

# Development, Validation, and Application of an Agent-based Model for Simulating Large Herbivore Spatial Use

Diaz, Stephanie Grace https://scholarship.miami.edu/esploro/outputs/doctoral/Development-Validation-and-Application-of-an/991031659119202976/filesAndLinks?index=0

Diaz, S. G. (2022). Development, Validation, and Application of an Agent-based Model for Simulating Large Herbivore Spatial Use [University of Miami]. https://scholarship.miami.edu/esploro/outputs/doctoral/Development-Validation-and-Application-of-a n/991031659119202976

Open Downloaded On 2024/04/26 10:52:57 -0400

Please do not remove this page

## UNIVERSITY OF MIAMI

# DEVELOPMENT, VALIDATION, AND APPLICATION OF AN AGENT-BASED MODEL FOR SIMULATING LARGE HERBIVORE SPATIAL USE

By Stephanie Grace Diaz

A DISSERTATION

Submitted to the Faculty of the University of Miami in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Coral Gables, Florida

December 2021

©2021

Stephanie Grace Diaz All Rights Reserved

# UNIVERSITY OF MIAMI

## A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy

# DEVELOPMENT, VALIDATION, AND APPLICATION OF AN AGENT-BASED MODEL FOR SIMULATING LARGE HERBIVORE SPATIAL USE

Stephanie Grace Diaz

Approved:

Michael S. Gaines, Ph.D. Professor of Biology Donald DeAngelis, Ph.D. Professor of Biology

Rudi van Aarde, Ph.D. Professor of Zoology University of Pretoria Christopher Searcy, Ph.D. Professor of Biology

Douglas Fuller, Ph.D. Professor of Geography Guillermo Prado, Ph.D. Dean of the Graduate School

## Abstract of a dissertation at the University of Miami

Dissertation supervised by Professors Michael Gaines and Donald DeAngelis. No. of pages in text. (259)

Movement is a central process in ecology. An organism's internal state, reflecting the need to obtain critical resources such as food and water, and the spatiotemporal characteristics of these resources, interact to shape movement. Critical resources exist in environments that are both spatially and temporally complex, and susceptible to changes induced by natural and human-induced processes. How organisms interact with these resources and their environment and the way that these interactions shape movement patterns and spatial use is consequently of great interest to wildlife conservation planning and management.

Simulation models are virtual experimental systems that can be used to capture the complex nature of animal movement and its drivers. The underlying components of the system are known by the modeler and can be manipulated, making it possible to explore hypotheses related to movement ecology that would otherwise not be possible otherwise. Agent-based modeling (ABM/ABMs) provides a flexible framework well-suited to incorporate fitness-seeking behaviors and decision-making and thus realistically simulate animal movement and spatial use.

This dissertation aimed to develop, test, and validate an ABM for elephant movement and spatial use and to extend the ABM to explore how spatial variation in critical resources

influence variation in herbivore movement, spatial use, and foraging efficiency. I first used GPS data from African savanna elephants *(Loxodonta africana,* hereafter referred to simply as elephants) in two southern African parks to identify seasonal and intraspecific differences in spatial use characteristics, including home range size and displacement distances. I identified twelve patterns highlighting differences in spatial use between wet and dry seasons and between the two parks and discussed potential factors shaping those patterns.

I then developed and validated a spatially-explicit ABM to simulate the movement and spatial use of elephants by linking the internal and external drivers of elephant movement through hierarchical behavior-based movement rules. To qualitatively explore model performance, I assessed whether our model was able to reproduce the twelve movement patterns present in the empirical data. The ABM was successful at reproducing six out of the twelve identified movement patterns, including the greater diel displacement distances exhibited by elephants in the wet season compared to the dry season in CNP and in KNP, and the greater distances traveled from permanent water sources in the wet season compared to the dry season in CNP. The model reproduced four of the remaining patterns at least partially, including the larger home ranges in the wet season compared to the dry season, but this pattern was only present when comparing within parks. Simulated elephants also exhibited greater net daily displacement distances in the wet season compared to the dry season, but this pattern was only present when comparing within parks. For a quantitative comparison, I also used linear mixed models (LMMs) to identify differences in the movement characteristics between the simulated and empirical data. I found that four of the 16 statistical comparisons between empirical and simulated

movement patterns were categorized as discrepancies of large effect size, three as discrepancies of medium effect size, while the remainder were categorized as of small to very small differences. Discrepancies of large effect sizes associated with home range size, diel displacement distance, and net daily displacement distance, were mainly driven by the simulations underestimating movement characteristics in CNP while overestimating those in KNP. The temporal patterns of movement of the elephant agents were also similar to those observed in real elephants.

Finally, I used the validated ABM and artificial landscapes to explore how spatial differences in critical resources translate into differences in spatial use and foraging efficiency of large, water-dependent herbivores. I found that spatial differences in water source density, tree cover characteristics, and forage distribution led to differences in home range size, activity budgets, trip durations, and foraging efficiency among simulated herbivores in different artificial landscapes. Model results corroborated those from empirical studies stressing the importance of surface water availability in influencing spatial use patterns and foraging efficiencies for water-dependent herbivores within savannas. Additionally, model results pointed to a role for tree cover influencing movement and foraging efficiency regardless of water source density throughout the landscape. The results of my dissertation encourage the development, validation, and application of agent-based models in movement ecology, particularly for the exploration of ecological questions regarding animal movement.

This dissertation is dedicated to my PIs, Mike, Don, and Rudi. Thank you for always being available to chat and for giving the very best advice and suggestions. To Rudi, thank you for welcoming me into your lab with open arms, and for the wonderful week chasing elephants in Kruger. To Don, this dissertation would not have been possible without your patience and encouragement. To Mike, thank you for believing in my potential, for always remaining positive (even when I am not), and for having my back. I am finally at the finish line because you never let me give up.

Finally, this dissertation is dedicated to my family, who have never ceased supporting me even when I didn't see myself finishing this dissertation. To my mom and dad; I couldn't have done this without your love and constant encouragement. Thank you for raising me to be stubborn. This is as much your accomplishment as it is mine. To Karina, thank you for the 8 AM (and 12 PM, 5 PM, 9 PM) facetime calls, and for Annie. To Daniel, thank you for staying up with me to listen to Taylor Swift's new album every time. I am lucky to be your sister. And to my boyfriend David, thank you for being there for me at my worst and my best and all the in-betweens. But most of all, thank you for being the very best part of these 7 years.

I would like to acknowledge the Florida Education Fund, and the biology department for their financial support. This work would not have been possible without their interest and support.

I would also like to acknowledge Michael Mole and Andrew Purdon for being the best lab mates I could've asked for. I would not have reached the finish line without your help.

# TABLE OF CONTENTS

LIST OF FIGURES	viii
LIST OF TABLES	xii
LIST OF ABBREVIATIONS	xiii

# CHAPTER 1

## AGENT-BASED MODELING IN MOVEMENT ECOLOGY

1.1 Understanding and simulating animal movement	1
1.2 Models simulating animal movement	4
1.3 Agent-based modeling in movement ecology	7
1.4 Exploring the links between movement, spatial use, and foraging efficiency heterogenous environments using agent-based models (ABMs)	' in 10
1.5 African elephant movement ecology	12
1.6 Aims and objectives	14

# CHAPTER 2

## IDENTIFYING PATTERNS OF ELEPHANT MOVEMENT FOR ABM VALIDATION

2.1. Pattern-oriented modeling: patterns as "fingerprints" of a system's underlying processes	17
2.2 Methods	29
2.3 Results	34
2.4 Discussion	37
2.5 Concluding remarks	42

# CHAPTER 3

# DEVELOPMENT AND VALIDATION OF A SPATIALLY-EXPLICIT AGENT-BASED MODEL FOR ELEPHANT MOVEMENT AND SPATIAL USE

3.1 Theoretical framework	43
3.2 Methods	44
3.3 Results	51
3.4 Discussion	53
3.5 Conclusions	59

## CHAPTER 4

# AN ABM APPROACH FOR EXPLORING THE INFLUENCE OF FORAGE, WATER, AND TREE COVER CHARACTERISTICS ON THE MOVEMENT AND FORAGING EFFICIENCY AND OF HERBIVORES

4.1 Surface water availability and piospheres: influences on foraging area and activity budgets	61
4.2 Water and shade: influences on activity budgets, foraging trip durations an habitat use	d 62
4.3 Spatial variation of water and tree cover in savannas	63
4.4 Home ranges as large-scale expressions of movement decisions	65
4.5 Methods	70
4.6 Results	79
4.7 Discussion	85

## CHAPTER 5

## CONCLUSIONS AND FUTURE DIRECTIONS

5.1 Thesis overview	99
---------------------	----

5.2 Forage abundance and social interactions: fitting in the missing pieces to understanding spatial variation in movement and foraging efficiency of larg herbivores	o e 101
5.3 Limitations of using remote sensing products when modeling elephant movement	104
5.4 Potential model applications	110
5.5 Future directions	115
5.6 Concluding remarks	118
FIGURES	120
TABLES	145
WORKS CITED	159
APPENDIX	186

# List of Figures

Figure 2.1: Cartogram depicting wet and dry season water sources for one of our study
areas in northern Botswana, including CNP and surrounding protected areas. The
gray outline represents the specific areas included in the model
Figure 2.2: Cartogram depicting wet and dry season water sources for one of our study
areas in South Africa KNP 121
Figure 2 3: 95% contour isonleths of utilization distributions (home ranges) for CNP's
wet season (dark green) and CNP's dry season (vellow green) determined by
dynamic Brownian Bridge movement models
Eigure 2.4: 05% contour iconlethe of utilization distributions (home ranges) for KND's
Figure 2.4. 95% contour isopieurs of utilization distributions (nonie ranges) for KNF's
dynamia Brownian Bridge meyomant models
Eigune 2.5: Develote of home range size coloulated for both ampirical and simulated data
Figure 2.5. Boxplots of nome range size calculated for both empirical and simulated data $(n - 80  two is starting for KND's two second 71 two is starting for KND's day second$
(n = 80  trajectories for KINP's wet season, /1 trajectories for KINP's dry season, 20 trajectories for CNP's for CNP's for comparison for comparison for comparison for CNP's for comparison fo
29 trajectories for CNP's wet season, and 16 trajectories for CNP's dry season).
norizontal lines indicate median values, the top and bottom edges of the boxes
indicate the upper 25 <sup>th</sup> and lower 75 <sup>th</sup> percentile, respectively. The length of the
upper and lower whiskers indicates the data within 1.5 times the interquartile
range above the upper and below the lower quartile, respectively. The black dots
indicate outliers
Figure 2.6: Boxplots of diel displacement distances calculated for both empirical and
simulated data (n = 80 trajectories for KNP's wet season, /1 trajectories for $KNP'$
KNP's dry season, 29 trajectories for CNP's wet season, and 16 trajectories for
CNP's dry season). horizontal lines indicate median values, the top and bottom
edges of the boxes indicate the upper 25 <sup>th</sup> and lower 75 <sup>th</sup> percentile, respectively.
The length of the upper and lower whiskers indicates the data within 1.5 times the
interquartile range above the upper and below the lower quartile, respectively.
The black dots indicate outliers
Figure 2./: Boxplots of net daily displacement distances calculated for both empirical and
simulated data (n = 80 trajectories for KNP's wet season, /1 trajectories for $(1 + 1)$
KNP's dry season, 29 trajectories for CNP's wet season, and 16 trajectories for
CNP's dry season). horizontal lines indicate median values, the top and bottom
edges of the boxes indicate the upper 25 <sup>th</sup> and lower 75 <sup>th</sup> percentile, respectively.
The length of the upper and lower whiskers indicates the data within 1.5 times the
interquartile range above the upper and below the lower quartile, respectively.
The black dots indicate outliers
Figure 2.8: Boxplots of maximum distance traveled from a permanent water source
calculated for both empirical and simulated data ( $n = 76$ trajectories for KNP's
wet season, 70 trajectories for KNP's dry season, 28 trajectories for CNP's wet
season, and 15 trajectories for CNP's dry season). horizontal lines indicate
median values, the top and bottom edges of the boxes indicate the upper $25^{\text{un}}$ and
lower /5 <sup>th</sup> percentile, respectively. The length of the upper and lower whiskers
indicates the data within 1.5 times the interquartile range above the upper and
below the lower quartile, respectively. The black dots indicate
outliers127

Figure 3.1. Map showing the extent of the rasters (shown here is the raster used for Enhanced Vegetation Index (EVI)) utilized for KNP and CNP (along with surrounding protected areas outside of the red outline but within the raster's Figure 3.2. Simplified flow chart of the model decision tree for every time step ......129 Figure 3.3. Map showing an empirical trajectory from an elephant in CNP (gray trajectory), and two examples of corresponding simulated trajectories (red and Figure 3.4: Boxplots of A) home range sizes, B) diel displacement distances, C) net daily displacement distances and D) maximum distances traveled from a permanent water source calculated for both empirical and simulated data (n = 80 trajectories for KNP's wet season, 71 trajectories for KNP's dry season, 29 trajectories for CNP's wet season, and 16 trajectories for CNP's dry season). Data points corresponding to simulations represent a mean of all the data collected over ten simulation runs. The bold horizontal lines indicate median values, the top and bottom edges of the boxes indicate the upper 25th and lower 75th percentile, respectively. The length of the upper and lower whiskers indicates the data within 1.5 times the interquartile range above the upper and below the lower quartile, Figure 4.1: Forage layers with a clumped forage distribution (left), and a dispersed forage distribution (right). Clumped and dispersed forage landscapes have approximately similar means, sums, and standard deviations, but differ in the range of autocorrelation of cells. Cells with higher vegetation biomass are in white, while Figure 4.2: Tree cover layers with clumped distributions (top two layers), and dispersed distributions (bottom two layers). Tree cover layers were also characterized as having either high (top and bottom layers on the right), or low (top and bottom layers on the left) abundances of tree cover. Cells with tree cover are in white and cells without tree cover Figure 4.3: Clumped forage layers with low and high-water source density. The red inset shows a close-up of piospheres around water sources (water sources are Figure 4.4: Boxplots of foraging efficiencies calculated for landscapes with clumped forage distributions (left facets), and dispersed forage distributions (right facets), and tree cover characteristics (n=100 simulations for each landscape). The bold horizontal lines indicate median values, the top and bottom edges of the boxes indicate the upper 25<sup>th</sup> and lower 75<sup>th</sup> percentile, respectively. The length of the upper and lower whiskers indicates the data within 1.5 times the interquartile range above the upper and below the lower quartile, respectively. The black dots indicate Figure 4.5: Boxplots of forage consumption calculated for landscapes with clumped forage distributions (left facets), and dispersed forage distributions (right facets), and tree cover characteristics (n=100 simulations for each landscape). The bold horizontal lines indicate median values, the top and bottom edges of the boxes indicate the upper 25th and lower 75th percentile, respectively. The length of the

upper and lower whiskers indicates the data within 1.5 times the interquartile

range above the upper and below the lower quartile, respectively. The black dots	
indicate outliers	5
Figure 4.6: Boxplots of total distance traveled calculated for landscapes with clumped	
forage distributions (left facets), and dispersed forage distributions (right facets),	
and tree cover characteristics ( $n=100$ simulations for each landscape). The bold	
horizontal lines indicate median values, the top and bottom edges of the boxes	
indicate the upper 25th and lower 75th percentile respectively. The length of the	
unner and lower whiskers indicates the data within 1.5 times the interquartile	
range above the upper and below the lower quartile respectively. The black dots	
indicate outliers	7
Figure 4.7: A) Pownlots of home range sizes calculated for landscapes with alumned	/
Figure 4.7. A) Boxplots of nome range sizes calculated for landscapes with clumped	
forage distributions (feft facets), and dispersed forage distributions (fight facets),	
and tree cover characteristics ( $n=100$ simulations for each landscape), for both	
low and high-water landscapes. The bold horizontal lines indicate median values,	,
the top and bottom edges of the boxes indicate the upper 25th and lower 75th	
percentile, respectively. The length of the upper and lower whiskers indicates the	;
data within 1.5 times the interquartile range above the upper and below the lower	•
quartile, respectively. The black dots indicate outliers. B) Examples of home	
ranges for simulated trajectories in high water landscapes with clumped forage	
distributions. C) Examples of home ranges for simulated trajectories in low water	r
landscapes with clumped forage distributions. For both B and C, the blue dots	
represent water sources, the red polygons represent the 95% isopleths for each	
home range, and the black lines within the polygons represent the corresponding	
trajectory	3
Figure 4.8: Simulated trajectories of an agent in landscapes with low water, clumped	
forage, low tree cover, and either A) dispersed tree cover, or B) clumped tree	
cover. Green cells represent the presence of tree cover. Both trajectories converge	e
on one water point, and the color of the path represents the duration of the	
respective trip. Darker blue paths represent longer trip durations from water.	
Frequency distributions for both simulated trajectories are depicted in C	9
Figure 4.9: Boxplots of average time spent foraging per day for landscapes with clumped	í
forage distributions (left facets) and dispersed forage distributions (right facets)	*
and tree cover characteristics $(n=100 \text{ simulations for each landscape)}$ . The hold	
herizontal lines indicate median values the ten and bettern adges of the boyes	
indicate the unner 25th and lower 75th percentile, recreatively. The length of the	
indicate the upper 25th and lower 75th percentile, respectively. The length of the	
upper and lower whiskers indicates the data within 1.5 times the interquartile	
range above the upper and below the lower quartile, respectively. The black dots	~
indicate outliers	0
Figure 4.10: Boxplots of average time spent in shade per day for landscapes with	
clumped forage distributions (left facets), and dispersed forage distributions (righ	ıt
facets), and tree cover characteristics (n=100 simulations for each landscape). Th	e
bold horizontal lines indicate median values, the top and bottom edges of the	
boxes indicate the upper 25th and lower 75th percentile, respectively. The length	
of the upper and lower whiskers indicates the data within 1.5 times the	
interquartile range above the upper and below the lower quartile, respectively.	
The black dots indicate outliers	1

