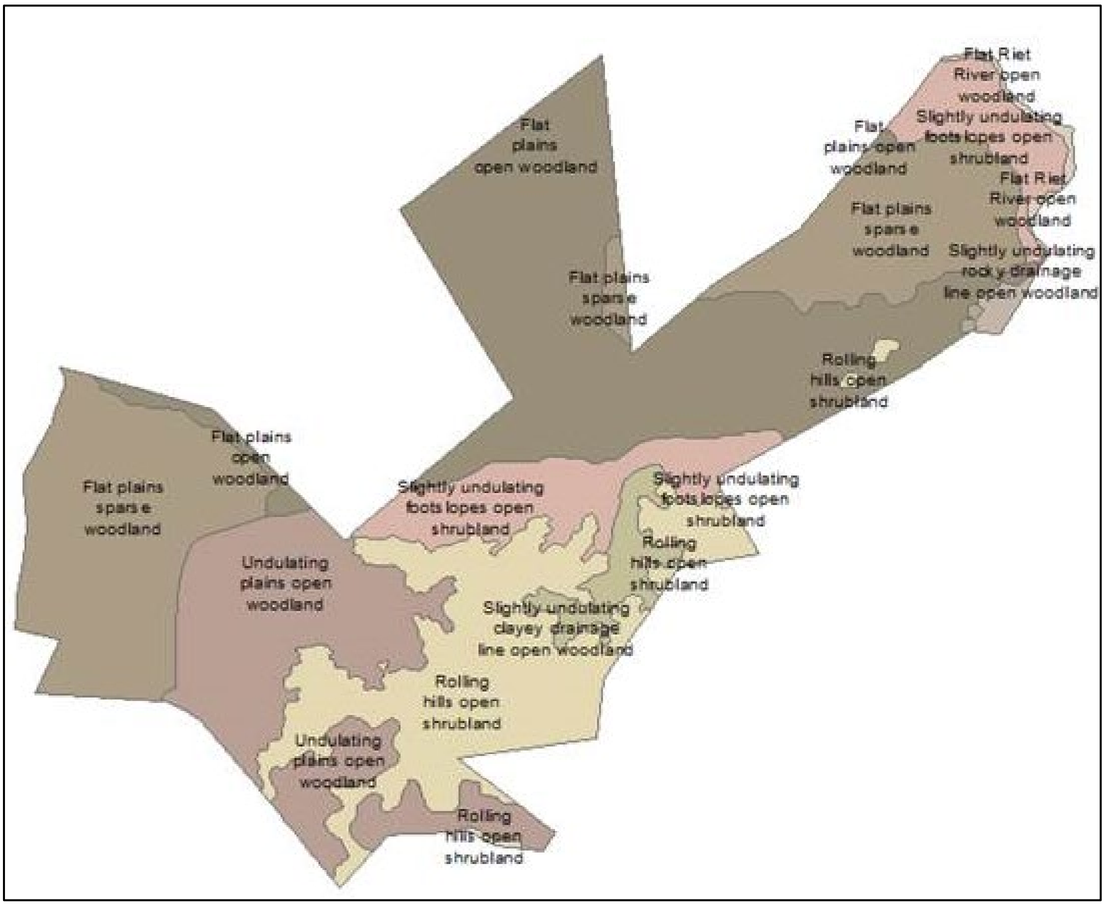


Fig 1. Map of Mokala National Park highlighting different habitat types. Source: Bezuidenhout et al (2015).

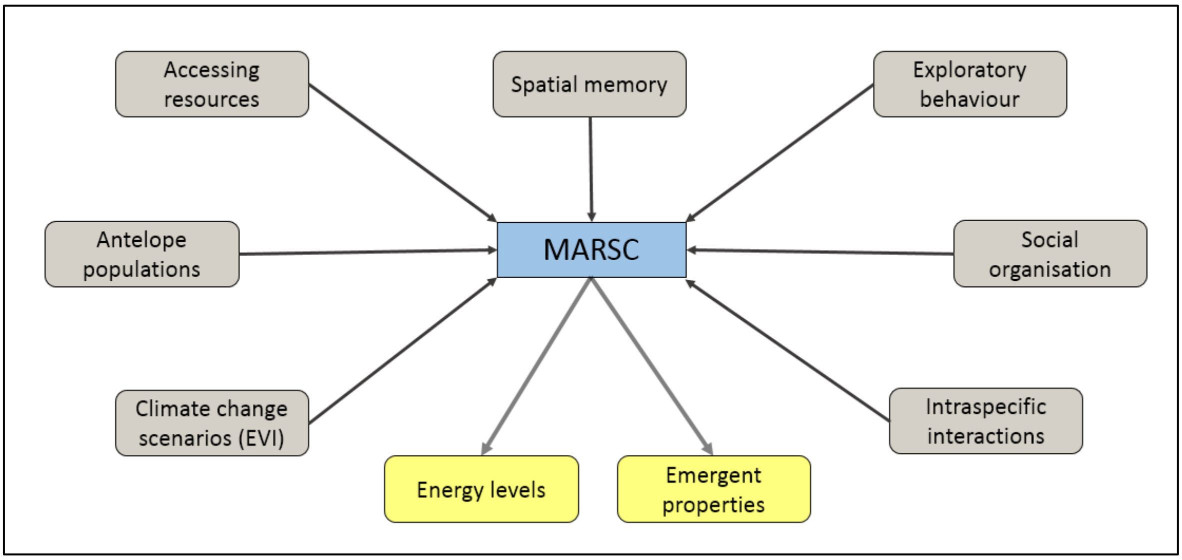


Fig 2. Key inputs (grey boxes) and outputs (yellow boxes) for the MARSC model.

Table 1. Ethogram used for focal sampling of the species during fieldwork

Behaviour	Description
Vigilant	animal is upright on 4 limbs, in an alert posture, staring at a fixed point with head high & ears erect, may stamp forefoot
Resting	animal appears relaxed, prone, dormant, no quadrupedal movement, not ruminating nor vigilant
Grazing	animal is searching for food or actively consuming food (taking grass into its mouth & chewing, with head lowered below vertebral column)
Ruminating	jaw movements associated with mastication, typically performed whilst prone
Standing	animal is upright on 4 limbs, stationary & receptive to environmental cues
Moving	locomotion on 4 limbs, not galloping, not part of foraging
Flight	animal galloping away from perceived threat
Other	other behaviour not listed above
Not visible	focal animal is not visible

Box 1. Methodology for converting EVI to energy intake (MJ) per pixel.

The process involved 3 stages: firstly, convert EVI value to biomass (kg/ha); secondly, convert biomass to a consumption rate (kg/min), i.e. the rate of forage consumed by an animal – this rate was then converted to the amount of forage consumed per pixel; thirdly, convert forage consumed per pixel to energy intake (MJ) per pixel. The result is an approximation and includes uncertainties, i.e. the consumption rate formula in stage 2 was based on red deer grazing in temperate grasslands; the intake per pixel (IP) assumes 80% grazing per time step when an animal is foraging i.e. the remaining 20% allows for local movement and vigilance.

1. Convert EVI to live biomass - BM1 (g DM/m2) (Kawamura et al., 2005a):

BM1 = 18.352e5.86X

where X = EVI on -1/+1 scale; DM = dry matter

Convert biomass from g/m2 to kg/ha as BM2:

BM2 = (BM1 * 10)

2. Convert biomass to consumption rate CR (kg/min) (adapted from Hudson & Nietfeld, 1985):

CR = (17.6 (1 – e-0.000505 BM2))/1000

Convert CR to actual (biomass) intake per pixel - IP (kg):

IP = CR * grazing time/pixel

3. Convert IP to Energy intake EI (MJ/pixel):

EI = IP * ME;

where ME (metabolizable energy) = (0.157 * DOMD %) = 7.85

where DOMD % (Digestible Organic Matter) = 50 (approximated from Murray, 1993)

Table 2. Key species attributes

	Mass - kg	Locomotion cost J/m	Initial energy level
Blue wildebeest	200	264	530
Black wildebeest	130	204	530
Hartebeest	180	248	480
Tsessebe	120	194	530

Table 3. Key parameters of grazers

Parameter or attribute	Description and rationale
Species	1 - blue wildebeest; 2 - black wildebeest; 3 - red hartebeest; 4 - topi
Grazer turn angle	Angle by which grazer may deviate from the 'true direction' when moving to a resource using memory (+/- 15°) - this is an arbitrary value used to reflect grazers' imperfect spatial memory.
General field of view	Panoramic field of view (330^0) for detecting water, the fence and other animals. Based on the panoramic field of view of other herbivores/prey species ranging from 330^0 - 360^0 (for horses, sheep, cattle - Blackshaw et al, 2003)
Scanning field of view	Field of view when scanning for forage (120^0) - requires depth perception (i.e. binocular vision). This may have been excessive (binocular vision ranges from 25^0 - 70^0 for horses, sheep, cattle - Blackshaw et al, 2003) but a further consideration was how this shape was displayed within Java. The shape would distort depending on the agents heading, affecting the number of cells within view.
Short view distance	Maximum distance for determining forage quality (4 pixels/106 m). This was an arbitrary value but was influenced by the above point about how the shape was displayed within Java.
Long view distance	Maximum distance for detecting water, the fence and other animals (15 pixels - approximately 400 m). Little/no literature exists on this detail, this was an estimated value based on how far I could see objects in a rural setting.
Move distance	Distance when moving locally - 6 pixels (approximately 160 m)
Move long distance	Distance moved in 1 hour/cycle, when moving to a specific resource using spatial memory - 70 pixels (which equates to approximately 1.9 km hr^{-1}). This value was well within the