# List of Tables

Table 2.1: Twelve patterns present in the empirical data
Table 3.1: Variables used within the model, their descriptions, associated entities and
possible values146
Table 3.2: Model parameters and relevant values or ranges used in the ABM, along with
supporting references
Table 3.3: Agent behaviors and their corresponding cell selection strategies and
supporting references
Table 3.4: Patterns present in the empirical movement data for both CNP and KNP, and
those produced by the ABM. Bolded patterns represent those that fully matched
the respective pattern in the empirical data
Table 3.5: Model validation results. P-values and effect sizes for models comparing empirical and simulated movement patterns across different ecological
contexts
Table 3.6: Patterns associated with activity budgets present in the relevant literature, and
those produced by the model
Table 4.1: Percent changes in foraging efficiency, forage consumed, distance traveled,
home range size, trip duration, and time spent employing foraging, shade use, and
wetting and drinking for each landscape factor. Percent changes attributed to each
factor were averaged across landscapes with all different combinations of the
other three landscape factors. Blue cells indicate a percent increase and red cells indicate a percent decrease. The direction of the abange is described under each
landscape factor (e.g. foraging efficiency is associated with a 7.2 percent increase
when we shift from considering a low-water landscape to a high-water
landscape) 155
Table 4.2: Percent changes in foraging efficiency forage consumed distance traveled
home range size, trip duration and time spent employing foraging, shade use, and
wetting and drinking due to tree cover abundance and distribution, assessed
separately for low- and high-water landscapes. Percent changes attributed to each
factor were averaged across landscapes with all different combinations of the
other two landscape factors. Blue cells indicate a percent increase and red cells
indicate a percent decrease. The direction of the change is described under each
landscape factor (e.g., foraging efficiency is associated with a 2.1 percent increase
when we shift from considering a low tree cover landscape to a high tree cover
landscape, assuming water availability remains low)156
Table 4.3: Hypotheses, whether the hypotheses were supported, and the model's
results

# **List of Abbreviations**

ABM/ABMsAgent-based modeling/agent-based modelsCRW/sCorrelated-random walk/sSSMState-space model

## **CHAPTER 1**

### Agent-based modeling in movement ecology

## 1.1 Understanding and simulating animal movement

Movement is central to many ecological processes. At small temporal and spatial scales individual organisms use movement to maximize their fitness, or the ability to survive and reproduce, within their local environments (Morales et al., 2005; van Moorter et al., 2013). This influences population dynamics over larger temporal and spatial scales (Doherty & Driscoll, 2018; Ims & Andreassen, 2005). An organism's internal state, reflecting the need to obtain critical resources such as food and water, and the spatiotemporal characteristics of these resources, interact to shape movement (Nathan et al., 2008). Critical resources exist in environments that are both spatially and temporally complex, and susceptible to changes induced by natural processes, as well as those resulting from human encroachment on natural systems and global climate change (Doherty & Driscoll, 2018). How organisms interact with these resources and their environment and the way that these interactions shape movement patterns and spatial use is consequently of great interest to wildlife conservation planning and management (Fraser et al., 2018).

Studies of animal movement can be characterized as being part of either of two areas of research (Dodge, 2016). The first aims to understand how the interactions between individuals and their environmental context influence movement by analyzing movement data (Dodge, 2016). It often involves calculating movement parameters, such as step length and turning angle, from tracking data, and relating these parameters to the environmental landscape via statistical models (Dodge, 2016; Schick et al., 2008).

1

Statistical models, including Hidden Markov Models (HMMs) and State Space Models (SMMs), have been successful at inferring "hidden" behavioral states from movement data of elk (Forester et al., 2007), leatherback turtles (Jonsen et al., 2006), and wolves (Franke et al., 2006) etc. These models have been primarily used to link environmental covariables to simplified behavioral states, such as "transit" and "resident", or "encamped" and "exploratory" (Deruiter et al., 2017.; Jonsen et al., 2006; Morales et al., 2005). However, statistical models are limited in the kind of environment-movement interaction questions that they can answer for several reasons (Schick et al., 2008). One such question that is difficult to answer with statistical models is: how and why do spatial differences in resource characteristics lead to spatial differences in movement (Goosens et al., 2020)? First, this question is difficult for statistical models because it is not an easy feat to disentangle and isolate the effects of specific environmental variables versus other possible variables on movement, particularly when the influences of certain variables cooccur with others (Aarts et al., 2009; Amoroso, 2020; Doherty et al., 2019). In the laboratory, it is possible to perform controlled experiments on systems to systematically examine the effects of certain variables on a given outcome (Jenerette & Shen, 2012; Shaw, 2020). In the field, however, empirical investigation of environment-movement questions via controlled experiments is often not possible, primarily because large-scale (ecosystem-level) manipulation of habitat is not feasible (Synes et al., 2016). Additionally, incorporating an organism's internal state, a key factor driving an individual's motivation to fulfill certain goals (Getz & Saltz, 2008; Nathan et al., 2008) , into statistical models is challenging because it is difficult to measure internal states in the field (Latombe et al., 2014). Consequently, statistical models cannot readily capture

the relationship between an individual's internal states (e.g., hunger, heat stress) and the environment (e.g., location of food, tree cover, water sources), and how this relationship drives movement (Hooten et al., 2019). Thus, it is difficult to obtain a deeper understanding of the underlying causes for variation in movement and spatial use in heterogenous environments.

The second area of research consequently focuses on developing models to simulate realistic animal movement to make predictions and to provide a greater conceptual understanding of animal movement by "making more with less data" (Dodge, 2016; Technitis et al.,2015; Vuilleumier & Metzger, 2006).Simulation models are virtual experimental systems that can be used to capture the complex nature of animal movement and its drivers (Peck, 2004). The underlying components and processes generating movement patterns are known by the modeler and can be manipulated, making it possible to explore hypotheses related to movement ecology that would not be possible otherwise (Getz & Salter, 2020).

Several studies suggest that advances in the field of movement ecology should now be geared towards developing realistic simulation models that capture the complex interactions between organisms and their dynamic environments (Dodge, 2016; Wood et al., 2018). Realistic movement models can then be used to explore hypotheses related to how movement and patterns are influenced by organism-resource interactions and to forecast responses to novel environmental changes.

#### **1.2 Models simulating animal movement**

Models have been extensively and successfully used for analyzing movement paths but perhaps have been used less for simulating realistic animal movement. The earliest of models used to simulate animal movement include random walk and diffusion models (Bell, 1991; Codling et al., 2008; Fraenkel & Gunn 1940; Gunn & Walshe, 1941; Jones, 1988; Preisler et al., 2004). The simplest random walk model assumes that the direction of relocation of an individual is unbiased, or not geared towards the direction of a specific target, and uncorrelated, such that turning angles characterizing relocations are drawn randomly from a uniform distribution (Codling et al., 2008). While random walks are generally unrealistic representations of animal movement, especially for individuals that respond to the external environment and modify their movement accordingly (Nathan et al., 2008), they serve as a foundation for more realistic models of animal movement (Fronhofer et al., 2013).

Correlated random walks (CRWs) represent one of these more realistic models. Displaying some degree of correlation in the turning angles of successive relocations, CRWs have been successfully used to model animal movement as the paths of many animals display directional persistence (Bartumeus et al., 2005; Bergman et al., 2000; Duffy, 2009; Schultz & Crone, 2016). For example, van Moorter (2009) used a correlated random walk to simulate the diffusive component of movement when a simulated individual moved away from the center of a point of attraction, ultimately generating realistic home ranges (Van Moorter et al., 2009). Another type of CRW includes biased correlated random walks, where movement is directed towards a target (Codling et al., 2008).

While CRWs do generate movement paths that more closely resemble those of animals, such as the dispersal movements of caribou in the winter (Bergman et al., 2000) and the movement of pea aphids (Nilsen et al., 2013), there are particular drawbacks. Perhaps the greatest pitfall of CRWs and other types of random walks used to simulate animal movement is these models' unrealistic assumption that the individual's external environment is homogeneous (Codling et al., 2008; Vuilleumier & Metzger, 2006). This assumption impedes the realistic simulation of animal movement because the movement decisions of individuals in nature are strongly influenced by the spatiotemporal heterogeneity of the landscape, which can include the distribution of forage and water availability (Johnson et al., 1992; Turner et al., 1993), and as such, simulated movement cannot capture organism-environment interactions. In response, "context aware random walks" have been developed to incorporate the environmental context in simulating movement (Ahearn et al., 2016; Long, 2018). For example, Ahearn et al., (2016) introduced a context-sensitive simulation model that combined a correlated random walk with contextual factors known to influence movement, such that that movement from one location to the next was a product not only of turning angles and movement steps, but also of how environmental factors influenced the visitation probability of a given area. The authors simulated tiger movement using the context-sensitive simulation model incorporating slope as a contextual factor, and a correlated random walk model, and compared the resulting trajectories with empirical data of tiger movement. The contextsensitive simulation model reproduced tiger movement realistically. It was considered a better approach for simulating movement because the resulting simulated trajectory reflected a fitness-seeking behavior and local movement decisions influenced by the

environment rather than simply simulating changes in geometric metrics such as step length and turning angle (Ahearn et al., 2016).

In addition to the different types of random-walk models, SSMs represent another approach to analyze and predict animal movement (Patterson et al., 2008), in which a hypothetical mechanistic movement model, such as a one-dimensional random walk, and an observation model dependent on the type of movement data obtained, are combined. When combined, the mechanistic movement and observation models can be used to "fill in the gaps" of an animal's trajectory by predicting the animal's state throughout its movement path. While these models have provided a better understanding of how the movement decisions of different species change over time and space, they have not been as useful in simulating realistic animal movement (Wijeyakulasuriya et al., 2020). Moreover, the application of SSMs is complex, computer-intensive, and requires knowledge of statistical modeling (Patterson et al., 2017, 2008). It is thus unclear how well SSMs perform as predictive tools.

The movement path of an animal is the result of continuous relocations driven by the complex interplay of abiotic and biotic factors, and the physiological and behavioral state of the individual (Nathan et al., 2008; Tang & Bennett, 2010). If a model is expected to realistically simulate movement and make robust predictions, it must be flexible enough to incorporate how these factors influence the various decisions that individuals make as they move. In other words, models should somehow incorporate fitness-seeking behaviors to reflect how animals modify their decisions and adjust their behaviors in response to both biotic and abiotic factors (Grimm & Berger, 2016; Tang, & Bennett, 2010).

#### 1.3 Agent-based modeling in movement ecology

An alternative modeling approach widely used in the movement ecology field, agentbased modeling (ABM/ABMs) provides a flexible framework well-suited to incorporate fitness-seeking behaviors and decision-making and thus realistically simulate animal movement and spatial use (Tang & Bennett, 2010a). ABM is a "bottom-up" modeling method in which system-level processes are the consequence of interactions at the individual level. ABMs simulate "agents", which represent real-world entities, and an environment that agents can interact with and in which they can also interact with other agents. Each agent can have a number of variables representing internal physiological states, as well as variables for behavioral states, all of which may be dynamic and are often interdependent, capturing the complexity of real-world organisms (DeAngelis & Diaz, 2019; DeAngelis & Grimm, 2014; DeAngelis & Mooij, 2005; Grimm & Railsback, 2005).

When ABMs are also spatially-explicit, such that every entity within the model is associated with a location, they can effectively capture the spatial relationships between landscape elements, and between landscape elements and agents (Duning, 1995). Spatially-explicit ABMs are often associated with grid-based environments on which agents interact. New advances in remote sensing technology and geographic information systems have enabled ecological modelers to represent landscapes and their attributes realistically, defining the complex spatial relationship between individuals and their environment (DeAngelis & Yurek, 2016; Duning, 1995). For example, remotely sensed Normalized Difference Vegetation Index (NDVI) has been used as a measure of food availability in ABMs for elephants (Boult et al., 2018b), and digital elevation models (DEMs) have been used to represent slope in ABMs developed for moose (Semeniuk et al., 2012). Many ABMs combine individual layers comprised of different types of spatial data into one model environment where a cell can be associated with many underlying attributes, such as distance to water, forage level, and slope.

ABMs are ideally suited to simulate animal movement. They can incorporate the dynamic internal and physiological states of individuals and the changing external factors that influence those internal states that ultimately lead to movement. Furthermore, the navigation capacity and motion capabilities of agents can be tailored to realistically portray the navigation capacities and motion capabilities of any given species (Nathan et al., 2008).

## 1.3.1 When to move

Moving individuals must continually make two decisions: when to move, and where to move (DeAngelis & Diaz, 2019). ABMs for movement generally incorporate rules that dictate when an individual agent decides to move from its current location. The onset of movement at fine scales may depend on the individual's current internal state, including its physiological and psychological conditions, the condition of the current area that the individual is in, and the presence of competition and predation (Doherty et al., 2019; Martin et al., 2013; Semeniuk et al., 2011). As such, ABMs simulating the fine-scale movement of individuals often keep track of temporal changes in the individual agent's internal state and its local surroundings. These changes generally prompt agent movement if they somehow increase (or at the very least, not decrease) the agent's fitness.. For example, an increased risk of predation in an area may elicit fear and prohibit movement through the area (Doherty & Driscoll, 2018), while decreased energy reserves

may result in an individual seeking out forage areas within the landscape. Large scale movement, such as migration, may be triggered by temporal changes in resource availability (Van Moorter et al., 2013) along with a number of other factors, ABMs have been utilized to explore the potential decision-rules that may dictate the timing of such behavior for various species.

## 1.3.2 Where to move

Many organisms can process information about their environment and make movement decisions to satisfy internal needs. When deciding where to move, mobile animals rely on their navigation capacity, which links the animals' internal states and external variables leading to either non-oriented, oriented, or memory-driven movement (Doherty & Driscoll, 2018; Fagan et al., 2013; Nathan et al., 2008). The ABM framework lends itself to representing dynamic environmental cues, particularly when the spatiotemporal relationships between the agent and the environment are explicitly represented, as in spatially explicit ABMs. The internal states of individuals can be represented as dynamic state variables and integrated with the cognitive capabilities of individuals, which allows model agents to assess various movement decisions within complex landscapes and ultimately decide on their next destination (Tang & Bennett, 2010). Additionally, some stochasticity in selecting an area to move to is incorporated within many ABMs by using a combination of probabilistic and logical rules, reflecting imperfect knowledge of the environment and perception capabilities. Many ABMs simulating animal movement explicitly represent and track various components of an individual agent's internal state in detail, resulting in movement characteristics that closely mimic those of organisms in natural environments. Movement is often the result of decision rules related to fitnessseeking or adaptive behaviors, which make the agents more "life-like" (Railsback, 2001), and movement more realistic. Fitness-related decision-making rules remain consistent even as the environment changes, and as such, the predictions made by ABMs regarding responses to the environment are more reliable than predictions based on parameters taken directly from empirical data (i.e. step lengths and turning angles) (Grimm & Berger, 2016; Stillman et al., 2015).

# 1.4 Exploring the links between movement, spatial use, and foraging efficiency in heterogenous environments using agent-based models (ABMs)

The survival of herbivores in savanna environments depends on their ability to obtain resources critical for growth and development, and herbivores must continually make movement decisions to acquire resources (Abrahms et al., 2021; Nathan et al., 2008). The "when to move" and "where to move" components of movement decisions may vary from environment to environment because the availabilities and distributions of critical resources are both spatially and temporally changing (Massé & Cote, 2013; Roshier et al., 2008), which differentially influences distances traveled (Mcintyre & Wiens, 1999), turning rates (Fauchald & Tveraa, 2006), and activity budgets. Consequently, different distributions and availabilities of critical resources can be linked to differences in movement patterns and spatial use across populations.

Simulation models have been developed to explore the response of herbivores to landscape heterogeneity, with most of these models focusing on the influence of the abundance and distribution of food resources on differences in movement patterns and spatial use. These include spatially explicit agent-based models in which movement and foraging is driven by generalized "good" and "bad" areas of forage resources (Vincenot et al., 2015), specific species of vegetation across the landscapes (Roese et al., 1991), or "resource" and "non-resource" sites (Boyer & Walsh, 2010; Turner et al., 1993). Such models have yielded theoretical contributions to the understanding of movement ecology, particularly at larger spatial scales. However, models incorporating only the distribution and abundance of forage resources paint an incomplete picture of movement dynamics, as several studies have acknowledged that the distributions of critical non-forage resources also influence foraging and movement (Bailey et al., 1996; Larson-Praplan et al., 2015; Redfern, 2003, Street et al., 2015).

As an herbivore forages, it must simultaneously respond to biotic and abiotic environmental factors, and it may use non-forage resources to survive, depending on the environmental context at that time (Bailey et al., 1996). In savannas, many herbivores depend on surface water and must make regular trips to water sources to drink (Redfern, 2003; Smit & Grant, 2009, but see Purdon & van Aarde 2017). Additionally, large herbivores must regularly contend with thermoregulatory challenges in the form of high temperatures for parts of the year and must rely on shade and water to reduce heat stress (Veldhuis et al., 2019). The need to respond to these requirements may place a constraint on foraging in the form of trade-offs and may influence space use patterns that arise from foraging movements (Chamaillé-Jammes et al., 2013; Street et al., 2015; Valeix et al., 2008; Veldhuis et al., 2019).

Savanna landscapes exhibit differences in the spatial characteristics of forage, water, and tree cover (House et al., 2003; Sankaran et al., 2005), and these differences may translate

to spatial variation in foraging efficiency by differentially influencing the movement patterns of large herbivores (De Knegt et al., 2007, Naidoo et al., 2012). The efficiency of foraging, defined as the ratio of energy gained to energy expended while searching for food resources has strong implications for herbivore survival (Wiggins et al., 2006). Their ability to obtain these resources is dependent on movement decisions, and, as such, there is an inherent link between herbivore movement and foraging efficiency (Bartumeus et al., 2005) that merits exploration.

Manipulation of the spatial characteristics of resources would allow for a controlled method to elucidate the relative impacts of different resources on movement; however, manipulating resource abundances and distributions in real landscapes is not feasible. Combining realistic movement models with artificial landscapes generated to reflect different abundances and distributions of resources allows for investigation of the reasons associated with complex herbivore-resource interactions that drive movement in different landscapes.

## 1.5 African elephant movement ecology

Savanna elephants *(Loxodonta africana)* are a prime example of large herbivores faced with continually changing environments, caused by both anthropogenic and natural disturbances. Understanding how elephant movement are influenced by the environment is critical because it sheds light on the extent to which elephant populations may alter the environment and impact other organisms (Jones et al., 1997; Wright & Jones, 2006), and their demography (Young & van Aarde 2010). Consequently, advances in location-based

tracking have been leveraged to gain insights into the movement of the African savanna's largest herbivore for management and conservation purposes.

Elephant movement patterns and subsequent spatial distribution are strongly determined by a combination of factors (Duffy et al., 2011; Harris et al., 2008; Western & Lindsay, 1984), including vegetation greenness, distribution of water sources, and environmental temperature (Harris et al., 2008; Loarie, et al., 2009a; Loarie et al., 2009b; Wall et al., 2013; Western & Lindsay, 1984). These same factors also play a role in shaping the movement patterns and habitat selection of other large savanna herbivores (Hirst 1975; Traill 2004), including white rhino (Ceratotherium simum) (Shrader et al., 2006; Tichagwa et al., 2019), African buffalo (Syncerus caffer) (Naidoo et al., 2012; Sianga et al., 2017; Roug et al., 2020), and wildebeest (Connochaetes taurinus) (Yoganand & Owen-Smith 2014; Weeber et al., 2020). Elephants prefer landscapes that are greener than average throughout the year (Loarie et al., 2009b), and generally remain closer to water during the dry season (Stokke & Du Toit, 2002; Western & Lindsay, 1984; Young et al., 2009). By inducing behavioral changes aimed at thermoregulation, such as shade use and wetting, environmental temperature also influences how elephants and other large herbivores utilize space (Dunkin et al., 2013; Kinahan et al., 2007; Mole et al., 2016).

Recently, an ABM has been developed to simulate elephant presence and absence in Kenya and Tanzania's Amboseli Basin, wherein daily relocations to and from dispersal areas were assumed to be driven by vegetation quality, vegetation quantity, and the availability of water (Boult et al., 2018b). Their model results fit the observed presence and absence of real elephants relatively well, suggesting that resource-driven models are effective at predicting the onset of range shifts. However, many of the environmental changes that are likely to impact elephants and other large herbivores in the future may elicit behavioral responses at finer scales. For example, increases in environmental temperature increase the need for thermoregulatory behaviors, such as shade use and wetting, possibly at the expense of foraging (Mole et al., 2016; Veldhuis et al., 2019). Thus, to explore how spatial differences in resources lead to variation in movement patterns and spatial use of large herbivores, movement must first be simulated at finer spatiotemporal scales. Once tested and validated, such an agent-based spatially explicit movement model could then be used to explore responses to animal-resource interactions.

## 1.6 Aims and objectives

This dissertation aimed to develop, test, and validate an ABM for elephant movement and spatial use and to extend the ABM to explore how spatial variation in critical resources influence variation in herbivore movement, spatial use, and foraging efficiency.

The first objective of this thesis was to identify spatiotemporal patterns emerging from movement data of elephants in southern Africa. In Chapter 2, I obtained GPS-telemetry data for elephant cows in South Africa's Kruger National Park (KNP) and Botswana's Chobe National Park (CNP) and surrounding protected areas, and segmented movement paths into trajectories spanning two weeks. I calculated home range size, diel displacement distance, net daily displacement distance and maximum distances traveled from a permanent water source for each trajectory and identified relevant patterns, which I then used for model validation purposes in Chapter 3. In Chapter 3, I developed a spatially explicit ABM to simulate the movement and spatial use of elephants in CNP and KNP. I utilized remote sensing data, including vegetation indices, percent tree cover, and water source presence, and real-time environmental temperature data, to build a virtual environment that is distinct to each park and season and representative of the known drivers of elephant movement. I linked the external and internal drivers of elephant movement to the external environment through hierarchical behavior-based movement rules, in which the highest priorities were assigned to responding behaviorally to ambient temperature and the need to drink water, and in which foraging became an option only once those needs were met. The same movement characteristics calculated in Chapter 2, along with activity budgets, were allowed to emerge from the conditions experienced by the ABM agent. I also conducted a sensitivity analysis and identified the parameter changes that had the greatest influence on model outputs. Model outputs were compared to empirical movement data both qualitatively, by determining whether the model reproduced the patterns uncovered in Chapter 2, and quantitatively, by using statistical models to identify significant differences in the movement characteristics between the simulated and empirical data.

In Chapter 4, I used the ABM developed and validated for elephants in Chapter 3 to explore how differences in water source density, tree cover characteristics (including distribution and abundance), and forage distribution can translate into differences in spatial use and foraging efficiency of generic water-dependent herbivores. I created artificial landscapes differing in water source density (low and high), tree cover abundance (low and high), tree cover distribution (dispersed and clumped) and forage distribution (dispersed and clumped) using a full factorial approach and allowed movement characteristics, activity budgets, and foraging efficiencies to emerge from interactions between the simulated herbivores and the landscape. I calculated movement characteristics such as home range size and foraging trip duration, activity budgets, and foraging efficiency for each trajectory, and determined how these characteristics differed under different environmental contexts. In this chapter, I was particularly interested in uncovering whether and how spatial differences in tree cover characteristics drive spatial differences in movement and foraging efficiency, and whether these spatial differences are consistent in landscapes with different abundances of surface water.

In Chapter 5, I discuss some limitations of the ABM developed and used in Chapters 3 and 4 related to the use of remote sensing products in modeling elephant movement. I also detail potential model applications, and future directions, including the incorporation of social interactions, predators, and energy budgets in the model.

## **CHAPTER 2**

## Identifying patterns of elephant movement for ABM validation

# 2.1. Pattern-oriented modeling: patterns as "fingerprints" of a system's underlying processes

The development and use of agent-based models (ABMs) is best described as a cycle. The initial development of ABMs involves formulating a question, and developing hypotheses related to the elements of the model that are reproducing the observed components of the system (Grimm & Railsback, 2005). The entities (generally representing different organisms), and parameters defining the system are then translated into a model structure capturing the system's dynamics. The model is then implemented, analyzed, tested, and validated. The process of testing and validating ABMs is necessary to assess their predictive value (Grimm & Railsback, 2005), and is primarily done by comparing the model outputs to natural systems. For ABMs of animal movement, testing and validating usually involves comparing model outputs to empirical movement data (Tang & Bennett, 2010).

Pattern-oriented modeling (POM) is a strategy to guide the development and testing of bottom-up models, such as ABMs (Grimm & Railsback, 2005; Grimm & Railsback, 2016; Grimm & Ginot, 2006; Grimm & Railsback, 2012; Kramer-Schadt & Grimm, 2007; Wiegand & Grimm, 2020). Patterns are structures in nature that can exist at different spatiotemporal scales and are generated by the underlying mechanisms of a system (Gallagher et al., 2021; Grimm et al., 1996). In movement ecology, patterns may include spatial and seasonal differences in movement characteristics such as home range

17

size and displacement distances, which reflect the interactions between the individual and the environment.

Grimm and Railsback (2012) suggest the use of multiple patterns to test applicability of an ABM; that is, to assess the ABM by its ability to fit multiple observed patterns in data rather than focusing on fitting it to one observed pattern (Grimm & Railsback, 2012). Many ABMs developed for simulating animal movement have used POM to validate model results. Semeniuk et al., (2012) used a POM approach to validate an ABM that was developed to explore the behavioral strategies used by caribou to select winter habitat in Alberta, Canada. The authors identified several patterns from GPS-telemetry data of caribou during the winter, including more restricted home ranges, and decreases in daily distance traveled, and compared these patterns to the patterns produced by various simulation models representing different behavioral strategies for habitat selection. The authors were able to identify the most likely behavioral strategy used by caribou, as it produced the majority of the patterns found in the empirical data, such as decreases in daily distances traveled during late winter (Semeniuk et al., 2012). Chudzinska et al., (2021) developed AgentSeal, an ABM for simulating movement of marine central-place foragers and used harbor seals as a case study. The authors modeled movement decisions based on optimal foraging theory, their internal state, and the availability of prey across the landscape. Movement patterns, including the core areas of the seals' spatial distribution s, foraging trip characteristics, step lengths, and turning angles extracted from GPS data of adult harbor seals, were used to validate model outputs. The model reproduced most of the patterns, suggesting that it captured the
underlying mechanisms that produced seal movement. For example, simulated seals exhibited the same core areas of distribution as those of wild seals.

In the case of modeling animal movement, if expected patterns arise under multiple conditions or scenarios, there is a greater possibility that the structure of the model accurately represents the processes that shape the spatiotemporal movements of individuals through complex environments (Grimm & Railsback, 2012). Using POM for validation of ABMs ensures rigorous testing of the model's internal structure. Patterns of animal movement and spatial use are commonly detected in movement characteristics including home range size, diel displacement distances, net daily displacement distances, and maximum distances from a water source. Below I discuss each movement characteristic as it relates to elephants and patterns found in the literature.

#### 2.1.1 Home range size

The home range represents the space that the individual uses for the purpose of day-today activities (Mcloughlin, 2000; Powell & Mitchell, 2012), and its size is determined by many factors, including the individual's size (McNab, 1963), the spatial distribution of critical resources (Powell & Mitchell, 2012), climate (Lindstedt et al., 1986), and predation risk (Tufto et al., 1996). Home range sizes are also dependent on the time scale over which they are calculated. Home ranges calculated over shorter time periods may be smaller than those calculated over longer time periods (Wiens, 1989). In addition, spatial differences in the distribution of critical resources such as forage and water can account for differences in home range size among populations (Beest et al., 2011), while seasonal changes in the same resources can produce temporal differences in home range size for a single population.

2.2.1.1 Seasonal differences in home range size

Elephants typically return to water sources every one to two days to drink (Purdon & van Aarde, 2017). Moreover, elephants use water for thermoregulatory purposes, as the evaporative cooling effects resulting from behaviors such as wetting and mud bathing dissipate heat when temperatures are high (Dunkin et al., 2013; Mole et al., 2016). Because of elephants' reliance on water, surface water availability is a strong determinant of spatial use for elephants, and differences in surface water availability between the rainy season and the dry season explain seasonal differences in home range size. Generally, home ranges in semi-arid areas are smaller during the dry season when elephant movement and spatial use is concentrated around permanent water sources, and larger during the rainy season when elephants can expand their ranges, as they are no longer constrained by water availability (Legget et al., 2006, Loarie et al., 2009a, Western & Lindsay, 1984; Young et al., 2009). Seasonal differences in vegetation productivity in concert with water availability also contribute to the general pattern of elephants having larger home ranges during the wet season compared to the dry season. As the onset of the rainy season increases water availability and vegetation productivity, elephants make exploratory movements in search of greener areas (Loarie et al., 2009a; Tsalyuk et al., 2019; Young et al., 2009), leading to large home ranges. When vegetation productivity decreases in the dry season, the risk of making exploratory movements generally becomes too great, which may translate to smaller home ranges (Tsalyuk et al., 2019).