	walking speed of 4.1 km hr^{-1} suggested by Curtin et al (2018), whereas Hopcraft et al (2014) refer to "> 12 km/day" – assuming avoidance of the midday heat and therefore walking for 8 hours, this would be 1.5 km hr^{-1}.
Location	Grazer's location - X and Y map coordinates
Heading	Grazer's heading
Memory distance	Arbitrary values (500 m for exploratory grazers; 3 km for those with a home range) based on the broad range of home ranges for the four species, which range from < 1 ha to 10 km^2 (Estes, 1992).
Grazing memory	Contains: grazer ID; location of grazing patch; day that patch was grazed; number of pixels at the location that exceed the foraging threshold; distance from agent to patch; pixScore (see Section 2.3.3 - Spatial memory). Note these last 2 fields vary with the agent's location, i.e. they are regularly amended, as is the day the patch was grazed.
Avoid recently grazed areas for 9 days	There is little or no research on the period of avoidance of recently grazed areas, though Howery et al (1999) state that "animals may remember and avoid recently grazed areas".
Short-term grazing memory	Contains angle and distance to each pixel (above the requisite threshold of 111) within the local patch.
Waterhole memory	Grazer ID; location of waterhole; distance from agent to waterhole. Note this last field varies with the agent's location, i.e. it is regularly amended.
Energy level	Energy level in MJ acquired during each day, this is reset at the start of each day.
Water hour	Hour of day when grazer visits waterhole
Herd	ID of herd that grazer is associated with (if applicable)
Day joined herd	Day grazer joined herd (if applicable)
Leader	Indicates if grazer is the herd leader.
Boldness	Grazer's boldness score
Sociability	Grazers were assigned to one of three social classes: antisocial, social, intermediate

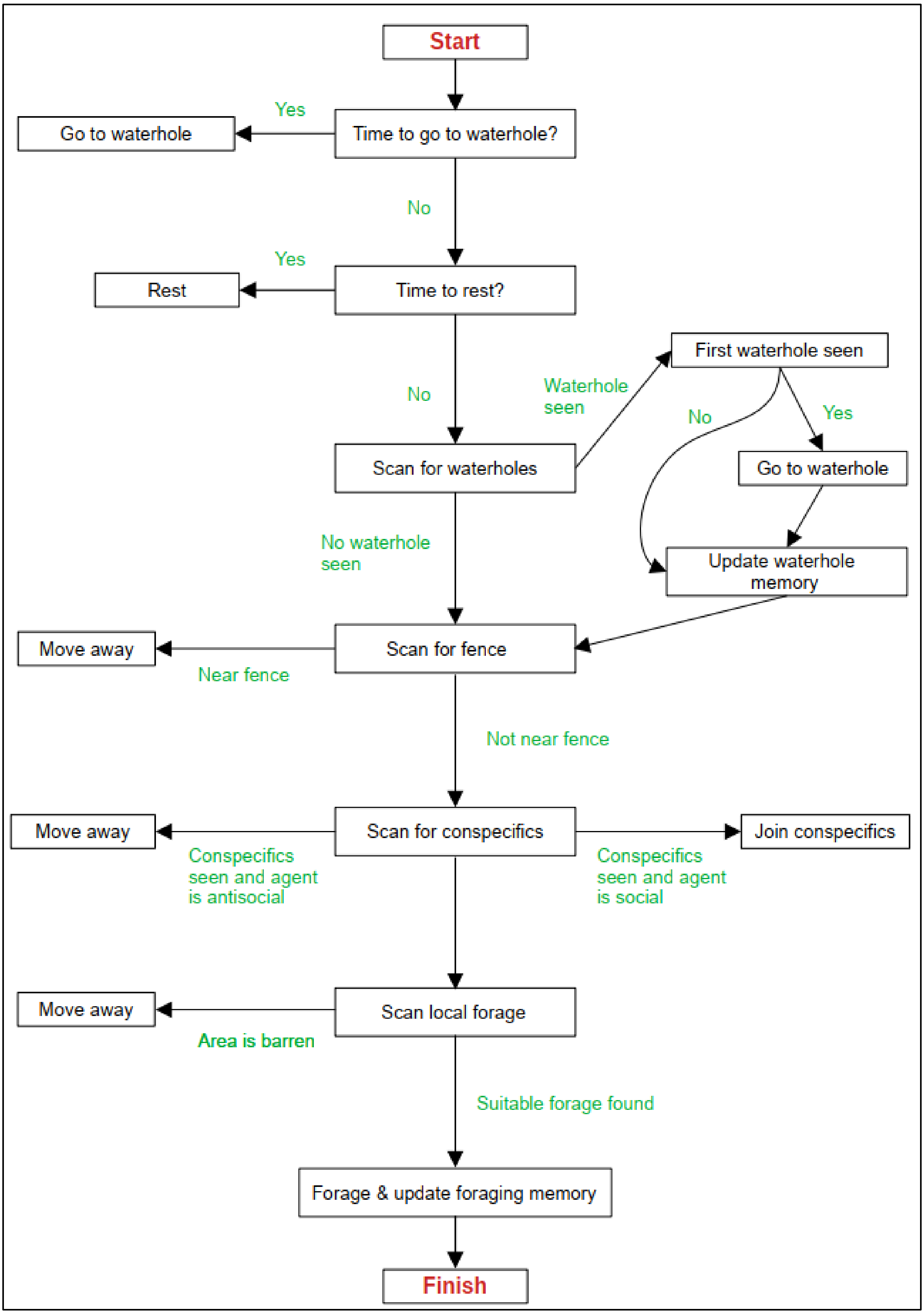
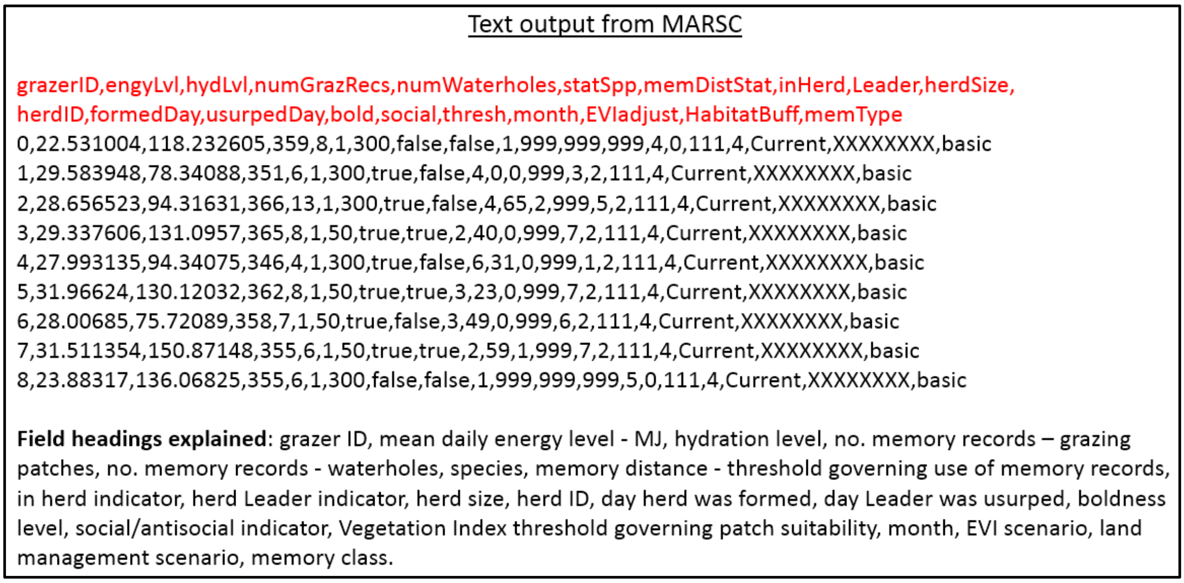


Fig 3. Flowchart representing a typical cycle based on an agent using “basic” memory-based foraging, during daylight hours.



Text output from MARSC

```
grazerID,engyLvl,hydLvl,numGrazRecs,numWaterholes,statSpp,memDistStat,inHerd,Leader,herdSize,
herdID,formedDay,usurpedDay,bold,social,thresh,month,EVIadjust,HabitatBuff,memType
0,22.531004,118.232605,359,8,1,300,false,false,1,999,999,999,4,0,111,4,Current,XXXXXXXX,basic
1,29.583948,78.34088,351,6,1,300,true,false,4,0,0,999,3,2,111,4,Current,XXXXXXXX,basic
2,28.656523,94.31631,366,13,1,300,true,false,4,65,2,999,5,2,111,4,Current,XXXXXXXX,basic
3,29.337606,131.0957,365,8,1,50,true,true,2,40,0,999,7,2,111,4,Current,XXXXXXXX,basic
4,27.993135,94.34075,346,4,1,300,true,false,6,31,0,999,1,2,111,4,Current,XXXXXXXX,basic
5,31.96624,130.12032,362,8,1,50,true,true,3,23,0,999,7,2,111,4,Current,XXXXXXXX,basic
6,28.00685,75.72089,358,7,1,50,true,false,3,49,0,999,6,2,111,4,Current,XXXXXXXX,basic
7,31.511354,150.87148,355,6,1,50,true,true,2,59,1,999,7,2,111,4,Current,XXXXXXXX,basic
8,23.88317,136.06825,355,6,1,300,false,false,1,999,999,999,5,0,111,4,Current,XXXXXXXX,basic
```

Field headings explained: grazer ID, mean daily energy level - MJ, hydration level, no. memory records – grazing patches, no. memory records - waterholes, species, memory distance - threshold governing use of memory records, in herd indicator, herd Leader indicator, herd size, herd ID, day herd was formed, day Leader was usurped, boldness level, social/antisocial indicator, Vegetation Index threshold governing patch suitability, month, EVI scenario, land management scenario, memory class.