For some elephant populations, a contradictory pattern has been documented, with dry season home ranges found to be larger than wet season home ranges (Shannon et al., 2006). In these areas, decreased vegetation productivity in the dry season may be associated with more widely dispersed habitats of higher nutritional quality, resulting in elephants expanding their ranges away from water to reach areas with remaining forage (Shannon et al., 2006).

### 2.2.1.2 Intraspecific differences in home range size

Unsurprisingly, differences in elephant home range sizes in different areas can be explained by variation in surface water availability. Grainger et al., (2005) and de Beer et al., (2008) described inverse relationships between home range size and water point density. In contrast, Wall et al., (2021) found that 16-day home ranges were larger where there was a greater availability of permanent water. Spatial differences in vegetation productivity, related to annual rainfall, also drive intraspecific variation in home range (Young et al., 2009). For example, elephants in "wet" savannas, which have higher vegetation productivity, had smaller home range sizes during wet and dry seasons compared to elephants in "dry" savannas, which have lower vegetation productivity (Young et al., 2009), suggesting that elephants could meet their nutritional demands within a smaller area. Differences in landscape heterogeneity, described by factors such as number, shape, and proportion of patches across a landscape, can also explain differences in home range size among family groups in a similar way that vegetation productivity does (Grainger et al., 2005). In Kruger National Park (KNP), home range sizes for cows decreased as the number of patches in their home range increased, indicating that elephants did not have to range over larger areas to locate food resources

(Grainger et al., 2008). Similarly, home range sizes in Etosha decreased with increasing patch density for some dry seasons (de Beer & van Aarde, 2008).

Certain anthropogenic features also have profound effects on areas over which elephants roam. Perhaps the most controversial features are artificial water sources. Supplying water through boreholes in areas that are typically devoid of water sources allows elephants and other herbivores to range over greater areas than they would if there were no artificial water provisioning (Loarie et al., 2009a; Shannon et al., 2009). During the dry season, artificial water sources allow elephants to utilize areas across the landscape that would otherwise be unavailable to them due to the lack of surface water (Loarie et al., 2009a; Vanak et al., 2010). Fences erected around protected areas may also influence home range size by restricting elephant movements, leading to smaller home ranges relative to those in areas without fences (Wall et al., 2021).

#### 2.1.2 Diel displacement distance and net daily displacement distance

Diel displacement distance, or the total distance traveled over a 24-hour period, has been used as a measure of movement frequency and energy expenditure in elephant family units (Polansky et al., 2013) and has been used as a proxy for foraging effort (Young & van Aarde, 2010). Net daily displacement distance, the straight-line distance between the start and end location of a 24-hour period, has proved useful for determining movement path tortuosity (Vanak et al., 2010). Lower net daily displacement distances indicate greater changes in direction and more intense use of an area (Patterson et al., 2008). 2.1.2.1 Seasonal differences in diel displacement distances and net daily displacement distances

Seasonal differences in diel and net daily displacement distances are most likely the result of the same factors causing seasonal differences in home range size. During the dry season,he costs of traveling long distances outweigh the benefits of finding resources, generally prohibiting movement from water as the costs of. Diel and net daily displacements are therefore generally lower during the dry season compared to the wet season. Loarie et al., (2009a) found that elephants had smaller net displacements during the dry season when vegetation productivity was poor and surface water was less readily available. A similar pattern was found in Samburu and Buffalo Springs National Reserves Complex. As the availability of forage decreased in the dry season, the diel displacement distances of elephants also decreased, indicating that elephants used an 'energy conservation' foraging strategy as increased movement would not likely have led to an increase in energy in the form of forage resources (Polansky et al., 2013).

For some populations, diel displacement distances may be greater during the dry season, for similar reasons as to why the home ranges of some populations are greater during the dry season. If nutritional demands cannot be met when staying close to water during the dry season, elephants may increase movement to travel the long distances between water and forage. Increased elephant densities at critical resource sites, such as water holes, during the dry season may further deplete forage resources near water and induce a 'crowding effect', also resulting in increased movement during the dry season to meet daily requirements (Young & van Aarde, 2010). For example, Young et al., (2010) found

that diel displacement distances were greater in the dry season when vegetation productivity was lower, indicating greater effort to reach food and water resources.

2.1.2.2 Intraspecific differences in diel displacement distances and net daily displacement distances

As with home range size, differences in diel and net daily displacement distances among elephant populations in different areas can be ascribed to spatial variation in rainfall which results in spatial differences in vegetation productivity and surface water availability. Seasonal vegetation productivity is higher in savannas with higher mean annual rainfall (Young et al., 2009), and as such, elephants in "wet" savannas may not have to venture far from within their range to locate forage resources. Young et al., (2010) found that as vegetation productivity decreased across 13 different study sites, diel displacement distances of elephants increased during the dry season (Young et al., 2010), a pattern also observed in Loarie et al., (2009a) for net inter-annual displacements of several elephant populations across southern Africa.

Several studies have found that habitat type and vegetation greenness can influence the tortuosity (convolutedness) of an elephant's movement path, thereby influencing net displacement distances. More tortuous movements are generally associated with foraging. Elephants in South Africa's Pongola Game Reserve display the most tortuous movements in riverine thickets, suggesting that elephants are foraging in riverine habitats where trees are plentiful (Duffy et al., 2011). Where forage resources are abundant, movements characterized as having greater turning angles and therefore lower net displacements increase the chances of remaining in a profitable area. Straighter movements achieve the

opposite, and thus allow for movement away from an area if resources are scarce (Bartumeus et al., 2005; De Knegt et al., 2007).

Anthropogenic features also influence the net displacement characterizing an elephants' movement path. Elephant movement in the proximity of the fence surrounding South Africa's Pilanesburg National Park is characterized by greater net displacements, while lower net displacements are exhibited away from the fence (Vanak et al., 2010). An increase in net displacements close to the fence is indicative of avoidance behavior likely related to anthropogenic activities on the opposite side of the fence. The opposite pattern was observed when exploring the influence of fences on elephant movement patterns in southern African countries, as elephant paths tended to "bunch up" when close to fence, indicating lower net displacements (Loarie et al., 2009a).

Areas of human habitation and areas where poaching occurs can form part of the "landscape of fear" for elephants. Several studies have shown that elephants modify their movement so that they move through these risky areas more quickly. For example, elephant movement in the Laikipia-Samburu ecosystem was characterized as having greater net displacement distances when in areas close to human habitation or in locations associated with poaching risks (Ihwagi et al., 2019). In Tsavo, Kenya, the risk of being close to areas of human habitation is seemingly outweighed by the benefits of eating crops, as elephants were less likely to move in a straight direction once in farmland (Troup et al., 2020). 2.1.3 Maximum distance traveled from a permanent water source.

2.1.3.1 Seasonal differences in maximum distances traveled from a permanent water source

Seasonal differences in distances traveled from permanent water sources are driven by differences in surface water availability between the wet and dry seasons. During the dry season, elephants are limited in their movements to the vicinity of water sources (Harris et al., 2008; Loarie et al., 2009a). Increased rainfall during the wet season fills temporary pans and pools across the landscape, allowing elephants to take advantage of the increased surface water availability and move away from permanent water sources (Harris et al., 2008; Loarie et al., 2009a).

2.1.3.2 Intraspecific differences in maximum distances traveled from a permanent water source

Conceivably, elephants in fenced areas can only travel so far from permanent water sources before they are restricted from moving farther. Consequently, it is possible that elephants in unfenced areas travel greater distances from permanent water compared to elephants in fenced areas.

It is not known whether spatial differences in tree cover or environmental temperatures influence intraspecific differences in maximum distances traveled from a permanent water source. Rozen-Rechels et al., (2020) found that elephants' foraging trip durations (the time spent foraging between returns to water) were shorter when temperatures were warmer. Shorter foraging trips are probably associated with elephants foraging closer to water (Rozen-Rechels et al., 2020). It is thus possible that spatial differences in

temperature may influence differences in trip durations and distances traveled from water.

Rozen-Rechels et al., (2020) suggests that micro-habitats (including shade from tree cover), might mitigate the effects of high temperature as elephants return to water. It is this possible that elephants may be able to travel further distances from water if there is shade available throughout their foraging trips, rather than having to return to water quickly to employ wetting behavior.

## 2.1.3.3 Objectives

In this chapter, I examined patterns related to four movement characteristics, home range size, net daily displacement distance (the straight-line distance between the first and last location of a 24-hour period), diel displacement distance (the total distance traveled over a 24-hour period), and maximum distance traveled from a water source, of elephants in two southern African parks. This involved determining whether there were overall seasonal differences in these movement characteristics, and whether there were overall differences in these movement characteristics between KNP and CNP. The patterns were used for comparisons to patterns produced by the ABM described in Chapter 3.

# I predicted the following:

## Seasonal differences in movement characteristics

1. Wet season home range sizes would be larger than dry season home range sizes due to the greater availability of forage resources and surface water availability.

- 2. Diel displacement distances would be greater in the wet season compared to the dry season due to the greater availability of forage resources and surface water availability.
- Net daily displacement distances would be greater in the wet season compared to the dry season due to the greater availability of forage resources and surface water availability.
- Distances traveled from permanent water would be greater in the wet season compared to the dry season as surface water availability increases and elephants are no longer tied to permanent water.

## Between-park differences in movement characteristics

- 5. Home range sizes in CNP would be larger than KNP due to CNP being slightly more arid than KNP (at least when comparing rainfall between the areas the trajectories were located) and having less surface water.
- Diel displacement distances would be greater in CNP then KNP for the same reason as described in 2, and because of the presence of human settlements in CNP.
- 7. Net daily displacement distances would be greater in CNP compared to KNP.
- Distances traveled from permanent water would be greater in CNP compared to KNP.

#### 2.2 Methods

#### 2.2.1 Study areas

Chobe National Park (CNP) spans approximately 11,000 square kilometers in northern Botswana, and is characterized by woodland, savanna, and grassland ecosystems (Figure 2.1). The nearest town, Kasane, has a population of approximately 7,500, and serves as the northern entrance to the park. The Chobe River runs along the northern edge of CNP before flowing into the Linyanti swamp in the northwestern corner of the park and is one of CNP's only sources of permanent water. Northern Botswana has two distinct seasons; a dry season that extends from May to October, and a wet season that extends from November to March. The mean annual rainfall is approximately 650 mm. Daytime environmental temperatures are highest in September and October, with mean maximum temperatures of approximately 34 degrees Celsius, and lowest in June and July, with mean maximum temperatures of approximately 27 degrees Celsius. CNP is unfenced and consequently wildlife is free to move between the park and several bordering reserves, wildlife management areas (WMAs), and pastoral/residential areas.

The Kasane Forest Reserve Extension, Kazuma Forest Reserve, Maikaelelo Forest Reserve, and Chobe Forest Reserve border the park in the north-east and north-west. The Nungu Wildlife Management Area, a vast expanse to the east and south of CNP, serves as a buffer zone for the protected areas. The former CH/1 hunting concession, now a pastoral/residential area, borders the Chobe River to the north-west of CNP. Botswana banned commercial hunting nationwide in 2013, with former hunting zones subsequently declared "photographic" or "safari" zones. All the elephant movement paths used for analyses were within the aforementioned areas.

On the edge of South Africa's northeastern border, Kruger National Park (KNP) is the largest reserve in South Africa with an area of approximately 19,000 square kilometers (Figure 2.2). The Park boasts a diversity of fauna and flora, and the elephant population peaked at more than 17,000 individuals in 2015 (Ferreira, 2017). Arid bushveld and lowveld bushveld are present in the north and south, respectively (Codron et al., 2006, Venter et al., 2003). Vegetation is dominated by mopane (*Colophospermum mopane*) woodlands in the north, and *Combretum* and *Acacia* species in the south. The geology of KNP also differs from east to west; the eastern region of the park contains fertile balsitic soil, while the west contains less fertile granitic soil (Codron et al., 2006). The northern region of the park receives 300-500 mm of annual rainfall while the southern regions receives 500-700 mm of annual rainfall (Macfadyen et al., 2018; Venter et al., 2013). Several ephemeral rivers traverse KNP, including the Shingwedzi, Letaba, and Olifants, generally drying up in the winter when rainfall is low. The wet and dry seasons span November through March, and June to October, respectively, with the highest temperatures reaching about 30 degrees Celsius in January and February. In the early 1990's the neighboring private reserves removed the fences separating them from KNP, effectively allowing wildlife to roam over a greater area. The outermost border of the park, however, remains fenced. All of the elephant movement paths from KNP used for analyses were within the fenced area.

Between 2012 and 2014, satellite collars (Africa Wildlife Tracking, Pretoria, SA) were placed on cows from areas within and surrounding CNP and cows from within KNP. Elephant cows and their offspring, comprising family units, travel across the landscape as one unit. Therefore, the movement patterns of one cow represents those of the entire family unit (Young & van Aarde, 2010). The satellite collars recorded fixes at approximately hourly intervals. Movement paths were segmented into two-week (14 day) trajectories, such that each individual was usually associated with two trajectories per month. I excluded any trajectories that were outside of the study areas (see raster extents in Figure 2.1). Consequently, only movement data from four cows from areas within and surrounding CNP and nine cows from within KNP was used.

#### 2.2.3 Estimating home range size

The package 'move' was implemented within R statistical computing environment (R Core Team, 2014) to estimate the 95% utilization distribution (UD) for each trajectory using a dynamic Brownian-Bridge Movement Model (dBBMM). The UD is a probability distribution that determines an individual's probability of occurrence in a twodimensional area (Keating et al., 2006). Traditional Brownian Bridge Movement models (BBMMs) predict movement paths between successive fixes by utilizing continuous conditional random walk models, thereby estimating the probability of occurrence for an individual in an area (Horne et al., 2007). The probability estimates are dependent on a location error, the time between successive fixes, and a Brownian motion variance parameter, which is a measure of path irregularity and is fixed for a given trajectory in BBMMs. In utilizing a fixed Brownian motion variance parameter, the BBMM makes the

unrealistic assumption that animal movement is uniform along a trajectory, whereas, movement essentially represents changing behavioral states (Gurarie, 2018; Kranstauber et al., 2012, McClintock et al., 2017). To mediate this, the dBBMM estimates a dynamic Brownian motion variance parameter for sections of a trajectory by incorporating changes in turning angles and speed from one section to the next (Kranstauber et al.2012). Resulting UDs estimated with dBBMMs thus better represent the changing behavioral states that characterize animal movement, circumventing under- or overestimates of UDs for given sections of a trajectory. To estimate UDs using dBBMM for individual two-week trajectories, I used a window size of 7 hours and a margin of 5 hours, and the location error was set to 23 meters. The window size indicates the number of fixes considered to quantify the variation in step lengths and turning angles along a trajectory. Larger window sizes are not able to capture frequent behavioral changes as well as a smaller window size (Kranstauber et al., 2012). The margin size is used for the behavioral change point analysis which detects where a behavioral change occurs in along a trajectory.2.2.4 Determining diel displacement distance and net daily *displacement distance* 

I calculated diel displacement distances for individual trajectories as the total distance traveled per day averaged over two weeks. Net daily displacement distances were determined by calculating the distance between the first relocation and last relocation of a 24-hour period. I then took the arithmetic mean of these values over two weeks for each trajectory. In calculating net and diel displacement distances, I only included days within each trajectory that had at least 20 fixes to avoid negatively biasing our daily averages as days with fewer fixes may be associated with smaller distances traveled and lower net daily displacement distances.

# 2.2.5 Determining maximum distance traveled from a permanent water source

Two shapefile layers of points representing permanent water across CNP and surrounding areas and KNP were used for this analysis. Permanent water was defined as water sources containing water year-round. For both study areas, I used the permanent water source layer used in Robson et al., (2017). The authors used Landsat 8 imagery and supervised classification to generate a layer of points representing water sources with a resolution of 30 m for protected areas in Africa (Robson et al., 2017, supporting information). I supplemented the layer with data from the Global Surface Water dataset (Pekel et al., 2016). Specifically, I downloaded the "Water Seasonality (2014-2015)" dataset. Permanent sources that were not included in the original layer were added using the "Editor" toolbox in ArcGIS 10.5.

I also used high-resolution satellite imagery from Google Earth to locate permanent bodies of water smaller than 30 meters for both CNP and KNP. The "Historical imagery" toolbar was used to determine whether these smaller sources of water contained water year-round for 2012, 2013 or 2014. I was able to confirm the permanency of many of these sources through the internet. For example, some water sources near lodges are pumped year-round to attract game for the viewing enjoyment of tourists, and this is generally stated on the lodges' respective websites. For other water sources, there was no information about their permanency available on the internet and no historical imagery available for the dry season months of 2012, 2013 or 2014. In this case, I considered the water source to be permanent if there was water available during, at least, two dry season months of other years. The distance between each relocation in the trajectory to the closest permanent water source was calculated, and the maximum of these distances was determined.

# 2.2.6 Analyzing trajectories

I used linear mixed models (LMMs) to identify differences in the mean of the four movement characteristics between parks and seasons for the empirical data. The full model for each response variable included season (dry vs. wet), park (KNP vs. CNP), and their interaction as fixed effects, with a random effect of year nested within individual elephant ID to account for both repeated observations of individuals and individual variation in movement patterns among years. P-values for each model effect were determined using likelihood ratio tests comparing simpler nested models lacking the effect with the more complex model including the effect using the "anova" function in R. To approximate normality, home range size, diel displacement distances, and maximum distances traveled from a water source were transformed using the Yeo-Johnson transformation method, and net daily displacement distances were log-transformed. Median values and interquartile ranges (IQR) are presented.

# 2.3 Results

# 2.3.1 Home range size

For elephants in CNP, the median home range size for the wet season was 113.62 km<sup>2</sup> (IQR= 62.41-178.42 km<sup>2</sup>). Median home range size for elephants in the hot, dry season was 42.65 km<sup>2</sup> (IQR= 23.57-119.61 km<sup>2</sup>) (Figure 2.3). For elephants in KNP, the median

home range size for the wet season was  $49.82 \text{ km}^2$  (IQR=  $33.02-80.03 \text{ km}^2$ ). Median home range sizes for elephants in KNP for the hot, dry season was  $31.77 \text{ km}^2$  (IQR=  $21.91-48.58 \text{ km}^2$ ) (Figure 2.4).

There was no interaction present between park and season, and thus, I found two patterns related to home range size. 1) In general, home range sizes for elephants in CNP were larger than home range sizes for elephants in KNP (P=.0072), and 2) home range sizes were significantly larger in the wet season compared to home range sizes in the dry season (P<.001) (Figure 2.5).

## 2.3.2 Diel displacement distance

Median diel displacement distances for elephants in CNP in the wet season and the hot, dry season were 13.67 km (IQR= 11-14.88 km) and 12.13 km (IQR= 11.21-18.08 km), respectively. The median diel displacement distances for KNP's elephants in the wet and hot, dry season were 9.84 km (IQR= 8.33-11.93 km) and 7.66 km (IQR= 6.42-9.5 km), respectively.

Significant interactions were present between park and season, and there were four patterns present related to diel displacement distance. 1) There was no significant difference in diel displacement distances during the wet and hot, dry season for elephants in CNP (P=.974). 2) For KNP, however, wet season diel displacement distances were significantly different than hot, dry season diel displacement distances, with wet season diel displacement distances being significantly greater (P<.001). 3) Additionally, diel displacement distances in CNP's wet season were significantly greater than diel displacement distances in KNP's wet season (P=.021). 4) I also found that diel displacement distances in CNP's hot, dry season were significantly greater than diel displacement distances in KNP's hot, dry season (P<.001) (Figure 2.6).

# 2.3.3 Net daily displacement distance

Median net daily displacement distances for elephants in CNP in the wet and hot, dry seasons were 6.67 km (IQR= 5.37-8.03 km) and 4.64 km (IQR= 2.04-8.65 km), respectively. Median net daily displacement distances for elephants in KNP in the wet and hot, dry seasons were 4.42 km (IQR= 3.55-5.5 km) and 3.4 km (IQR= 2.86-4.34 km), respectively.

There were no interactions present between park and season, and thus, I found two patterns related to net daily displacement distance. 1) Elephants in CNP exhibited significantly greater net daily displacement distances compared to elephants in KNP (P=.004). 2) Additionally, elephants had significantly greater net daily displacement distances in the wet season compared to the hot, dry season (P<.001) (Figure 2.7).

#### 2.3.4 Maximum distance traveled from a permanent water source

Median maximum distances traveled from permanent water sources for elephants in CNP during the wet and hot, dry seasons were 15.3 km (IQR= 13.03-25.72 km) and 8.88 km (IQR= 7.03-11.06 km), respectively. Maximum distances traveled from permanent water sources for elephant in KNP during the wet and hot, dry seasons were 7.8 km (IQR= 6.14-10.44 km) and 5.94 km (IQR= 5.24-7.55 km), respectively.

Significant interactions were present between park and season, and there were four patterns present related to maximum distance traveled from a permanent water source. 1) Elephants in CNP traveled significantly greater distances from permanent water in the wet season compared to the dry season (P<.001). 2) The same pattern was found for elephants in KNP (P<.001). 3) Additionally, elephants traveled greater distances from a permanent water source in CNP's wet season compared to KNP's wet season (P=.01). 4) I found no difference in maximum distances traveled from a permanent water source between CNP's hot, dry season and KNP's hot, dry season (P=.051) (Figure 2.8).

## 2.4 Discussion

As predicted, I found seasonal and between-park differences in the four movement characteristics I calculated for CNP and KNP. In total, twelve patterns were uncovered from the data (Table 2.1).

#### 2.4.1 Seasonal differences in movement characteristics

Seasonal differences in movement characteristics of elephant populations in CNP and KNP corroborate those of previous studies (Loarie et al., 2009a; Stokke & Du Toit, 2002; Vanak et al., 2010; Young et al., 2009) and present further evidence for elephants responding to changes in the availability and distribution of critical resources, particularly water, by modifying their spatial use patterns even at the two-week scale.

I found that wet season home ranges were larger than dry season home ranges (consistent with prediction 1), the result of elephants expanding their movement beyond areas near permanent water sources at the onset of the rains (Leggett, 2006; Loarie et al., 2009a; Redfern et al., 2005). This pattern is consistent with many other studies in other conservation areas across southern Africa, including the Kunene region of Namibia (Leggett., 2006), Tanzania (Galanti et al., 2006), South Africa (Thomas et al., 2008), and

other African countries (Loarie et al., 2009a). Interestingly, my results contradict those of other studies that have found no significant seasonal differences in elephant home range sizes within KNP. For example, Grainger et al., (2005) found no differences between wet season and dry season home ranges in KNP, likely the result of the abundance of water available year-round due to the provisioning of artificial water sources (Grainger et al., 2005). This discrepancy may be due to differences in the temporal and spatial scale of analysis. Grainger et al., (2005) examined differences in home range size at a seasonal scale, while I analyzed home range size at a 2-week scale. Additionally, there was a mismatch in wet and dry season months considered between my study and Grainger et al., (2005). Specifically, I only analyzed dry season trajectories during the hotter months, August through October, while Grainger et al., (2005) analyzed dry season trajectories during all dry season months (May to August).

Consistent with prediction 2, I found that diel displacement distances were significantly greater in the wet season compared to the dry season, but this was only true for elephants in KNP. These results suggest that resource scarcity during the dry season led KNP elephants to utilize an 'energy conservation' foraging strategy while remaining near permanent water sources, while the rainy season allows elephants to use more widely available and dispersed resources (Polansky et al., 2013). Thomas et al., (2011) and Thaker et al., (2019) also noted the same seasonal differences in diel displacement distances for elephants in KNP (Thaker et al., 2019; Thomas et al., 2011). In CNP, median diel displacement distances for elephants in the dry season, but these differences were not significant.

Consistent with prediction 3, I also found that elephants exhibited lower net daily displacement distances during the dry season compared to the wet season. This pattern is also noted by other studies (Loarie et al., 2009a; Vanak et al., 2010), suggesting that the energetic costs of moving to more profitable areas may outweigh the benefits during the dry season, and movements are over small areas (Birkett et al., 2012) generally centered around water points. The onset of the rainy season releases this restriction, and greater net daily displacements during this time may be related to exploratory movements made to exploit high quality areas (Wittemyer et al., 2007; Young et al., 2009).

The onset of the rainy season also led to greater distances traveled from permanent water sources in the wet season compared to the dry season within each park, consistent with prediction 4, as water and vegetation become more readily available across the landscape. Elephants in both CNP and KNP traveled less than 10 km from a permanent water source during the dry season, a pattern that is ubiquitous across elephant populations in southern Africa (Stokke & Du Toit, 2002; Loarie et al., 2009a).

## 2.4.2 Between-park differences in movement characteristics

Elephants range across protected and unprotected areas in southern Africa that differ in surface water availability, vegetation characteristics, and elephant population density. Variation in these factors from one location to the next explains differences in the movement patterns and spatial use of elephant populations across space (Loarie et al., 2009; Wall et al., 2021; Young et al., 2009; Young & van Aarde, 2010).

Consistent with predictions 5 and 6, I found that elephants in CNP had larger home ranges, and greater diel displacement distances than elephants in KNP. Spatiotemporal

variability in rainfall drives geographic differences in important key resources, including food and water. Rainfall is a key factor in determining the vegetation characteristics, including vegetation growth, biomass (Scholes et al., 2003), and structure (Fuller & Prince, 1996), and subsequently controls the distribution of food resources for large herbivores in savannas. Rainfall also drives surface water availability, filling ephemeral pans across the landscape during the wet season (Brennan et al., 2020; Sutherland & Sutherland, 2021; Venter & Bristow, 1986). Where annual rainfall is lower, primary productivity and water availability are also lower, and patches of food resources and water may be far apart. Elephant home range size and movement thus increases with decreasing rainfall as more movement is required to reach high quantity and quality vegetation and water (Leggett et al., 2006, Loarie et al., 2009). Most of the trajectories within KNP (90% of dry season trajectories and of 85% of wet season trajectories) were in the wetter southern region of the park (south of the Olifants River), which may partly explain the larger home ranges and longer diel displacement distances in the slightly more arid CNP compared to KNP. Smaller home ranges and shorter diel displacement distances in KNP may also be the result of the perimeter fence surrounding a large portion of KNP. Fences around conservation areas can cause "edge-effects" (Vanak et al., 2010), limiting elephant movement and bounding home ranges, particularly during the wet season when more extensive ranging usually occurs (Loarie et al., 2009a). Furthermore, elephants in fenced areas cannot expand their ranges to more potentially profitable areas when faced with resource scarcity (Shrader et al., 2010).

I found that elephants in CNP exhibited greater net daily displacement distances compared to elephants in KNP, a pattern that was consistent with prediction 7 and that

may be partially attributed to lower annual rainfall in CNP compared to KNP's southern region. Greater net daily displacement distances in CNP may also be a result of elephants avoiding human settlements, as well as poaching hotspots, within CNP. While there are no villages within KNP, there are several villages within the area in northern Botswana considered in our study. When moving through areas of human habitation, elephant movement tends to be much straighter and of longer duration in order to quickly move through the area (Graham et al., 2009; Ihwagi et al., 2019; Troup et al., 2020).

We note that there was a greater difference in maximum distances traveled from permanent water sources in CNP compared to KNP, consistent with prediction 8. Historically, KNP has greater surface water availability, partly as a result of the construction of hundreds of boreholes and dams to provide water for wildlife year-round (Smit, 2013). More than half of the water holes were closed after it was realized that there were extensive ecological effects of water provisioning within the park, including a reduction of rare antelope populations (Harrington et al. 1999; Smith, 2013, Owen-Smith & Mills 2006) and overgrazing (Smit et al., 2007). However, approximately 10% of the park is still within 10 km of the closest water source year-round (Smit, 2013). This is in stark contrast to CNP, where permanent water is less widespread (Verlinden & Masogo, 1997). The difference in surface water availability between the wet and dry season may thus not be as pronounced in KNP as it is in CNP (Grainger et al., 2005). Stokke du Toit et al., (2002) recorded elephant observations at various transects in the northeastern section of Chobe National Park and noted that elephants traveled an average distance of 7 km and 3.5 km from permanent water in the wet season and dry season, respectively (Stokke du Toit et al., 2002). Our calculated distances are almost double those of Stokke

du Toit (2002) likely because our study area encompassed a much larger portion of the park and surrounding protected areas, and elephants used other permanent water sources in addition to the Chobe and Zambezi Rivers.

#### 2.5 Concluding remarks

The spatiotemporal patterns characterizing movement and spatial use of elephants are complex and can be inconsistent from the dry season to the wet season, and from one population to the next, as shown in this study. I speculate that these inconsistencies for elephants in CNP and KNP may reflect variation in responses to spatiotemporal differences in vegetation quality and quantity, water, and anthropogenic disturbances, among other factors.

In the next chapter, I will use the patterns uncovered in this chapter to validate an ABM developed for simulating elephant movement. Questions that have been posed regarding any model developed for simulating movement include the following: how well does the model describe the space utilization patterns of individuals? Further, can the model be applied to other ecological systems of similar type in different geographical areas or spatial contexts? (Latombe et al., 2011; Sun et al., 2016). Confidence that models adequately capture the mechanisms that comprise the natural system may be limited if they are tested only under a limited set of conditions. To ascertain that the ABM developed in the next chapter is structurally realistic and that it captures the underlying mechanisms of spatial use of elephants, it must be able to reproduce the multiple patterns uncovered in this chapter.

## **CHAPTER 3**

# Development and validation of a spatially-explicit agent-based model for elephant movement and spatial use

# **3.1 Theoretical framework**

The flexibility of the ABM framework makes it a useful tool for simulating fine-scale animal movement, as empirical data on the assumed drivers of movement (e.g., extrinsic and intrinsic factors) can be employed to devise movement rules associated with habitat utilization. These rules can in turn be linked to a model environment characterized by relevant attributes, including but not limited to habitat quality, resource availability, and prey densities (Aben et al., 2014; Carter et al., 2015; Philips, 2020; Watkins et al., 2015). Consequentially, ABMs enable the emergence of movement properties from small-scale interactions through time and allow for predictions of patterns at a larger scale.

To test the applicability of a resource-driven model of elephant space utilization, I developed a spatially explicit ABM for their movement. I aimed to assess the utility of the ABM in simulating finer-scale elephant movement patterns and subsequent space utilization than the model used by Boult et al., (2018b). I simulated movement at an hourly scale, as this scale can reflect switches in elephant behavior due to changes in internal states and short-term responses to the local availability and distribution of critical resources including forage, water, and shade. The goal of this chapter was to validate a model for elephant movement and use it to reproduce movement responses to spatial and temporal heterogeneity.

43

I used published information derived from the extensive literature (see Tables 3.2 and 3.3 for model assumptions, relevant parameters, and supporting references), rather than directly calibrating the model with empirical data. The ABM then allowed movement characteristics, including commonly calculated home range sizes, diel displacement distances (total distance traveled over a 24-hour period), and net daily displacement distances (straight-line distance between first location and last location of a 24-hour period), to emerge from conditions experienced by the individual elephant or family unit (termed 'agent' in the ABM), such as the sensitivity of the agent to ambient temperatures.

To test the model's robustness to different landscape conditions, I implemented a cellbased or raster approach, representing two geographical areas with different spatiotemporal characteristics and patterns of food abundance, water availability and distribution, tree cover, and temperature. I incorporated published external and internal drivers of elephant movement and linked these drivers to the external environment through hierarchical behavior-based movement rules. In this way, I extended the modeling framework to test the generality of an ABM for elephant movement over a range of environmental conditions.