Fig 4. Extract of text output from MARSC, listing agent's key data for analysis.

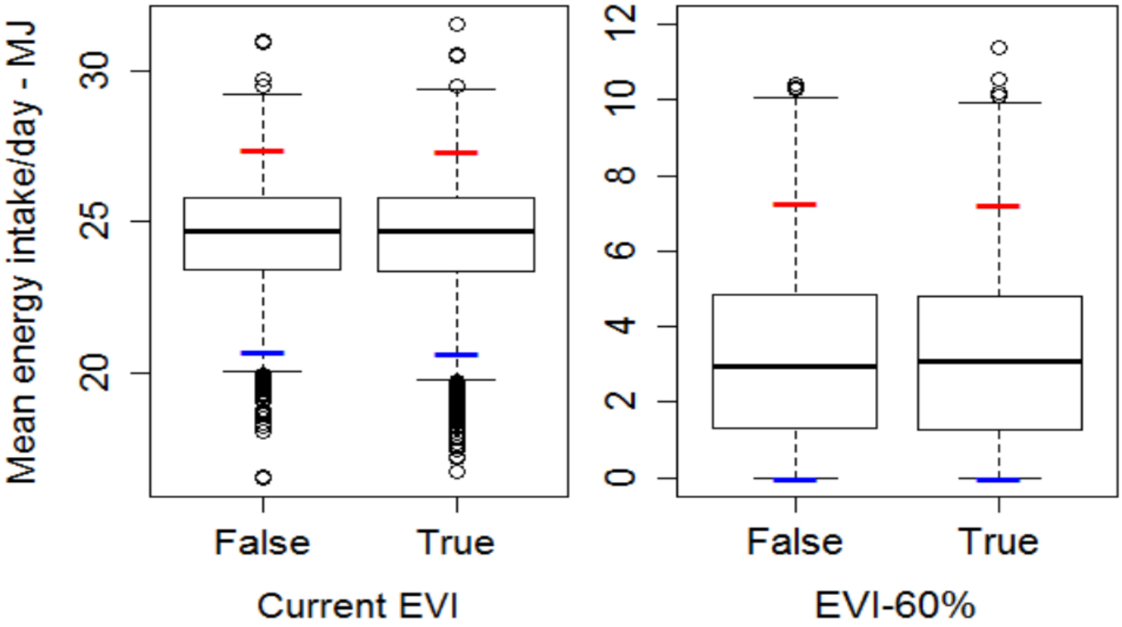


Fig 5. Comparison of the impact of immediate regrowth of grazed pixels (True) and pixels with no regrowth (False). Simulation covered a period of 9 days for the month of May and comprised blue wildebeest only.

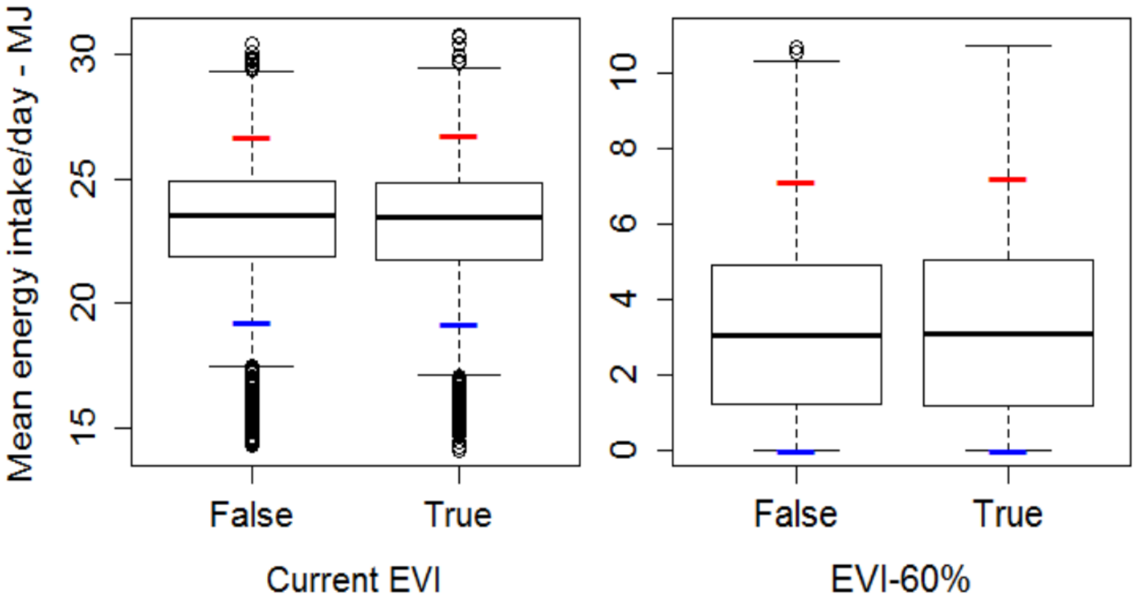


Fig 6. Comparison of the impact of immediate regrowth of grazed pixels (True) and pixels with no regrowth (False). Simulation covered a period of 9 days for the month of May and comprised all four species.

A brief description of the target species

The four species which form the focus of this project are briefly discussed below, in terms of their physical description, behaviour, reproduction, distribution and habitat choice.

Alcelaphines

The tsessebe, hartebeest and both wildebeest species, are all members of the tribe Alcelaphini (Estes, 1992). Alcelaphines are typical plains antelopes (although the common wildebeest prefers acacia savanna) with a distinctive appearance: sloping backs resulting from having forequarters higher than hindquarters (Estes, 1992). Depending on available resources, the full range of spatial behaviour (from completely sedentary to highly nomadic) and social organisation (territorial males, bachelor groups, females with young) is evident across populations of these species, or within the same population at different times (Estes, 1992). When resources are lacking during the dry season, populations exhibit instability; with the rains, populations become more stable in composition and are more likely to be sedentary (Estes, 1992). Where wildebeest, hartebeest and tsessebe overlap, wildebeest are ecologically dominant, yet the smaller tsessebe dominates encounters with hartebeest (Estes, 1992).

Blue Wildebeest

Wildebeest behaviour and social organisation is flexible and responsive to environmental conditions; in some cases resident populations have formed from previously migratory populations (Estes, 1992). The species prefers short grass, either on open plains or acacia savanna, but also consumes a limited amount of browse (Estes, 1992). The broad muzzle and wide incisor row - wider than hartebeest and tsessebe - of both wildebeest species facilitate grazing short grass (Murray & Brown, 1993). Blue wildebeest reportedly need to drink water daily or at least every other day, yet they exist in waterless regions of the Kalahari (obtaining water through melons and tubers) (Estes, 1992). In South Africa - the only country where the natural ranges of blue wildebeest and black wildebeest overlap - the 2 species are generally allopatric (Figs 7 and 8). The blue wildebeest occupies the savanna biome, whereas the black wildebeest favours the grassland biome. Blue wildebeest are the most migratory alcelaphine (Estes, 1992).

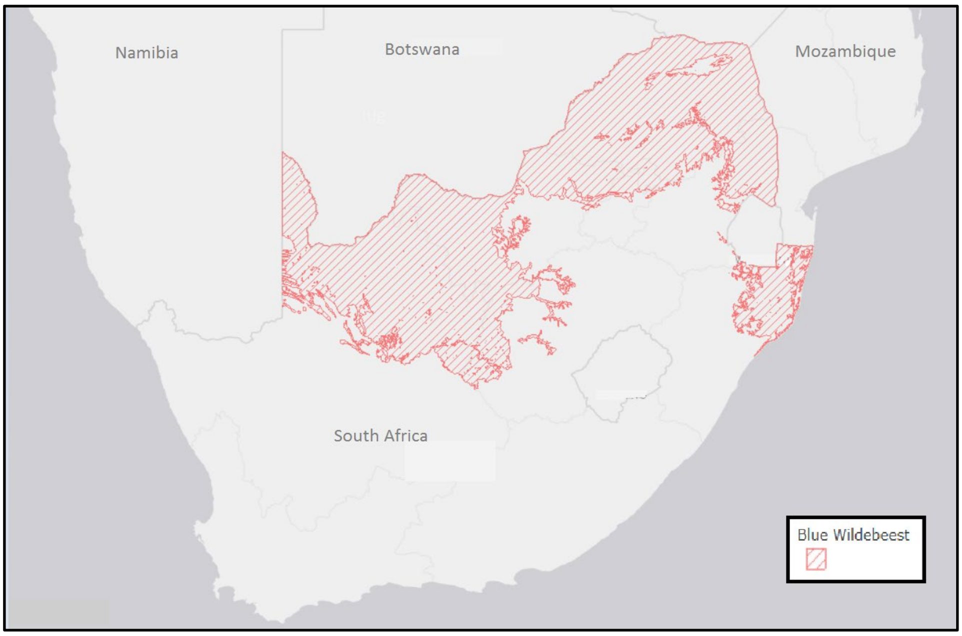


Fig 7. The distribution of blue wildebeest within South Africa corresponds strongly with the savanna biome. Modified from Dept of Environmental Affairs, SA Govt., http://mapservice.environment.gov.za/tomviewer.

Black Wildebeest

In behaviour, reproduction and social organisation, both wildebeest species are very similar, although human intervention has impacted heavily on the black wildebeest (Estes, 1992). The species also used to undertake migrations, but the level of fencing in South Africa means black wildebeest are now sedentary (Estes, 1992). No research exists for the “natural” ecology of black wildebeest, i.e. when the species was migrating across an intact ecosystem and subject to predation (Estes, 1992).