#### **3.2 Methods**

#### 3.2.1 Study Sites/Model Landscapes

Chobe National Park (CNP) and surrounding protected areas in Botswana, and Kruger National Park (KNP) in South Africa are home to large populations of elephants. These two areas were used as our model landscapes, and movement data from elephants living there were used for model validation. Simulations were run separately for each study site. I excluded the northern portion of the area comprising CNP (see Figure 3.1) and all movement data there, as towns and human activity in the area may have altered elephant movement (see Tempe et al., 2017). For both parks, the dry season extends from June to October, while the wet season extends from November to March. April and May signal the end of the wet season, and beginning of the dry season, respectively. CNP and the surrounding reserves used in the model span about 17,000 km<sup>2</sup> in northern Botswana, and are characterized by woodland, savanna, and grassland ecosystems. CNP is unfenced and elephants moved between the park and several bordering areas. KNP spans an area of about 19,000 km<sup>2</sup> and is partially fenced. Arid bushveld and lowveld bushveld are present in the north and south, respectively (Codron et al., 2006, Venter et al., 2003). Vegetation is dominated by mopane (*Colophospermum mopane*) woodlands in the north, and *Combretum* and *Acacia* species in the south.

### 3.2.2 Model Overview

Movement was simulated by incorporating the assumed main drivers of elephant movement into a hierarchal decision-making process, where the higher priorities were to respond behaviorally to ambient temperature and the need to drink water, and foraging became an option once those needs were met. Each behavioral response was accomplished by directed movement. A complete and detailed model description following the Overview, Design concepts, Details protocol (Grimm et al., 2006; Grimm et al., 2010, Grimm et al., 2020) is contained in Appendix A.1.

The *entities* within the model were the agents, landscape cells, and environment. Here, the agent was represented by an elephant family unit, which is one of the simplest levels of social hierarchy in elephant populations (Wittemyer et al., 2005). The agent was mobile and responded to the environment by changing its movement across the landscape. The agent was characterized by the following *state variables* and *attributes*: 1) its state, which represented the sensitivity of the agent to ambient temperatures, 2) its position on the landscape (x and y coordinates), at any given time step, 3) the time since it last visited a water source, 4) the behavior that it was employing (i.e., wetting, shadeuse, drinking, or foraging) , and 5) the ambient temperature that it was experiencing at a given time step ("perceived temperature"). Model entities and state variables are described in Table 3.1.

Attributes of landscape cells were 1) greenness, updated every time step to reflect vegetation change, 2) percent tree cover, and 3) a binary value indicating whether water sources were present in the cell. State variables included 1) environmental temperature (hourly temperature was downloaded from the National Oceanic and Atmospheric Administration's National Center for Environmental Information, and missing values were estimated using spline interpolation (Samanta et al., 2012), and 2) the number of cells within the landscape that increased in greenness. The model landscapes comprised separate rasters representing the aforementioned attributes of the study areas during the wet and dry season (Figure 3.1). The *spatial extent* for the two areas differed and was approximately 360 km by 120 km for KNP, and 160 km by 128 km for CNP and surrounding protected areas. Each of the cells comprising the model landscape had a *spatial resolution* of 30 m by 30 m. For greenness, I utilized Landsat's remotely sensed Enhanced Vegetation Index, a spectral vegetation index calculated as the ratio of

EVI). EVI is a useful proxy for resource availability and the quality of vegetation (He et al., 2015; Kumar et al., 2019; Pettorelli et al., 2011; Ryan et al., 2012). The date associated with the EVI data used for each simulation corresponded to the time of movement tracking for elephants in each park and each season.

Simulations were run for 336 time-steps, representing a temporal resolution of one hour and a temporal extent of two weeks. We used 336 time-steps as the duration of the simulations to strike a balance between having a trajectory that was ecologically meaningful in representing spatial use and to minimize computational intensity. Additionally, a simulation duration of 2 weeks closely matched the time differences in consecutive satellite images (16 days) used to determine changes in vegetation greenness through-out the simulation. Each empirical trajectory was paired with one simulated trajectory that started at the same location. The main processes within the model, which were repeated every time step, constituted the agent's decision-making as it moved through a landscape. The agent first decided whether it sought shade or water to maintain homeothermy. This decision was influenced by the current perceived temperature, the agent's state, and the temperature threshold above which behavioral thermoregulation was likely to occur. Agents moved within a specified "search radius", which represented the maximum distance that elephants were likely to move in one hour and differed depending on the behavior employed. There was a higher probability of forming a smaller search radius than a larger search radius (0.9 km and 1.8 km, respectively) when employing thermoregulatory behavior. We assumed that elephants preferred to employ wetting behavior if a water source was within the search radius, due to the benefits of

evaporative cooling. If no water source was present in the search radius, the agent employed shade use within the smaller search radius.

The agent's state was a binary variable meant to represent the differences in sensitivity to environmental temperatures between family groups with calves and those without calves (Mole et al., 2016), and differences in mobility between family groups with and without calves (Ngene et al., 2010). If the agent did not have to employ behavioral thermoregulation, it then decided whether to drink. This decision was determined based on the time since the agent last visited a water source (including instances of wetting), and the perceived environmental temperature. As the time since the agent last visited a water source increased, and as the environmental temperature increased, there was an increased probability of it drinking. I incorporated spatial memory relating to water sources in the model by allowing agents to "sense" the location of water sources across the landscape and to move in the direction of the closest water source. At least two studies reported that elephants make directed movements towards close water sources and have knowledge of the spatial distribution of water sources in the landscape (Polansky et al., 2015; Wato et al., 2018). Agents could move within a search radius of 1.8 km.

If the agent did not employ thermoregulatory behavior or drinking, the model assumed it would forage. I incorporated memory relating to the vegetation quality of areas that the agent has recently visited by allowing the agent to "remember" the quality of recently visited areas and adjust its movement tortuosity to remain in relatively higher quality areas. The agent was assumed to be aware of the EVI values for areas within its search radius that were visited recently (within the last three time-steps) and used a running

average of these values to decide which cell was likely to be the best to next visit to forage. Movement resembling area-restricted search was performed if EVI values were greater than or equal to the running average in its memory, and more directed movement was performed if EVI values were less than the running average. The agent moved anywhere within a smaller or larger search radius depending on its state. Agents representing family groups with calves moved up to 0.9 km when foraging, while those without calves moved up to 1.8 km. This difference represented the limitations that calves may impose on family groups when moving. Table 3.2 describes model parameters for each behavior and supporting references, and Table 3.3 describes cell selection strategies the agent uses for each behavior and supporting references. A simplified flowchart of the agent's decision-making process is depicted in Figure 3.2.

I ran ten simulations for each empirical trajectory, with each simulated trajectory starting at the same location as its corresponding empirical trajectory. I aimed to generate enough simulated trajectories per empirical trajectory such that the resulting average value of each movement characteristic calculated from the ten simulated trajectories would be a representation of model performance. Examples of an empirical trajectory and corresponding simulated trajectories are depicted in Figure 3.3. The figure depicts the stochasticity inherent in model runs, and that no two simulated trajectories are the same.

# 3.2.3.1 Activity budgets of real elephants

To validate the activity budgets calculated from the ABM, I used parameters derived from the relevant literature (see Table 3.6 for patterns present in the literature: Chamaillé-Jammes et al., 2013; Mole et al., 2016; Purdon & van Aarde, 2017; Shannon et al., 2008).

# 3.2.3.2 Analyzing movement patterns of elephants

I calculated movement characteristics for elephant agents in CNP and KNP as I did for actual elephants in Chapter 2. For a qualitative comparison between simulated and empirical data, rather than identifying whether significant differences existed between the simulated and empirical data, I used LMMs to determine whether the model was able to reproduce the patterns in movement characteristics of the empirical data. The full model for each response variable included season (dry vs. wet), park (KNP vs. CNP), and their interaction as fixed effects, with a random effect of year nested within individual elephant ID to account for both repeated observations of individuals and individual variation in movement patterns among years.

For a quantitative comparison, I also used linear mixed models (LMMs) to identify differences in the movement characteristics between the simulated and empirical data. A final term to indicate whether the data was simulated or empirical was included within these LMMs, as well as interactions between this term and the fixed effects. Data were transformed to meet assumptions of parametric statistics (Pinheiro et al., 2011). I then standardized the data to express all parameter estimates in terms of effect sizes. A one-factor-at-a-time local sensitivity analysis of the model determined the sensitivity of the model outputs to parameter uncertainties. I varied each input parameter from the original reference values (Appendix Table A.4) by 10% and observed the magnitude of the corresponding change in model outputs as effect sizes. This was again accomplished using LMMs, in which I compared the original model outputs (home range size, diel and net daily displacement, and maximum distance traveled from a permanent water source) with the outputs obtained when a given parameter was altered.

### **3.3 Results**

### 3.3.1 Qualitative comparison to empirical data

To qualitatively explore model performance, I assessed whether our model was able to reproduce the twelve movement patterns present in the empirical data (see Table 3.4). Six movement patterns, including those associated with diel displacement distance and maximum distances traveled from a permanent water source, were reproduced (Figure 3.4). Four of the other movement patterns were at least partially reproduced (Table 3.4).

# 3.3.2 Quantitative comparisons to empirical data

Four of the 16 statistical comparisons between empirical and simulated movement patterns were categorized as discrepancies of large effect size, three as discrepancies of medium effect size, while the remainder were categorized as of small to very small differences (Cohen 1988; Table 3.5). Discrepancies of large effect sizes associated with home range size, diel displacement distance, and net daily displacement distance, were mainly driven by the simulations underestimating movement characteristics in CNP while overestimating those in KNP.

# 3.3.3 Activity budgets

Table 3.6 shows patterns associated with activity budgets for simulated agents and those found in relevant literature, including the time spent employing thermoregulatory and foraging and the links between these behaviors and environmental temperature. Agents spent approximately 20-25% of the time employing thermoregulatory behaviors. This was similar the time actual elephants spent employing thermoregulatory behaviors (approximately 30% of the time as observed in Mole et al., 2016 and Guy 1976). As with actual elephants, agents employed thermoregulation most often in the afternoon hours when temperatures are generally highest. Like actual elephants which spend approximately 12-18 hours foraging per day (as observed in Guy 1976, Wyatt & Eldringham 1974, and Mole et al., 2016), agents also spent approximately 18 hours foraging per day. On average, agents spent the least amount of time foraging in the afternoon hours when the temperatures are high, consistent with what has been observed in actual elephant populations (Shannon et al., 2008).

# 3.3.4 Sensitivity analysis

Movement characteristics were most sensitive to (in the order of importance) : 1) increases and decreases in the parameters determining the turning angles when the agent foraged, 2) decreases in the temperature threshold for employing behavioral thermoregulation, and 3) increases in the probability of employing 'drinking' behavior at any given time since the agent last visited a water source (Tables A.5-A.8). Changes in the paramaters associated with turning angles resulted in the greatest effect sizes ranging from -0.133 to -0.359, indicating that simulated movement is particularly sensitive to changes in this parameter. Of the four movement characteristics, home range size and net daily displacement were most sensitive to changes in the parameters associated with turning angles. A more detailed description of the sensitivity analysis is provided in the Appendix A.2.

# 3.4 Discussion

Simulated and empirical home range sizes differed statistically between parks and between seasons, however, the direction of the seasonal and park effect generally matched between simulated and empirical home range sizes. The ABM was also successful at reproducing some differences in diel displacement distances (DDD) and net daily displacement distances (NDD) between seasons, particularly for KNP. The increased rainfall associated with the transition from dry to wet season increased the availability of forage and water, relaxing movement constraints to permanent water and triggering an expansion of movement and of the home range (Birkett et al., 2012; Buchholtz et al., 2019; Loarie et al., 2009a; Stokke & Du Toit, 2002). The seasonal differences in water availability were likely the major reason why the ABM simulated the increased movement.

The wet season is associated with increased fine-scale heterogeneity as forage resources increase in both quantity and quality (compared to the dry season, in which conditions are

"uniformly poor" (Polansky et al., 2013; van Moorter et al., 2013). Increased fine-scale heterogeneity may have prompted increased movement as the potential gain from food resources outweighed the cost of moving (see Polansky et al., 2013). Simulated elephants moving through areas with consistently homogenous forage quality (when the average EVI of the search radius was greater than or equal to the running average EVI of recently visited locations), tended to display more tortuous and shorter movements to increase the likelihood of remaining in high EVI areas. However, if the EVI raster layer captured the increased fine-scale heterogeneity associated with the wet season, simulated elephants should have increased daily displacements relative to the dry season because the quality of cells that are farther away from the agent may inevitably outweigh the cost of moving to those cells.

Simulated elephants traveled farther from permanent water in the wet season compared to the dry season, a general pattern found in real elephant populations (Bastille-rousseau et al., 2020; Jackson et al., 2008; Loarie et al., 2009a; Stokke & Du Toit, 2002). Simulated elephants also traveled farther from permanent water in CNP compared to KNP. In CNP and the surrounding protected areas, the Chobe River constitutes the major source of permanent water (Fox & Alexander, 2015), and elephants often disperse many kilometers inland to seasonal water sources (Alwij et al., 2010). This is in contrast to the abundance and wide distribution of both seasonal and permanent water in KNP, where it is physically not possible for elephants to move too far from permanent water (Purdon & van Aarde, 2017b; Redfern, 2003).

The temporal patterns of movement of elephant agents are similar to those observed in real elephants. Model agents spent a total number of hours foraging that were comparable
to real elephants and spent more time avoiding heat in the afternoon when temperatures were higher (Guy, 1976; Mole et al., 2016; Shannon et al., 2008).

### 3.4.1 Discrepancies between the model outputs and empirical data

Discrepancies of medium to large effect size in three of the four movement characteristics between the empirical and simulated data were not unexpected, as model outputs rarely fit actual data perfectly. Rather than try to explain why there were some quantitative differences between movement characteristics calculated for simulated and empirical data, I focused on identifying potential reasons for the model's limited ability to reproduce certain patterns between study areas and between seasons.

### 3.4.2 Human interference

The model was not able to reproduce the significantly greater NDD and DDD observed in CNP compared to KNP based on the empirical data. These discrepancies may be due in part to the exclusion of anthropogenic influences on elephants within the model. Throughout the time period that elephant movement was monitored, KNP experienced one instance of elephant poaching (Lunstrum, 2014). In Botswana, however, a steady increase in poaching has been documented since 2010 (Lindsay et al., 2017, Schlossberg et al., 2019; Schlossberg et al., 2020). Poaching affects the movement of elephant populations by creating a "landscape of fear" in which individuals move in straighter lines (Ihwagi et al., 2019), or shift their ranges (Goldenberg et al., 2018) away from areas where poaching activity is higher. Neil et al (2020) developed an ABM that incorporated adaptive poacher agents, rangers, and elephants to predict how the interactions between

these entities affect elephant poaching levels. The authors suggested that incorporating avoidance of poaching hotspots in the model could alter elephant distribution and subsequent poaching levels (Neil et al., 2020).

Within the model, areas favorable for foraging will generally elicit movement with greater tortuosity and shorter step lengths. However, if the corresponding area in the real world is also a risky area, the movements of actual elephants may be straighter and of longer duration in order to quickly move through the area (Graham et al., 2009; Ihwagi et al., 2019; Vollrath, 2005). Villages and commercial farms border some of KNP (Cook et al., 2015), but there are no villages within our study area in KNP. There are, however, several villages bordering the Chobe Forest Reserve included within our study area near CNP. Failing to account for the increased risk perceived by elephants passing through these human-impacted areas may have contributed to the model producing trajectories with lower DDDs and NDDs than expected in CNP.

Including poaching 'hot spots' and areas of human habitation as raster layers within the model may be more important for CNP compared to KNP and would allow agents to employ realistic avoidance behavior (Roever et al., 2012b). Other models have incorporated risky areas into habitat selection models for elephants (Roever et al., 2013a). For example, by including carcass density as representations of risky areas in a habitat selection model for elephants in northern Botswana, Roever et al., (2013a) found that protected areas were not necessarily associated with decreases in mortality risk as one would expect (Roever et al., 2013a).

### 3.4.3 Environmental predictability and spatial memory

Spatial memory can shape animal space utilization patterns by allowing for non-random returns to locations within the landscape (Gautestad & Myrsterud 2010). Tsalyuk et al., (2019) found that elephant movement was influenced by long-term vegetation conditions more so than current conditions. It is possible to simulate long term spatial memory within ABMs by incorporating past conditions into the model environment and allowing the agent to make decisions based on these conditions. Bracis & Mueller (2017) developed an ABM in which zebra agents remembered long-term averages of past habitat conditions, represented by averaging remotely sensed vegetation indices in the past, and made movement decisions based on these long-term averages of habitat conditions rather than on current conditions. Spatial memory may be represented by two "streams" that make up a memory map; one stream prevents an individual from returning to areas recently visited, while the other draws individuals to attractive habitats, also referred to as reference and working memory, respectively (Bracis et al., 2017; Folse, 1989; Van Moorter et al., 2009). Whether spatial memory influences fine-scale movement decisions in areas where the quality of forage resources is not easily predictable remains to be studied.

I suggest that modeling spatial memory relating to water sources, arguably the strongest driver of elephant movement during the dry season, was sufficient to produce a relatively good fit between the model and the empirical data. In the dry season, the need to return to water sources may regularly override the desire to re-visit traditionally favorable foraging sites. During the wet season, the increased abundance and quality of food may decrease the need to remember specific areas and increase exploratory movements (Tsalyuk et al.,

2019). Spatial memory may thus play a less important role in accessing food resources for elephants than it does in accessing water sources. To augment our foraging submodel to capture spatial memory processes related to food resources, we would need a better understanding of the extent to which spatial memory related to vegetation characteristics plays a role in dictating movement decisions during the wet season.

### 3.4.4 Foraging preferences and the issue of scale

To improve my foraging sub-model, I would need a greater understanding of the spatial scale at which elephants make foraging decisions at hourly time steps. Whether the vegetation greenness (EVI) raster's resolution of 30 meters represents too fine of a spatial scale for elephants to base their foraging decisions on remains to be tested. De Knegt et al., (2011) contended that fine-scale foraging decisions may be made after elephants select larger-scale areas of high forage availability within the spatial constraints of water. We know that elephants prefer greener than average vegetation at the scale of 250 and 500 meters (Loarie et al., 2009b), and can select favorable patches even at scales of 100 square meters (Pretorius et al., 2011). Thus, it is possible that elephants may make hourly foraging decisions at spatial scales as fine as 30 meters to exploit preferential feeding sites.

My model does not include any spatial information that would allow our agents to base their movement decisions on preferences for specific feeding sites. In the wet season when vegetation is more variable, elephants may make exploratory movements to seek out areas with high quality forage (Loarie et al., 2009a; Tsalyuk et al., 2019; Young et al., 2009). If real elephants are exploring the landscape for preferred feeding sites in the wet season rather than simply selecting for greenness within their vicinity, they may travel greater distances than our elephant agents, and display less tortuous movement. The inability of our simulated elephants to make exploratory movements may be one of the reasons for our model underestimating wet season home range sizes, diel displacement distances, and net daily displacement distances for CNP.

### **3.5 Conclusions**

I have shown that a resource-driven model with relatively simple decision rules generates trajectories with movement characteristics that are mostly comparable to those calculated from empirical data. By analyzing the differences in the model's ability to reproduce realistic movement for elephants in CNP and KNP, I was able to identify potential causes for the discrepancies between model outputs and empirical data. The addition of location-specific information on "risky" areas may be the most immediately feasible way to extend the applicability of our movement model, particularly for CNP.

Coarser-scale movement models, such as Boult et al.' (2018), which predicts the presence or absence of elephants in the study area, are suitable for predicting how dispersal movements may be influenced by landscape features. In contrast, simulating hourly movement (as our model does) may be more useful in predicting how finer-scale patterns of space use, such as those created by foraging movements, are influenced by finer spatio-temporal changes in the environment. These include changes in daily temperatures and in the distribution of water and shade that in the future may change in response to climate change. Validated movement models such as the one developed herein can also serve as virtual laboratories to explore hypotheses *in silico* related to how movement and foraging efficiency are influenced by organism-resource interactions.

### **CHAPTER 4**

### An ABM approach for exploring the influence of forage, water, and tree cover characteristics on the movement and foraging efficiency of herbivores

The movement decisions that animals make are perhaps most obviously influenced by the spatial characteristics of food resources across the landscapes, as they are the source of energy herbivores need for survival. Indeed, food is often the most discussed factor shaping movement (Gallagher et al., 2017) and is considered by many to be the major factor shaping animal spatial use (Klappstein & Potts, 2021; Morales et al., 2010; Thums et al., 2018). The spatial distribution and abundance of food resources partially determines the distances that an herbivore must travel between areas, and ultimately alters foraging and the characteristics of movement (Bailey et al., 1996, De Knegt et al., 2007; Mueller & Fagan 2008). Spatial variation in topography, disturbances, moisture availability, and competitive interactions can all play large roles in creating differences in the distribution and abundance of herbaceous biomass in different savanna habitats (Augustine, 2012). It is not surprising that empirical studies often link spatial differences in the movement patterns and foraging efficiency of herbivores, including black rhinoceros (Seidel & Boyce, 2015), buffalo (Naidoo et al., 2012), and elephants (Young et al., 2009), to spatial differences in the abundance and distribution of food resources. Many theoretical studies exploring the effects of habitat heterogeneity on foraging and movement have also focused on the influence of food spatial distribution and abundance (Roese et al., 1991; Vincenot et al., 2015; Wallis De Vries, 1996). An herbivore's foraging efficiency, generally described as the ratio of energy gained over energy expended over a period of time, is strongly determined by the movement decisions it

60

makes while foraging (De Knegt et al., 2007; Roese et al., 1991), and is a determinant of herbivore survival (Bailey et al., 1996; Hainsworth, 1974; Nagaoka, 2002). Understanding how spatial differences in resource characteristics influence movement patterns may consequently lay the foundation for "building the bridge between animal movement and population dynamics" (Morales et al., 2010).

# 4.1 Surface water availability and piospheres: influences on foraging area and activity budgets

In savannas and other ecosystems, surface water availability drives the movement decisions of herbivores, and the spatial and temporal limitations placed by water dependence is well documented. First, the configuration of water sources influences the areas available to herbivores (Choquenot & Ruscoe, 2003; Illius & Connor, 2000; Loarie et al., 2009; Redfern, 2003). For many large herbivores, 5 km is the typical maximum distance traveled from water daily during the dry season (Kanga & Ogutu, 2013; Owen-Smith, 1996; Redfern et al., 2005), and areas farther than 5 km from water sources are less accessible for foraging than areas closer to water (Owen-Smith 1996). This foraging area, and subsequently the dispersal range, becomes greater if water sources are placed close enough together such that they are within the traveling distance of an herbivore (Owen-Smith, 1996). Furthermore, when water sources are close together, their piospheres, or areas of degradation of vegetation that radiate from a water point due to trampling and grazing (Foran, 1980; Owen-Smith, 1996), may overlap. While the overlapping of piospheres may lessen the intensity of individual effects at each water point (Landman et al., 2012; Owen-Smith, 1996; Thrash & Derry, 1999), it leads to

homogenization of vegetation, particularly the grass layer, across the landscape (De Leeuw et al., 2001; Owen-Smith, 1996). This ultimately has consequences for foraging dynamics. Isolated water sources are subject to more intense piosphere effects (Thrash, 2000) as herbivores concentrate their foraging efforts in the vicinity of one water source. Consequently, herbivores may have to travel even longer distances from water to reach areas that are not degraded. Because water-dependent species, including elephant, wildebeest, zebra and buffalo, generally return to water every one to two days (Purdon & van Aarde, 2017; Redfern et al., 2005), it is often at the expense of foraging (Cain et al., 2012; Owen-Smith et al., 2020). Surface water availability may consequently affect the foraging efficiency of large herbivores by influencing spatial use and activity budgets (Bailey et al., 1996; Redfern, 2003).

## 4.2 Water and shade: influences on activity budgets, foraging trip durations and habitat use

When faced with high environmental temperatures, herbivores often modify their behavior and seek out water or shade to reduce thermal stress (Boyers et al., 2019, Terrien et al., 2011). Water allows animals to take advantage of evaporative cooling through wetting and drinking. Large and relatively hairless herbivores, including white rhinoceros and buffalo, are particularly reliant on water and mud to cool off (Vanschoenwinkel et al., 2011). African buffalo prefer wallowing over using shade, suggesting that water is more effective at ameliorating the stress of high environmental temperatures (Tullocha & Litchfieldb, 1981). High temperatures may ultimately modify the durations of foraging trips, that is, the time spent foraging between returns to water. The foraging trips of elephants, for example, tended to be shorter when the temperatures at the beginning of the trips were higher (Rozen-Rechels et al., 2020). Shorter foraging trips due to higher temperatures may limit how far individuals can forage from water and thus constrain access to forage resources.

In areas where water is scarce, shade may be the most readily available resource for large herbivores (Giotto et al., 2013; Hetem et al., 2011). Using behavioral strategies to respond to high environmental temperatures may affect foraging by altering daily activity budgets, such that less time is allocated to foraging and employing behavioral thermoregulation takes priority. For example, both wildebeest and chamois spend less time feeding when temperatures are warm (Maloney et al., 2005; Mason et al., 2014). Additionally, the need to employ behavioral thermoregulation influences habitat use associated with foraging. For example, in response to high ambient temperatures, male alpine ibex occupy areas at higher altitudes, which, while lower in ambient temperatures, are also characterized as having lower quality vegetation compared to areas at lower altitudes (Mason et al., 2017). Herbivores may also move less when temperatures are high, possibly associated with the need to stay close to sources of shade when temperatures are high and thus benefit thermoregulation (Alston et al., 2020).

### 4.3 Spatial variation of water and tree cover in savannas

Savanna landscapes can have differing availabilities and distribution of water sources and tree cover, and these differences can be naturally occurring or due to human interference. In arid and semi-arid savannas, the upper bound of woody cover is driven by mean

annual precipitation (Sankaran et al., 2005). The distribution of tree cover may vary from clumped aggregations to more randomly or evenly dispersed patterns, and these differences are often attributed to the effects of fire, herbivory, soil patchiness, and intraspecific competition. In mesic savannas, fire can induce a more clumped distribution of trees across a landscape (Hochberg & Menaut, 1994; Jeltsch et al., 1996), while more dispersed distributions are suggestive of competitive effects in relation to limiting factors, such as water and nutrients (Caylor et al., 2003). The area of tree clusters in savannas can reach hundreds of square meters (Boggs, 2010). Moustakas et al. (2007) found patches of trees with canopy surface areas of 300 square meters in the southern Kalahari, South Africa. Anthropogenic disturbances are also responsible for changes in the woody cover layers of savannas. Illegal wood cutting and farming in savannas have been associated with decreases and fragmentation in woody cover in Burkina Faso (Dimobe et al., 2017). Conversely, increased atmospheric carbon dioxide associated with global climate change has been considered a major driver of woody cover increase in African savannas (Kgope et al., 2010). Piosphere effects around water holes are often associated with decreases in woody cover (Chamaillé-Jammes et al., 2009). Generally, water sites are not as abundant as shade provided by woody cover, however, water availability in parks is often supplemented by artificial water holes, increasing surface water distribution (Epaphras et al., 2008; Smit et al., 2007). Distances between water sources may also vary substantially.

#### 4.4 Home ranges as large-scale expressions of movement decisions

Differences in movement influenced by variation in abundance and distribution of resources such as food and water can translate to intraspecific variation in patterns of space use, such as home range size. Many studies linking patterns of spatial use and resource distribution show that larger home ranges are often associated with more dispersed and less available resources, as more movement is required to encounter these resources (Mcnab, 1963; Sai & Bourgoin, 2009; Seigle-ferrand et al., 2021).

Spatial differences in surface water availability due to differences in rainfall can result in intraspecific variation in home range size. In general, rainfall is positively associated with surface water availability and vegetation productivity (Chamaillé-jammes et al., 2007a; Chamaillé-Jammes et al., 2007b; Chamaillé-Jammes et al., 2008; Illius & Connor, 2000; Pandey & Singh, 1992), two major interacting drivers of herbivore movement in savannas. Home ranges in 'dryer' areas having less surface water availability and lower vegetation productivity should be larger than home ranges in 'wetter' areas, which have greater surface water availability and greater vegetation productivity, as more movement is required to reach those critical resources that are limited and sparsely distributed (Doherty et al., 2019; Said et al., 2009; Schopef et al., 2015). This apparently holds for elephants (Grainger et al., 2005; de Beer & van Aarde 2008; Young et al., 2009), and buffalo (Western 1975) across Africa.

Intraspecific variation in home range size can also arise from spatial differences in surface water availability due to surface water supplementation in the form of artificial water points. Provisioning of artificial water points is not linked to greater vegetation productivity as occurs with increases in rainfall. Artificial water points may increase

65

home range size as increased surface water availability allows for more extensive ranging to areas that are otherwise inaccessible (Du Toit & Cumming, 1999; Norman Owen-Smith, 1996). For example, elephants had larger home ranges where water was more widely available (Wall et al., 2021) and they ranged over greater areas in the dry season when water was provided (Loarie et al., 2009a).

Environmental temperature can also influence an individual's home range size indirectly, as access to water and shade affects space utilization. Female feral pigs exhibited smaller home range with increased air temperatures, suggesting that their movement is restricted to areas with water and shelter (Dexter, 2003). Similarly, beira antelope (*Dorcatragus megalotis*) home ranges were smaller during the hot season, with movement restricted to areas near shade, such as trees or rock shelters (Giotto et al., 2013).

Clearly, the movement decisions that herbivores must make extend beyond those related to food acquisition and occur within the context of landscapes that are complex and characterized by spatial variation in critical resources. While most fine-scale models of herbivore movement have focused on exploring the effects of forage abundance and distribution on the movement and foraging efficiency of herbivores (Boyer & Walsh, 2010; Roese et al., 1991; Vincenot et al., 2015), less attention has been given to elucidating the effects of additional factors on movement and foraging efficiency, namely, the abundance and distribution of water and tree cover. Furthermore, few studies have connected how differences in movement and foraging efficiency due to spatial differences in resources translate to differences in larger-scale spatial use patterns, such as home range size.

The objective of this chapter was to explore how spatial differences in the availability and distribution of water and tree cover can produce differences in movement patterns and subsequent foraging efficiencies, which is the energy gained through forage consumption / total distance traveled, and spatial use patterns of water-dependent herbivores.

I used an existing movement ABM validated for elephants in Chapter 3 to simulate hourly movements of agents representing herbivores. The agents had to drink water approximately every 24 hours and were sensitive to high temperatures similar of many large herbivores in African savannas. ABMs are ideally suited for exploring the influences of various abiotic factors on animal movement and foraging efficiency, as forage consumption and distances traveled can be a direct response to the agent's interaction with landscape elements and its internal state. Spatially explicit ABMs are able to represent the distances between resources and the spatial configuration of landscape elements, both of which play critical roles in shaping movement. Because altering real landscapes to reflect variation in the distribution and abundance of resources is practically impossible, artificial, or *in silico*, computer-simulated landscapes are useful in reproducing differences in landscape composition and physiognomy (Duning, 1995). I utilized artificial landscapes to create environments representing savanna landscapes varying in distributions of forage, abundance of water (low vs high water source density reflecting low and high-water source densities), and distribution and abundance of tree cover. I did not manipulate forage abundance, focusing instead on the effects of forage distribution, water and tree cover characteristics, but I did incorporate piospheres within each landscape. Consequently, forage was not necessarily limited across the artificial landscapes.