Wildebeest social organisation comprises territorial males, females with young and bachelor herds (Estes, 1992). No longer migratory, black wildebeest males differ from blue wildebeest males by maintaining perennial territories (Estes, 1992). Whilst short grass is preferred, black wildebeest will browse during the winter period (Skinner & Smithers, 1990). Black wildebeest are the least tolerant of woodland and high grass and rarely seek shade (Estes, 1992). Rather, they are more likely to orient towards or away from the sun to reduce heat load, whereas blue wildebeest are more likely to seek shade (Lease et al, 2014). Differential use of microclimates within the same habitat may facilitate wildebeest syntopy and inhibit hybridisation (Lease et al, 2014).

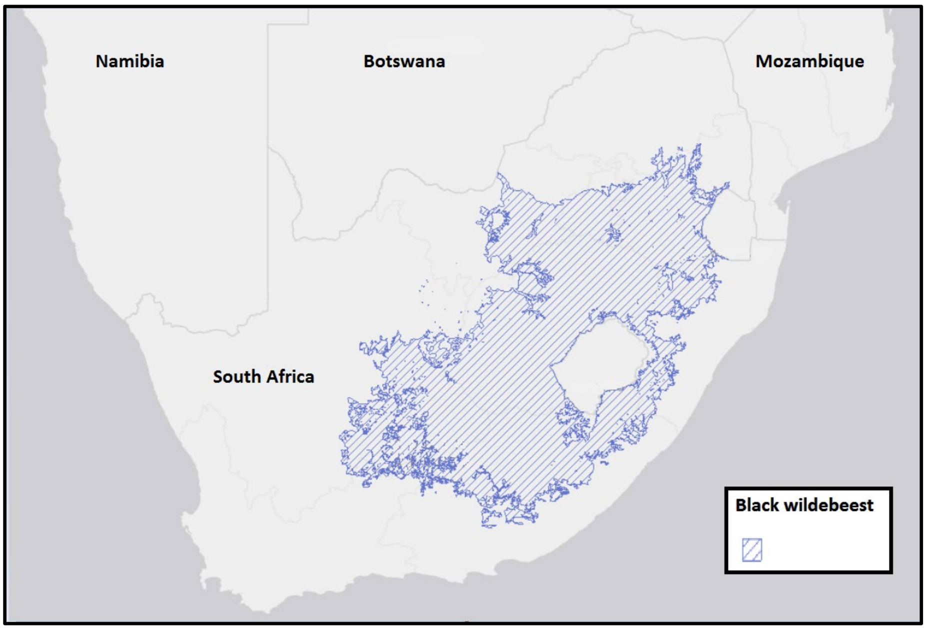


Fig 8. The distribution of black wildebeest within South Africa corresponds strongly with the grassland biome (see Fig 6). Modified from Dept of Environmental Affairs, SA Govt. http://mapservice.environment. gov.za/tomviewer

Hartebeest

The red hartebeest (*A. b. camma*) ranges across most of South Africa, with the exception of the north-west and the extreme north-east (Fig 9). More of an ecotone species, hartebeest will occupy woodland and high grass more readily than other alcelaphines (Estes, 1992). Tolerant of arid country, hartebeest have the lowest metabolic rate among alcelaphines (Estes, 1992). Hartebeest are less selective of green leaves than wildebeest or tsessebe, but more selective of leaves on senescent vegetation (Murray & Brown, 1993). Presumably this explains their efficiency at obtaining nutrition from dry grass (Gosling, 2011), which may give them a competitive advantage under climate change, if rainfall is reduced. Skinner & Smithers (1990) list different accounts of red hartebeest diet, varying from predominantly grass to 40-44% browse. Given also their broad tolerance of habitat and conditions, it is unsurprising that hartebeest are the least migratory alcelaphine (Estes, 1992).

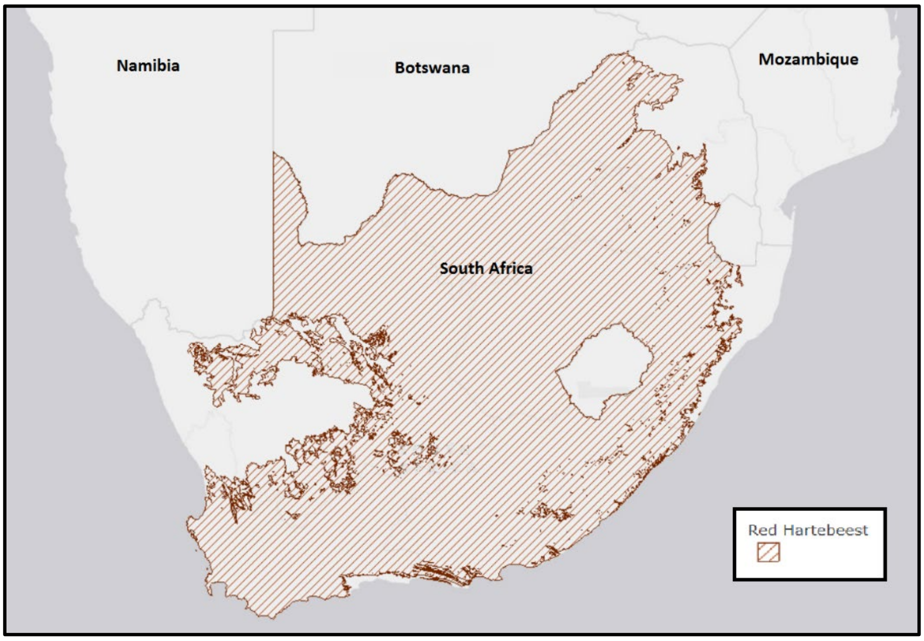


Fig 9. Distribution of red hartebeest within South Africa. Modified from Dept of Environmental Affairs, SA Govt. http://mapservice.environment. gov.za/tomviewer

Tsessebe

Tsessebe (along with blue wildebeest) are the dominant herbivores of acacia savanna and plains and the most social alcelaphines (Estes, 1992). This enigmatic species demonstrates a remarkable level of variation in terms of social and reproductive organisation, in adapting to varying environmental conditions (Estes, 1992). The flexible behaviour of the species may be beneficial in adapting to climate change. Populations may adopt any gradation between perennial sedentary-dispersed and perennial mobile aggregations; males may hold large territories with attendant harems and young, or small temporary territories within mobile aggregations, or may compete for females in a lek (Estes, 1992). In Uganda's Queen Elizabeth National Park, aggregations of up to 2000 individuals roam constantly across the plains in unpredictable fashion; transient territorial networks are established by males for a few hours or days when the herd settles temporarily (Estes, 1992).

Predominantly a grazer, tsessebe are intermediate in their preference for green leaves that are more mature than the green flush favoured by wildebeest, but less mature than the late growth stages favoured by hartebeest (Murray & Brown, 1993). Tsessebe are the most water dependent alcelaphine (Estes, 1992). As with blue wildebeest, the distribution of tsessebe corresponds with the savanna biome (Fig 10).

Fig 10. Distribution of tsessebe within South Africa is limited to the savanna biome (see Fig 6). Modified from Dept of Environmental Affairs, SA Govt. http://mapservice.environment.gov.za/tomviewer.

List of References

Note: only first 3 authors are listed for references for multi-author papers.

Abaigar, T., Rodríguez-Caballero, E., Martínez, C. et al. (2019). The first reintroduction project for mhorr gazelle (Nanger dama mhorr) into the wild: knowledge and experience gained to support future conservation actions. Global Ecology and Conservation, 19.

Akçakaya, H., Butchart, S., Watson, J. et al. (2014). Preventing species extinctions resulting from climate change. Nature Climate Change, 4.

Ali, A., Ford, A., Evans, J. et al (2017). Resource selection and landscape change reveal mechanisms suppressing population recovery for the world's most endangered antelope. Journal of Applied Ecology, 54.

Allen, T. & Hoekstra, T. (1992). Toward a unified ecology. Columbia University Press.

Anderson, T., Hopcraft, J., Eby, S. et al. (2010). Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. Ecology, 91.

Araújo, M., Pearson, R., Thuiller, W. et al. (2005) Validation of species-climate impact models under climate change. Global Change Biology, 11.

Araújo, M. & Petersen, A. (2012) Uses and misuses of bioclimatic envelope modelling. Ecology, 93.

Araújo, M. & Rahbek, C. (2006). How does climate change affect biodiversity? Science, 313.

Bailey, D. (1995) Daily Selection of Feeding Areas by Cattle in Homogeneous and Heterogeneous Environments. Applied Animal Behaviour Science, 45.

Balmford, A., Gaston, K., Blyth, S. et al. (2003) Global variation in terrestrial conservation costs, conservation benefits, and unmet conservation needs. Proceedings of the National Academy of Sciences, 100.

Barbosa, A., Real, R. & Vargas, J. (2009). Transferability of environmental favourability models in geographic space: the case of the Iberian desman (Galemys pyrenaicus) in Portugal and Spain. Ecological modelling, 220.

Bauer, S. & Klaassen, M. (2013). Mechanistic models of animal migration behaviour - their diversity, structure and use. Journal of Animal Ecology, 82.

BBC News (2002) Lioness adopts third baby antelope. Accessed 30/3/2016 from: http://news.bbc.co.uk/2/hi/africa/1905363.stm.

Beauchamp, G. & Ruxton, G. (2005) Harvesting Resources in Groups or Alone: The Case of Renewing Patches. Behav Ecol, 16.

Beecham, J. & Farnsworth, K. (1998). Animal foraging from an individual perspective: an object orientated model. Ecological Modelling, 113.

Beever, E., Embere Hall, L, Varner, J. et al. (2017) Behavioral flexibility as a mechanism for coping with climate change. Frontiers in Ecology and the Environment, 15.

Bennett, A. (1987). Interindividual variability: an underutilized resource. New directions in ecological physiology, 19.

Bennett, D. & Tang, W. (2006) Modelling adaptive, spatially aware, and mobile agents: Elk migration in Yellowstone. Intl. Journal of Geog. Info. Science, 20.

Berdahl, A., Kao, A., Flack, A. et al. (2018) Collective Animal Navigation and Migratory Culture: from Theoretical Models to Empirical Evidence. Phil. Trans. R. Soc. B, 373.

Bergeron, P., Montiglio, P., Réale, D. et al. (2013). Disruptive viability selection on adult exploratory behaviour in eastern chipmunks. Journal of Evolutionary Biology, 26.

Bergman, E., Bishop, C., Freddy, D. et al. (2014a) Habitat Management Influences Overwinter Survival of Mule Deer Fawns in Colorado. The Journal of Wildlife Management, 78.

Bergman, E., Doherty, P., Bishop, C. et al. (2014b) Herbivore Body Condition Response in Altered Environments: Mule Deer and Habitat Management. PLoS ONE, 9.

Bergman, E., Doherty, P., White, G. et al. (2015) Habitat and Herbivore Density: Response of Mule Deer to Habitat Management. The Journal of Wildlife Management, 79.

Bergman, G. & Donner, K. (1964). An analysis of the spring migration of the common scoter and the long-tailed duck in southern Finland. Acta Zool. Fennica, 105.

Berry, H. (1980). Behavioural and eco-physiological studies on blue wildebeest Connochaetes taurinus at the Etosha National Park. PhD Thesis. University of Cape Town, S. Africa.

Bezuidenhout, H., Bradshaw, P., Bradshaw, M. et al. (2015) Landscape units of Mokala National Park, Northern Cape Province, South Africa. Navors. nas. Mus., Bloemfontein, 31.

Blackshaw, J., Allan, D. & McGreevy, P. (2003). Notes on some topics in applied animal behaviour. J.K. Blackshaw.

Bocedi, G., Palmer, S., Pe'er, G. et al. (2014). RangeShifter: a platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. Methods Ecol. Evol., 5.

Bocedi, G., Palmer, S., & Travis, J. (2020) RangeShifter Version 2.0. User Manual.

Bocedi, G., Palmer, S., Malchow, A. et al. (2021). RangeShifter 2.0: an extended and enhanced platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. Ecography, 44.

Boyer, D. & Walsh, P. (2010) Modelling the Mobility of Living Organisms in Heterogeneous Landscapes: Does Memory Improve Foraging Success? Proc. R. Soc. A, 368.

Bracis, C., Gurarie, E., Van Moorter, B. et al. (2015) Memory effects on movement behavior in animal foraging. PLoS ONE 10.

Bracis, C. & Mueller, T. (2017). Memory, not just perception, plays an important role in terrestrial mammalian migration. Proc. R. Soc. B, 284.

Bro-Jørgensen, J. (2016). Our antelope heritage–why the fuss? In: Bro-Jørgensen, J. & Mallon, D. (Eds.). Antelope Conservation: from Diagnosis to Action. Conservation Science and Practice Series, John Wiley & Sons Ltd, W. Sussex, UK.

Brooks, C. & Harris, S. (2008). Directed movement and orientation across a large natural landscape by zebras, Equus burchelli antiquorum. Animal Behaviour, 76.

Bush, A., Mokany, K., Catullo, R. et al (2016). Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. Ecology Letters, 19.

Cahill, A., Aiello-Lammens, M., Fisher-Reid, M. et al. (2012) How does climate change cause extinction? Proc R Soc B, 280.

Cain, J., Owen-Smith, N. & Macandza, V. (2012). The costs of drinking: comparative water dependency of sable antelope and zebra. Journal of Zoology, 286.

Calkins, M., Beever, E., Boykin, K. et al. (2012) Not-so-splendid isolation: modelling climate-mediated range collapse of a montane mammal Ochotona princeps across numerous ecoregions. Ecography, 35.

Careau, V., Thomas, D., Humphries, M. et al. (2008) Energy Metabolism and Animal Personality. Oikos, 117.

Cartwright, S., Bowgen, K., Collop, C. et al. (2016). Communicating complex ecological models to non-scientist end users. Ecological Modelling, 338.

CBD (2018) Convention on Biological Diversity. Aichi Biodiversity Targets. Available from: https://www.cbd.int/sp/targets/

Chen, D. (2021). Impact of climate change on sensitive marine and extreme terrestrial ecosystems: Recent progresses and future challenges. Ambio, 50.

Chen, I., Hill, J., Ohlemueller, R. et al. (2011) Rapid Range Shifts of Species Associated with High Levels of Climate Warming. Science, 333.

Chimienti, M., Desforges, J., Beumer, L. et. al. (2020). Energetics as common currency for integrating high resolution activity patterns into dynamic energy budget-individual based models. Ecological Modelling, 434.

Codling, E. & Bode, N. (2014). Copycat dynamics in leaderless animal group navigation. Movement Ecology, 2.

Coppens, C., de Boer, S. & Koolhaas, J. (2010) Coping Styles and Behavioural Flexibility: Towards Underlying Mechanisms. Philosophical Transactions of the Royal Society B: Biological Sciences, 365.

Cuddington, K., Fortin, M., Gerber, A. et al. (2013) Process-based models are required to manage ecological systems in a changing world. Ecosphere, 4.

Curtin, N., Bartlam-Brooks, H., Hubel, T. et al, (2018). Remarkable muscles, remarkable locomotion in desert-dwelling wildebeest. Nature, 563.

D’Amen, M., Zimmermann, N. & Pearman, P. (2013). Conservation of phylogeographic lineages under climate change. Global Ecology and Biogeography, 22.

Dall'Olmo, G. & Karnieli, A. (2002). Monitoring phenological cycles of desert ecosystems using NDVI and LST data derived from NOAA-AVHRR imagery. International Journal of Remote Sensing, 23.

Darwin, C. (1859) The Origin of Species by means of Natural Selection. John Murray, London, UK.

DeAngelis, D. & Diaz, S. (2019). Decision-making in agent-based modeling: A current review and future prospectus. Frontiers in Ecology and Evolution, 6.

Dennehy, J. (2001). Influence of social dominance rank on diet quality of pronghorn females. Behavioral Ecology, 12.

Di Minin, E. & Toivonen, T. (2015) Global protected area expansion: creating more than paper parks. BioScience, 65.

Diane Fossey Gorilla Fund International (2016). Accessed 25/2/2016 from: http://gorillafund.org/news-events/pr_120721_young-gorillas-dismantle-snares?

Dorward, L. (2014) New record of cannibalism in the common hippo, Hippopotamus amphibius (Linnaeus, 1758). African Journal of Ecology, 53.

Dougherty, L. & Guillette, L. (2018) Linking Personality and Cognition: A Meta-Analysis. Phil. Trans. R. Soc. B, 373.

Druce, H., Pretorius, K. & Slotow, R. (2008) The Response of an Elephant Population to Conservation Area Expansion: Phinda Private Game Reserve, South Africa. Biological Conservation, 141.

Duncan, P. (1975). Topi and their food supply. PhD Thesis. University of Nairobi, Kenya.

Dukas, R. (1999) Costs of Memory: Ideas and Predictions. Journal of Theoretical Biology, 197.

Edgeworth, F. (1885). Methods of statistics. Journal of the Statistical Society of London, 181-217.

Elith, J. & Leathwick, J. (2009). Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics, 40.

Enstipp, M., Ballorain, K., Ciccione, S. et al (2016). Energy expenditure of adult green turtles (Chelonia mydas) at their foraging grounds and during simulated oceanic migration. Functional Ecology, 30.

Estes, R. (1992). The Behavior Guide to African Mammals. University of California Press, Los Angeles, USA.

Estes, R. (2014). The Gnu's world: Serengeti wildebeest ecology and life history. University of California Press, USA.

Fagan, W., Lewis, M., Auger-Méthé, M. et al (2013). Spatial memory and animal movement. Ecology Letters, 16.

Falcón-Cortés, A., Boyer, D., Merrill, E. et al (2021). Hierarchical, Memory-based Movement Models for Translocated Elk (*Cervus canadensis*). bioRxiv (preprint server, not peer-reviewed).

Fischhoff, I., Sundaresan, S., Cordingley, J. et al. (2007) Social Relationships and Reproductive State Influence Leadership Roles in Movements of Plains Zebra, Equus Burchellii. Animal Behaviour, 73.

Fuller, A., Mitchell, D., Maloney, S. K. et al. (2016) Towards a Mechanistic Understanding of the Responses of Large Terrestrial Mammals to Heat and Aridity Associated with Climate Change. Climate Change Responses, 3.

Garel, M., Cugnasse, J., Maillard, D. et al (2007). Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. Ecological Applications, 17.

Gies, M., Sondermann, M., Hering, D. et al. (2015). Are species distribution models based on broad-scale environmental variables transferable across adjacent watersheds? A case study with eleven macroinvertebrate species. Fundamental and Applied Limnology/Archiv für Hydrobiologie, 186.

Giles, S., Harris, P., Rands, S. et al (2020). Foraging efficiency, social status and body condition in group-living horses and ponies. PeerJ, 8.

Gilroy, J., & Lockwood, J. (2016). Simple settlement decisions explain common dispersal patterns in territorial species. Journal of Animal Ecology, 85.

Gomes, A., Guerra, S., Silva, P. et al. (2020) Proactive Common Waxbills Make Fewer Mistakes in a Cognitive Assay, the Detour-Reaching Task. Behav Ecol Sociobiol, 74.

Gompper, M. (1996) Sociality and Asociality in White-Nosed Coatis (Nasua Narica): Foraging Costs and Benefits. Behavioral Ecology, 7.

Gosling, L. (2011) Abstract in: Antelope Conservation in the 21st Century: from Diagnosis to Action. Symposium at Zoological Society of London.

Graham, L., Spake, R., Gillings, S. et al (2019). Incorporating fine-scale environmental heterogeneity into broad-extent models. Methods in Ecology and Evolution, 10.

Greenwood, O., Mossman, H., Suggitt, A. et al. (2016) Using in Situ Management to Conserve Biodiversity under Climate Change. Journal of Applied Ecology, 53.

Greggor, A., Berger-Tal, O., Blumstein, D. et al. (2016). Research priorities from animal behaviour for maximising conservation progress. Trends in Ecology & Evolution, 31.

Greives, T. & Bowden, R. (2019). The world is not flat: accounting for the dynamic nature of the environment as we move beyond static experimental manipulations. Integrative and Comparative Biology, 59.

Grimm, V., Berger, U., DeAngelis, D. et al. (2010). The ODD protocol: a review and first update. Ecological Modelling, 221.

Grimm, V., Railsback, S., Vincenot, C. et al (2020). The ODD protocol for describing agent-based and other simulation models: A second update to improve clarity, replication, and structural realism. Journal of Artificial Societies and Social Simulation, 23.

Guardian, The (2002) Lioness adopts another antelope. Accessed 13/3/2016 from: http://www.theguardian.com/world/2002/feb/17/_ jamesastill.theobserver.

Guisan, A. & Zimmermann, N. (2000). Predictive habitat distribution models in ecology. Ecological modelling, 135.

Hale, R., Blumstein, D., Nally, R. et al. (2020) Harnessing knowledge of animal behavior to improve habitat restoration outcomes. Ecosphere, 11.

Hale, R. & Swearer, S. (2017) When good animals love bad restored habitats: how maladaptive habitat selection can constrain restoration. Journal of Applied Ecology, 54.

Hall, L. & Chalfoun, A. (2018). Behavioural plasticity modulates temperature-related constraints on foraging time for a montane mammal. Journal of Animal Ecology, 88.

Hamby, D. (1994). A review of techniques for parameter sensitivity analysis of environmental models. Environmental Monitoring and Assessment, 32.

Hanson, J., Rhodes, J., Butchart, S. et al. (2020) Global Conservation of Species' Niches. Nature, 580.

Hart, B., Hart, L. & Pinter-Wollman, N. (2008) Large Brains and Cognition: Where Do Elephants Fit In? Neuroscience & Biobehavioral Reviews, 32.

Hefty, K. & Stewart, K. (2019). Flexible resource use strategies of a central-place forager experiencing dynamic risk and opportunity. Movement Ecology, 7.

Heinz Center for Science, Economics and Environment (2012) Climate-change Vulnerability and Adaptation Strategies for Africa's Charismatic Megafauna. Washington, US.

Helm, C. (2006) Ecological separation of the black and blue wildebeest on Ezemvelo Nature Reserve in the highveld grasslands of South Africa. MSc Thesis. University of Pretoria, S. Africa.

Hetem, R., Fuller, A., Maloney, S. et al. (2014) Responses of large mammals to climate change. Temperature, 1.

Hobbs, N., Baker, D., Bear, G. et al. (1996). Ungulate grazing in sagebrush grassland: mechanisms of resource competition. Ecological Applications, 6.

Hopcraft, J., Morales, J., Beyer, H. et al (2014). Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. Ecological Monographs, 84.

Houlahan, J., McKinney, S., Anderson, T. et al. (2017). The priority of prediction in ecological understanding. Oikos, 126.

Howery, L., Bailey, D. & Laca, E. (1999) Impact of spatial memory on habitat use. Grazing Behavior of Livestock and Wildlife, 70.

Huang, J. & Frimpong, E. (2016). Limited transferability of stream-fish distribution models among river catchments: reasons and implications. Freshwater Biology, 61.

Hudson, R. & Nietfeld, M. (1985). Effect of forage depletion on the feeding rate of Wapiti. Journal of Range Management, 38.

Hudson, L., Isaac, N., & Reuman, D. (2013). The relationship between body mass and field metabolic rate among individual birds and mammals. Journal of Animal Ecology, 82.

Hulbert, A. (2014). A sceptics view: “Kleiber’s Law” or the “3/4 Rule” is neither a law nor a rule but rather an empirical approximation. Systems, 2.

Ioannou, C., Singh, M. & Couzin, I. (2015) Potential Leaders Trade Off Goal-Oriented and Socially Oriented Behavior in Mobile Animal Groups. The American Naturalist, 186.

IPCC. (2014a) Summary for policymakers. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Cambridge University Press, UK.

IPCC. (2014b) Africa. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Cambridge University Press, UK.

IPCC, 2019: Summary for Policymakers. In: Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems. Cambridge University Press, UK.

IPCC, 2021: Technical Summary. In: Climate Change 2021: The Physical Science Basis. Cambridge University Press, UK. In Press.

Jiang, Z., Huete, A., Didan, K. et al. (2008). Development of a two-band enhanced vegetation index without a blue band. Remote sensing of environment, 112.

Jones, K. (2018). The impact of perturbations on patterns of movement and parasitism in a critically endangered marsupial, the woylie. PhD Thesis. Murdoch University, Australia.

Jordan, L. & Ryan, M. (2015). The sensory ecology of adaptive landscapes. Biology letters, 11.

Kawamura, K., Akiyama, T., Yokota, H. et al. (2005a). Monitoring of forage conditions with MODIS imagery in the Xilingol steppe, Inner Mongolia. International Journal of Remote Sensing, 26.

Kawamura, K., Akiyama, T., Yokota, H. et al. (2005b) Comparing MODIS vegetation indices with AVHRR NDVI for monitoring the forage quantity and quality in Inner Mongolia grassland, China. Grassland Science, 51.

Keith, S. & Bull, J. (2017). Animal culture impacts species' capacity to realise climate-driven range shifts. Ecography, 40.

King, A., Johnson, D. & Van Vugt, M. (2009) The Origins and Evolution of Leadership. Current Biology, 19.

Knight, M. (1991). Ecology of the gemsbok Oryx gazella gazella (Linnaeus) and blue wildebeest Connochaetes taurinus (Burchell) in the southern Kalahari. PhD Thesis. University of Pretoria, S. Africa.

Laca, E. (1998). Spatial memory and food searching mechanisms of cattle. Rangeland Ecology & Management/Journal of Range Management Archives, 51.

Lawson, C., Bennie, J., Thomas, C. et al (2014). Active management of protected areas enhances metapopulation expansion under climate change. Conservation Letters, 7.

Lawton, J., Brotherton, P., Brown, V. et al (2010) Making space for nature: a review of England’s wildlife sites and ecological network. Report to Defra, UK Govt.

Lea, J., Kerley, G., Hrabar, H. et al. (2016) Recognition and Management of Ecological Refugees: A Case Study of the Cape Mountain Zebra. Biological Conservation, 203.

Lease, H., Murray, I., Fuller, A. et al. (2014). Black wildebeest seek shade less and use solar orientation behavior more than do blue wildebeest. Journal of Thermal Biology, 45.

Luncz, L. & Boesch, C. (2014) Tradition Over Trend: Neighboring Chimpanzee Communities Maintain Differences in Cultural Behavior Despite Frequent Immigration of Adult Females. Am. J. Primatol., 76.

Malishev, M. & Kramer-Schadt, S. (2021). Movement, models, and metabolism: Individual-based energy budget models as next-generation extensions for predicting animal movement outcomes across scales. Ecological Modelling, 441.

Manel, S., Williams, H. & Ormerod, S. (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. Journal of Applied Ecology, 38.

Mantyka-Pringle, C., Martin, T. & Rhodes, J. (2012). Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Global Change Biology, 18.

Marcantonio, M., Metz, M., Baldacchino, F. et al (2016). First assessment of potential distribution and dispersal capacity of the emerging invasive mosquito Aedes koreicus in Northeast Italy. Parasites & vectors, 9.

Márcia Barbosa, A., Real, R., Muñoz, A. et al (2013). New measures for assessing model equilibrium and prediction mismatch in species distribution models. Diversity and Distributions, 19.

Mazza, V., Eccard, J., Zaccaroni, M. et al. (2018) The Fast and the Flexible: Cognitive Style Drives Individual Variation in Cognition in a Small Mammal. Animal Behaviour, 137.

McCullough Hennessy, S., Deutschman, D., Shier, D. et al (2016). Experimental habitat restoration for conserved species using ecosystem engineers and vegetation management. Animal Conservation, 19.

McNaughton, S. (1984) Grazing Lawns: Animals in Herds, Plant Form, and Coevolution. The American Naturalist, 124.

McNaughton, S. (1988). Mineral nutrition and spatial concentrations of African ungulates. Nature, 334.

Merkle, J., Fortin, D. & Morales, J. (2014). A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. Ecology Letters, 17.

Merkle, J., Sigaud, M. & Fortin, D. (2015) To Follow or Not? How Animals in Fusion - Fission Societies Handle Conflicting Information during Group Decision-Making. Ecology Letters, 18.

Merkle, J., Potts, J. & Fortin, D. (2016). Energy benefits and emergent space use patterns of an empirically parameterized model of memory-based patch selection. Oikos, 126.

Merrick, M. & Koprowski, J. (2017). Should we consider individual behavior differences in applied wildlife conservation studies? Biological Conservation, 209.

Mestre, F., Risk, B., Mira, A. et al. (2017). A metapopulation approach to predict species range shifts under different climate change and landscape connectivity scenarios. Ecological Modelling, 359.

Miller, B. & Morisette, J. (2014). Integrating research tools to support the management of social-ecological systems under climate change. Ecology and Society, 19.

Mokala National Park (2017) Mokala National Park Management Plan 2017 - 2027. SANParks Conservation Services Division, Pretoria, S. Africa.

Monzon, J., Moyer-Horner, L. & Palamar, M. (2011) Climate Change and Species Range Dynamics in Protected Areas. Bioscience, 61.

Morales, J., Fortin, D., Frair, J. et al (2005). Adaptive models for large herbivore movements in heterogeneous landscapes. Landscape Ecology, 20.

Moran, E., Hartig, F. & Bell, D. (2016) Intraspecific trait variation across scales: implications for understanding global change responses. Glob. Change Biol. 22.

Murray, J., Low Choy, S., McAlpine, C. et al. (2011) Evaluating model transferability for a threatened species to adjacent areas: Implications for rock-wallaby conservation. Austral Ecology, 36.

Murray, M. (1993). Comparative nutrition of wildebeest, hartebeest and topi in the Serengeti. African Journal of Ecology, 31.

Murray, M. & Brown, D. (1993) Niche separation of grazing ungulates in the Serengeti: an experimental test. J. Anim. Ecol., 62.

National Geographic (2013) Solo: The Wild Dog’s Tale. Accessed 25/2/16 from: http://tvblogs.nationalgeographic.com/2013/03/29/solo-the-wild-dogs-tale/.

Nawroth, C., Prentice, P. & McElligott, A. (2017) Individual Personality Differences in Goats Predict Their Performance in Visual Learning and Non-Associative Cognitive Tasks. Behavioural Processes, 134.

Nyambe, K., Chama, L., Siachoono, S. et al. (2017) Food Quality in Lusaka National Park: Tracking Mortality in Black Lechwe Antelopes. Journal of Applied Animal Welfare Science, 20.

Okayasu, S., Schoolenberg, M., Alkemade, R. et al (2019). Report on the workshop ‘Global Modelling of Biodiversity and Ecosystem Services’. June 2019, The Hague, the Netherlands.

Oloo, F. & Wallentin, G. (2017). An Adaptive Agent-Based Model of Homing Pigeons: A Genetic Algorithm Approach. ISPRS International Journal of Geo-Information, 6.

Osborne, P. & Seddon, P. (2012). Selecting suitable habitats for reintroductions: variation, change and the role of species distribution modelling. In: Ewen, J., Armstrong, D., Parker, K. et al (Eds.). Reintroduction biology: integrating science and management. John Wiley & Sons, W. Sussex, UK.

Osborne, P. & Suárez-Seoane, S. (2002) Should data be partitioned spatially before building large scale distribution models? Ecological Modelling, 157.

Owen-Smith, N., Hopcraft, G., Morrison, T. et al (2020). Movement ecology of large herbivores in African savannas: current knowledge and gaps. Mammal Review, 50.

Pandraud, A., Shrader, A., Sholto-Douglas, C. et al (2020). Factors driving the discovery and utilization of a newly available area by African elephants. Journal of Tropical Ecology, 36.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics, 37.

Patin, R., Fortin, D., Sueur, C. et al. (2019) Space Use and Leadership Modify Dilution Effects on Optimal Vigilance under Food-Safety Trade-Offs. The American Naturalist, 193.

Pauli, B., McCann, N., Zollner, P. et al (2013). SEARCH: spatially explicit animal response to composition of habitat. PloS one, 8.

Payne, B. & Bro-Jørgensen, J. (2016), Disproportionate Climate-Induced Range Loss Forecast for the Most Threatened African Antelopes. Current Biology, 26.

Paz-Y-Miño C, Leonard, S., Ferkin, M. et al. (2002) Self-Grooming and Sibling Recognition in Meadow Voles, Microtus Pennsylvanicus, and Prairie Voles, M. Ochrogaster. Animal Behaviour, 63.

Pearce-Higgins, J., Lindley, P., Johnstone, I. et al. (2019) Site-based adaptation reduces the negative effects of weather upon a southern range margin Welsh black grouse Tetrao tetrix population that is vulnerable to climate change. Climatic Change, 153.

Pearson, R. & Dawson, T. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography, 12.

Peterson, A. & Soberón, J. (2012). Species distribution modeling and ecological niche modeling: getting the concepts right. Natureza & Conservação, 10.

Pinter-Wollman, N., Isbell, L. & Hart, L. (2009) Assessing translocation outcome: Comparing behavioral and physiological aspects of translocated and resident African elephants (Loxodonta africana). Biological Conservation, 142.

Polansky, L., Kilian W, & Wittemyer G. (2015) Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state–space models. Proc. R. Soc., B282.

Possingham, H., Bode, M. & Klein, C. (2015) Optimal conservation outcomes require both restoration and protection. PLOS Biology, 13.

Pringle, R. (2017) Upgrading Protected Areas to Conserve Wild Biodiversity. Nature, 546.

Rabaiotti, D. & Woodroffe, R. (2019) Coping with Climate Change: Limited Behavioral Responses to Hot Weather in a Tropical Carnivore. Oecologia, 189.

Ranc, N., Moorcroft, P., Ossi, F. et al (2021). Experimental evidence of memory-based foraging decisions in a large wild mammal. Proceedings of the National Academy of Sciences, 118.

Razgour, O., Forester, B., Taggart, J. et al. (2019). Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections. Proceedings of the National Academy of Sciences, 116.

Reebs, S. (2010) Temporal Complementarity of Information-Based Leadership. Behavioural Processes, 84.

Reid, R. (2012). Savannas of our birth: people, wildlife, and change in East Africa. Univ of California Press, U.S.

Revilla, E., Wiegand, T., Palomares, F. et al. (2004) Effects of Matrix Heterogeneity on Animal Dispersal: From Individual Behavior to Metapopulation-Level Parameters. The American Naturalist, 164.

Richard-Hansen, C., Vie, J. & de Thoisy, B. (2000) Translocation of red howler monkeys (Alouatta seniculus) in French Guiana. Biological Conservation, 93.

Riek, A. (2008). Relationship between field metabolic rate and body weight in mammals: effect of the study. Journal of Zoology, 276.

Riginos, C. (2015) Climate and the Landscape of Fear in an African Savanna. Journal of Animal Ecology, 84.

Ripple, W., Newsome, T., Wolf, C. et al. (2015) Collapse of the World’s Largest Herbivores. Science Advances, 1.

Roach, N., Hunter, E., Nibbelink, N. et al. (2017). Poor transferability of a distribution model for a widespread coastal marsh bird in the southeastern United States. Ecosphere, 8.

Rocha, A. & Shaver, G. (2009). Advantages of a two band EVI calculated from solar and photosynthetically active radiation fluxes. Agricultural and Forest Meteorology, 149.

Rödel, H., Zapka, M., Talke, S. et al. (2015) Survival Costs of Fast Exploration during Juvenile Life in a Small Mammal. Behav Ecol Sociobiol, 69.

Román-Palacios, C. & Wiens, J. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. Proceedings of the National Academy of Sciences, 117.

Ruddell, B., Yu, R., Kang, M. et al. (2016) Seasonally Varied Controls of Climate and Phenophase on Terrestrial Carbon Dynamics: Modeling Eco-Climate System State Using Dynamical Process Networks. Landscape Ecol, 31.

Rysava, K., McGill, R., Matthiopoulos, J. et al (2016). Re-constructing nutritional history of Serengeti wildebeest from stable isotopes in tail hair: seasonal starvation patterns in an obligate grazer. Rapid Communications in Mass Spectrometry, 30.

SA Govt (2007) National Environmental Management: Biodiversity Act, 2004: Amendment of Critically Endangered, Endangered, Vulnerable and Protected Species List.

Savchenko, G., & Ronkin, V. (2018). Grazing, abandonment and frequent mowing influence the persistence of the steppe marmot, Marmota bobak. Hacquetia, 17.

Savolainen, O., Lascoux, M. & Merilä, J. (2013) Ecological Genomics of Local Adaptation. Nat Rev Genet, 14.

Scheele, B., Foster, C., Banks, S. et al. (2017) Niche Contractions in Declining Species: Mechanisms and Consequences. Trends in Ecology & Evolution, 32.

Schirmer, A., Herde, A., Eccard, J. et al (2019). Individuals in space: personality-dependent space use, movement and microhabitat use facilitate individual spatial niche specialization. Oecologia, 189.

Schlaepfer, M., Runge, M. & Sherman, P. (2002). Ecological and evolutionary traps. Trends in Ecology & Evolution, 17.

Schuster, A., Zimmermann, U., Hauer, C., et al (2017). A behavioural syndrome, but less evidence for a relationship with cognitive traits in a spatial orientation context. Frontiers in Zoology, 14.

Scillitani, L., Sturaro, E., Menzano, A. et al. (2012) Post-release spatial and social behaviour of translocated male Alpine ibexes (Capra ibex ibex) in the eastern Italian Alps. European Journal of Wildlife Research, 58.

Segan, D., Murray, K. & Watson, J. (2016). A global assessment of current and future biodiversity vulnerability to habitat loss–climate change interactions. Global Ecology and Conservation, 5.

Semeniuk, C., Musiani, M., Hebblewhite, M. et al. (2012). Incorporating behavioral–ecological strategies in pattern-oriented modeling of caribou habitat use in a highly industrialized landscape. Ecological Modelling, 243.

Seri, H., Chammem, M., Ferreira, L. et al (2018). Effects of seasonal variation, group size and sex on the activity budget and diet composition of the addax antelope. African Journal of Range & Forage Science, 35.

Sieck, M., Ibisch, P., Moloney, K. et al (2011) Current models broadly neglect specific needs of biodiversity conservation in protected areas under climate change. BMC Ecology, 11.

Sigaud, M., Merkle, J., Cherry, S. et al. (2017) Collective Decision-Making Promotes Fitness Loss in a Fusion-Fission Society. Ecology Letters, 20.

Sih, A. (2013) Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. Animal Behaviour, 85.

Sinclair, S., White, M. & Newell, G. (2010) How Useful Are Species Distribution Models for Managing Biodiversity under Future Climates? Ecology and Society, 15.

Singh, N. & Milner-Gulland, E. (2010) Conserving a moving target: planning protection for a migratory species as its distribution changes. Journal of Applied Ecology, 48.

Skinner, J. & Smithers, R. (1990) The Mammals of the Southern African Subregion. University of Pretoria, Pretoria.

Slotow, R. & van Dyk, G. (2001). Role of delinquent young 'orphan' male elephants in high mortality of white rhinoceros in Pilanesberg National Park, South Africa. Koedoe, 44.

Smeraldo, S., Di Febbraro, M., Ćirović, D. et al. (2017). Species distribution models as a tool to predict range expansion after reintroduction: A case study on Eurasian beavers (Castor fiber). Journal for Nature Conservation, 37.

Smid, H., Wang, G., Bukovinszky, T. et al. (2007) Species-Specific Acquisition and Consolidation of Long-Term Memory in Parasitic Wasps. Proc. R. Soc. B, 274.

Smit, I. & Simms, C. (2015) Internal SANParks report. Using high temporal satellite imagery to monitor vegetation condition in Mokala National Park.

Smith, J., Gavrilets, S., Mulder, M. et al. (2016). Leadership in mammalian societies: Emergence, distribution, power, and payoff. Trends in Ecology & Evolution, 31.

Soldati, F., Burman, O., John, E. et al. (2017) Long-term memory of relative reward values. Biol. Lett. 13.

Soto-Shoender, J., McCleery, R., Monadjem, A. et al (2018). The importance of grass cover for mammalian diversity and habitat associations in a bush encroached savanna. Biological Conservation, 221.

Stalmans, M., Massad, T., Peel, M. et al. (2019) War-induced collapse and asymmetric recovery of large-mammal populations in Gorongosa National Park, Mozambique. PLoS One, 14.

Stephens, D. (2008). Decision ecology: foraging and the ecology of animal decision making. Cognitive, Affective, & Behavioral Neuroscience, 8.

Stillman, R. & Goss-Custard, J. (2010). Individual-based ecology of coastal birds. Biological Reviews, 85.

Stillman, R., Railsback, S., Giske, J., et al. (2015). Making predictions in a changing world: the benefits of individual-based ecology. BioScience, 65.

Stillman, R., Wood, K. & Goss-Custard, J. (2016). Deriving simple predictions from complex models to support environmental decision-making. Ecological Modelling, 326.

Strandburg-Peshkin, A., Papageorgiou, D., Crofoot, M. et al. (2018). Inferring influence and leadership in moving animal groups. Philosophical Transactions of the Royal Society B: Biological Sciences, 373.

Strimas-Mackey, M. & Brodie, J. (2018) Reserve Design to Optimize the Long-Term Persistence of Multiple Species. Ecological Applications, 28.

Stutz, R., Bergvall, U., Leimar, O. et al. (2018) Cohesiveness Reduces Foraging Efficiency in a Social Herbivore. Animal Behaviour, 135.

Sulikowski, D. (2017) From Sensory to Social: The Information That Impacts Animal Foraging Decisions. Current Opinion in Behavioral Sciences, 16.

Suttle, K., Thomsen, M., Meredith A. et al. (2007) Species interactions reverse grassland responses to changing climate. Science, 315.

Swemmer, A., Bond, W., Donaldson, J. et al (2018). The ecology of drought-a workshop report. South African Journal of Science, 114.

Taylor, P., Ogony, L., Ogola, J. et al. (2017). South African mouse shrews (Myosorex) feel the heat: using species distribution models (SDMs) and IUCN Red List criteria to flag extinction risks due to climate change. Mammal Research, 62.

Tello-Ramos, M., Branch, C., Kozlovsky, D. et al. (2019) Spatial Memory and Cognitive Flexibility Trade-Offs: To Be or Not to Be Flexible, That Is the Question. Animal Behaviour, 147.

Thomas, C., Cameron, A., Green, R. et al. (2004) Extinction risk from climate change. Nature, 427.

Thomas, C. & Gillingham, P. (2015) The performance of protected areas for biodiversity under climate change. Biological Journal of the Linnean Society, 115.

Thornton, A. & Samson, J. (2012). Innovative problem solving in wild meerkats. Animal Behaviour, 83.

Thuiller, W., Broennimann, O., Hughes, G., et al. (2006) Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. Global Change Biology, 12.

Tolcha, A. & Shibru, S. (2020). Diurnal activity pattern and social behavior of Swaynes Hartebeest in Maze National Park, Southern Ethiopia. Journal of Ecology and The Natural Environment, 12.

Torney, C., Lamont, M., Debell, L. et al. (2018) Inferring the Rules of Social Interaction in Migrating Caribou. Phil. Trans. R. Soc. B, 373.

Trapanese, C., Meunier, H. & Masi, S. (2019) What, Where and When: Spatial Foraging Decisions in Primates. Biological Reviews, 94.

Turner, W., Rondinini, C., Pettorelli, N. et al. (2015). Free and open-access satellite data are key to biodiversity conservation. Biological Conservation, 182.

Urban, M. (2015) Accelerating Extinction Risk from Climate Change. Science, 348.

Urban, M., Bocedi, G., Hendry, A. et al (2016). Improving the forecast for biodiversity under climate change. Science, 353.

Vale. C., Tarroso, P. & Brito, J. (2014) Predicting species distribution at range margins: testing the effects of study area extent, resolution and threshold selection in the Sahara–Sahel transition zone. Diversity and Distributions, 20.

Valls-Fox, H., De Garine-Wichatitsky, M., Fritz, H. et al. (2018). Resource depletion versus landscape complementation: habitat selection by a multiple central place forager. Landscape Ecology, 33.

van der Vaart, E. & Verbrugge, R. (2008) Agent-based Models for Animal Cognition: A Proposal and Prototype. Proc. of 7th Int. Conf. on Autonomous Agents and Multiagent Systems. Estoril, Portugal.

Van Moorter, B., Visscher, D., Benhamou, S. et al. (2009). Memory keeps you at home: a mechanistic model for home range emergence. Oikos, 118.

VanDerWal, J., Shoo, L., Johnson, C. et al. (2009). Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. The American Naturalist, 174.

Varner, J. & Dearing, M. (2014) The Importance of Biologically Relevant Microclimates in Habitat Suitability Assessments. PLOS ONE, 9.

Velazco, S., Ribeiro, B., Laureto, L. et al (2020). Overprediction of species distribution models in conservation planning: A still neglected issue with strong effects. Biological Conservation, 252.

Von Maltitz, G., Scholes, R., Erasmus, B. et al. (2006). Adapting conservation strategies to accommodate impacts of climate change in southern Africa. In AIACC Working Paper (Vol. 35).

Ward, D. & Saltz, D. (1994). Forging at different spatial scales: Dorcas gazelles foraging for lilies in the Negev Desert. Ecology, 75.

Walker, R., King, A., McNutt, J. et al (2017). Sneeze to leave: African wild dogs (Lycaon pictus) use variable quorum thresholds facilitated by sneezes in collective decisions. Proc. R. Soc. B, 284.

Warren, C., Peek, J., Servheen, G. et al. (1996) Habitat use and movements of two ecotypes of translocated caribou in Idaho and British Columbia. Conservation Biology, 10.

Wasserstein, R. & Lazar, N. (2016) The ASA's Statement on p-Values: Context, Process, and Purpose. The American Statistician, 70.

Wasserstein, R., Schirm, A. & Lazar, N. (2019) Moving to a World Beyond “p<0.05”. The American Statistician, 73.

Weise, F., Lemeris, J., Stratford, K. et al. (2015) A home away from home: insights from successful leopard (Panthera pardus) translocations. Biodiversity and Conservation, 24.

Wilson, D. (1998). Adaptive individual differences within single populations. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 353.

Wolf, M. & Weissing, F. (2012) Animal personalities: consequences for ecology and evolution. Trends in Ecology & Evolution, 27.

Wood, K., Stillman, R. & Goss-Custard, J. (2015). Co-creation of individual-based models by practitioners and modellers to inform environmental decision-making. Journal of Applied Ecology, 52.

Wood, K., Stillman, R., Newth, J. et al (2021). Predicting avian herbivore responses to changing food availability and competition. Ecological Modelling, 441.

Zandberg, L., Quinn, J., Naguib, M. et al. (2017). Personality-dependent differences in problem-solving performance in a social context reflect foraging strategies. Behavioural Processes, 134.

Zhang, H., Zhang, S., Fu, M. et al (2019). Habitat manipulation preferred by Eld’s Deer in Hainan Island, China. Journal for Nature Conservation, 48.