Every simulated agent in the artificial landscapes faced environmental temperatures representing the hot, dry season, which is a limiting season for large herbivores, as higher temperatures drive greater employment of behavioral thermoregulation and forage biomass declines through time.

I calculated foraging efficiency, foraging trip duration, time spent foraging, time spent in shade, and time spent wetting/drinking to gain a more complete understanding of movement dynamics under the different combinations of landscape factors. I also calculated home range size to examine the consequences of differences in movement decisions on larger-scale spatial use patterns of simulated herbivores.

I asked the following main questions and pose hypotheses based on them:

## What factor has the greatest effect on movement and foraging efficiency when forage is not limited?

*Hypothesis 1*: Tree cover abundance would have the greatest effect on trip duration. High tree cover abundance will be associated with longer trip durations, as herbivores do not have to rely solely on water for behavioral thermoregulation.

*Hypothesis 2:* Water abundance would have the greatest effect on home range size as water-dependent herbivores must regularly return to water to drink and also use water for behavioral thermoregulation. When water source density is high, herbivores will be able to expand their ranges to access a greater portion of the landscape.

*Hypothesis 3*: Water abundance would have the greatest effect on foraging efficiency. When water source density is high, herbivores will be able to travel greater distances, and consume more forage. Does tree cover abundance and distribution affect movement patterns and foraging efficiency differently in low water source density vs high water source density landscapes?

*Hypothesis 4*: Differences in movement patterns due to differences in tree cover distribution and abundance will be more pronounced in landscapes with low water source abundances, as simulated herbivores would be most limited in movement where tree cover is low and clumped, and herbivores must remain in the vicinity of water. Home range sizes and foraging trip durations should be similar in high water source density landscapes regardless of tree cover abundance or distribution, while in low water density landscapes home ranges would be smallest and trip durations would be shorter when tree cover is low and clumped.

*Hypothesis 5:* Differences in foraging efficiency due to differences in tree cover distribution and abundance will be more pronounced in landscapes with low water source densities. In low water density landscapes, agents would be forced to take advantage of shade, while the presence of shade will not matter to the same extent in landscapes with high water source densities.

### If there are differences, what drives them?

*Hypothesis 6*: Variation in trip duration and home range size among low-water landscapes with differences in tree cover characteristics will be driven by differences in time spent wetting. In low water landscapes, trip durations will be shorter and home range sizes will be smaller when tree cover is low and clumped and agents must constantly return to water for wetting. In high water landscapes, trip durations and home range sizes will be similar regardless of tree cover characteristics.

*Hypothesis 7*: Variation in foraging efficiency among low-water landscapes with differences in tree cover characteristics will be driven by differences in forage consumption. When tree cover is low and clumped, agents will consume less forage due to less time spent foraging at the expense of traveling to and from water.

To our knowledge, no modeling study has examined how the spatial distribution and abundance of critical non-forage resources, namely water and tree cover, interact to influence forage consumption and energetic costs, and shape large scale movement patterns of large and water-dependent herbivores. The results of this modeling study may elucidate how differences in landscape configuration influence herbivore fitness and shed light on potential reasons for spatial variation in space use patterns by large herbivores. Table 4.3 summarizes the hypotheses which were supported, and the model's results.

### 4.5 Methods

### 4.5.1 Creating artificial landscapes

All artificial landscapes created for this study were 4000 by 4000 cell raster grids in which each cell represented an area of 30 meters by 30 meters. Each cell contained a forage level value, ranging from 0 to 1, a binary tree cover value, where values of 1 represented the presence of tree cover, and a binary water source value where values of 1 represented the presence of a water source. I used a factorial combination of two different forage layers, four different tree cover layers, and two different water source layers to create a total of 16 artificial landscapes.

### Forage layers

The forage layer for herbivores represented the distribution of green vegetation biomass across the landscape during the dry season, and each cell was set to a value between 0 to 90000 g. During times without rainfall, grasses generally cease growing (Owen-Smith 2002), and thus I assumed the growth rate throughout the course of the simulation is zero. I arbitrarily set the death rate of the forage layer across the landscape to 90 g per time step.

To simulate these differences in the spatial patterning of herbaceous biomass, I used the R package "nlm\_gaussianfield" with an autocorrelation range of 650 (19.5 km) for the "clumped" forage landscape and 5 (150 m) for the "dispersed" forage landscape (see Figure 4.1). The autocorrelation range within the function determines the maximum range of cells over which autocorrelation occurs, and larger values create more "clumped" landscapes. The values representing the correlation ranges for clumped and dispersed forage represents lower and upper values of spatial dependence for herbaceous biomass in a tropical savanna (Mutanga & Rugege, 2007). I set the mean value in the function to .5 and rescaled the values so that the values would be between 0 and 90000. I created 3 "clumped" forage landscapes and 3 "dispersed" forage landscapes, and for each simulation, I randomized the landscape selected. For details on the creation of the forage layer, refer to Appendix B.1.1.5. See Appendix Table B.1 for the descriptive statistics for each forage layer used in the model.

### Tree cover layers

Tree cover layers with the following characteristics were created:

- 1. Abundant and clumped tree cover
- 2. Abundant and dispersed tree cover
- 3. Scarce and clumped tree cover
- 4. Scarce and dispersed tree cover

Landscapes with abundant tree cover were defined as having 25 percent tree cover, an amount considered relatively high for savannas (for reference, woodlands have greater than 40 percent tree cover, and see Roever et al., 2012 for mean percent tree cover of parks within Africa). Landscapes with scarce tree cover were defined as having 5 percent tree cover, more reminiscent of a grassland. To generate different levels of spatial autocorrelation, I used the R package "nlm\_gaussianfield" with an autocorrelation range of 25 (750 m) for the "clumped" tree cover landscape and 5 (150 m) for the "dispersed" tree cover landscape. These values represent the smaller and larger sizes of tree clusters found in two savanna systems in southern Africa (Boggs 2010). The function "util\_binarize" was then used to convert the raster cell values to 0 (indicating no tree cover in the cell) to 1 (indicating tree cover within the cell) (Figure 4.2). No tree cover was present in areas that were within 63 cells from water to reflect piosphere effects on woody cover (see below for description of the different piosphere "zones").

### Water source layer and piospheres

Each of the above landscapes was also crossed with a low-density water source layer and a high-density water source layer. The low-density layer was characterized by a water

source density of 0.001 water sources per square kilometer, and the high-density layer was characterized by a water source density of 0.015 water source per square kilometer. These values for water source densities are consistent with densities in actual savannas (e.g., see Chamaillé -James et al., 2007b for water source densities in Hwange National park).

For each layer, I created piospheres around each water point. To reproduce the utilization gradient, I divided the distances from each water point into 5 different "zones" and decreased the initial forage level of the cells in each zone by a specific percent. The forage level of cells within 4 cells (120 m) of a water point was reduced to zero, representing the "sacrifice zone" (Thrash & Derry, 1999). The forage level of cells within 5 to 15 cells (450 m), 16 to 31 cells (930 m), 32 to 48 cells (1.4 km), and 49 to 63 cells (1.9 km), was reduced by 80, 60, 40, and 20%, respectively. In this way, I was able to achieve a realistic utilization gradient where forage levels increased with distance to water. Figure 4.3 depicts low and high-water source density landscapes and piospheres. Because high-water source density landscapes had more piospheres than low-water landscapes, forage levels in high-water landscapes were slightly lower than forage levels in low-water landscapes at the beginning of a simulation. See Appendix Figure B.1 for histograms of forage biomass/levels for example low-water and high-water landscapes.

### 4.5.2 Model Overview

Movement was simulated by incorporating drivers of water-dependent grazer movement into a hierarchal decision-making process, where the higher priorities were to respond behaviorally to ambient temperature and the need to drink water, and foraging became an option once those needs were met. Each behavioral response was accomplished by directed movement. I note that the ABM used in this chapter is identical to that developed in Chapter 3 except for two components. First, only one "state" is included in the model, and second, foraging is not simulated as area-restricted search. A complete and detailed model description following the Overview, Design concepts, Details protocol (Grimm et al., 2006; Grimm et al., 2010) is contained in Appendix section B.

The entities within the model were the agents, landscape cells, and environment. Here, the agent was representative of a generic large savanna grazer that is water-dependent (must return to water approximately every 24 hours), and sensitive to high temperatures. The agent was mobile and responded to the environment by changing its movement across the landscape. The agent was characterized by the following state variables and attributes: 1) position on the landscape (x and y coordinates), at any given time step, 2) the time since it last visited a water source, 3) the behavior that it was employing (i.e., wetting, shade-use, drinking, or foraging) , and 4) the ambient temperature that it was experiencing at a given time step ("perceived temperature"). Model entities and state variables are described in Appendix Table B.2.

Attributes of landscape cells were 1) forage level, updated every time step to reflect decreases in forage during the dry season, 2) a binary value indicating whether or not tree cover was present in the cell, and 3) a binary value indicating whether or not water sources were present in the cell. State variables included environmental temperature (representative hourly temperature from CNP and KNP were downloaded from the National Oceanic and Atmospheric Administration's National Center for Environmental Information, and missing values were estimated using spline interpolation (Samanta et al., 2012). The model landscapes comprised separate rasters representing the aforementioned attributes. The spatial extent was 120 km by 120 km (4000 by 4000 cells) and each of the cells comprising the model landscape had a spatial resolution of 30 m by 30 m.

Simulations were run for 336 time-steps, representing a temporal resolution of one hour and a temporal extent of two weeks. I used 336 time-steps as the duration of our simulations to strike a balance between having a trajectory that was ecologically meaningful in representing spatial use and to minimize computational intensity. The main processes within the model, which were repeated every time step, constituted the agent's decision-making as it moved through a landscape. The agent first decided whether it sought shade or water to maintain homeothermy. This decision was influenced by the current perceived temperature, the agent's state, and the temperature threshold above which behavioral thermoregulation was likely to occur. I set the temperature threshold at 30 degrees Celsius, as this approximates the temperature above which many herbivores seek cooler microclimates (Boyers et al., 2019). Agents moved within a specified "search radius", which represented a maximum distance that water-dependent herbivores were likely to move in one hour and differed depending on the behavior employed. There was a higher probability of forming a smaller search radius than a larger search radius (0.9 km and 1.8 km, respectively) when employing thermoregulatory behavior. I assumed that water-dependent herbivores preferred to employ wetting behavior if a water source was within the search radius, due to the benefits of evaporative cooling. If no water source was present in the search radius, the agent employed shade use within the smaller search radius.

If the agent did not have to employ behavioral thermoregulation, it then decided whether to drink. This decision was determined based on the time since the agent last visited a water source (including instances of wetting), and the perceived environmental temperature. As the time since the agent last visited a water source increased, and as the environmental temperature increased, there was an increased probability of it drinking. I incorporated spatial memory relating to water sources in the model by allowing agents to "sense" the location of water sources across the landscape and to move in the direction of the closest water source. Agents could move within a search radius of 1.8 km.

If the agent did not employ thermoregulatory behavior or drinking, the model assumed it would forage. There was a higher probability of selecting cells that maximized 'forage level/distance to the agent, and the agent moved within a search radius of 1.8 km. For many herbivores, the intake rate of food generally takes the form of a Holling type 2 response (Holling, 1959; Lindsay, 1994) where intake rate increases with food availability before reaching an asymptote. To reflect this process within our model, I determined the hourly intake rate for grazer agents during any given time step via the equation below:

## $\frac{mF}{1+mhF}$

where "m" is the rate of encounter of food resources in the cell and "F" is the food availability within the cell. 1/h is the maximum rate that food could be processed, i.e., the maximum rate of digestion. When there is a great abundance of food available for the agent, the rate of ingestion can reach an asymptote of 1/h. I did not take into account ungrazeable vegetation biomass, as the value for each cell in the forage layer was representative of green vegetation biomass, which was grazeable.

I chose to model a relatively large, generic grazing herbivore as the grazing agent. Taking note of reported wet bulk digestive capacity of kudu, I assumed that the digestive capacity, or "1/h" was 2 kg/day, or 83 g/hour (Owen-smith, 1993). I also assumed that "m" was .05.

I ran 100 simulations for each landscape. I aimed to generate enough simulated trajectories such that the resulting average value of each movement characteristic calculated from the simulated trajectories would be an accurate representation of model performance.

### 4.5.3 Quantifying foraging efficiency

I defined foraging efficiency as the ratio: 'E/D', where 'E' was the energy intake for each time step summed over the entire simulation, and 'D' was the total distance traveled throughout the entire simulation. Several simulation models have determined foraging efficiency (Boyer & Walsh, 2010). Energy intake was only counted for foraging, and not shade use or wetting behavior. While herbivores can feed while in the shade, generally, the employment of thermoregulatory behaviors has negative effects on resource acquisition (Mason et al., 2017).

### 4.5.4 Analyzing trajectories

I calculated percent changes in foraging efficiency, forage consumption, distance traveled, home range size, foraging trip duration, average time spent foraging per day, average time spent in shade per day, and average time spent wetting/drinking per day for water source density, forage distribution, tree cover distribution, and tree cover abundance, and assessed the direction of the changes. To calculate home range size, I used a kernel density estimator. The function 'kernelUD' from the package 'adehabitatHR' was implemented within R statistical computing environment (R Core Team, 2014) to calculate a utilization distribution for each trajectory using href as the adhoc smoothing parameter (Kie et al., 2010). I also calculated percent changes in the aforementioned for each factor pair (low tree cover to high tree cover), while keeping water source density the same.

Percent changes are described as increases or decreases in foraging efficiency, forage consumption, distance traveled, home range size, foraging trip duration, average time spent foraging per day, average time spent in shade per day, and average time spent wetting/drinking per day due to switching between landscapes with low vs high water source density , low vs high tree cover abundance, dispersed vs clumped tree cover distribution, and dispersed vs clumped forage distribution (unless otherwise noted). Table 4.3 summarizes whether the hypotheses were supported, and the model's results.

### 4.5.5 Sensitivity analysis

A one-factor-at-a-time local sensitivity analysis of the model determined the sensitivity of the model outputs to parameter uncertainties. I varied each input parameter from the original reference values (Appendix Table B.4) by 10% and calculated percent changes as described above. I then compared the direction of changes in foraging efficiency, forage consumed, distance traveled, home range size, trip duration, and time spent employing foraging, shade use, and wetting for each factor calculated from the original model outputs to the direction of changes in the same response variables for each factor calculated from the model run with parameter changes. I also compared the landscape factors with the greatest impact on each response variable between the original model and the model run with parameter changes.

### 4.6 Results

Percent changes are described as increases or decreases in switching between landscapes with low vs high water source density, low vs high tree cover abundance, dispersed vs clumped tree cover distribution, and dispersed vs clumped forage distribution (unless otherwise noted). Table 4.3 summarizes whether the hypotheses were supported, and the model's results.

### Foraging efficiency

Water abundance was the factor that had the greatest effect on foraging efficiency (7.2% increase with increased water source density). The remaining factors in order of importance were tree cover distribution (3.8% decrease with clumped tree cover), forage distribution (3.7% increase with clumped forage distribution), and tree cover abundance (3.2% increase with increased tree cover abundance). Landscapes with clumped tree cover, clumped forage, and high tree cover abundance had the greatest foraging efficiency (Table 4.1).

As hypothesized, the effect of tree cover distribution on foraging efficiency was greater in low water than in high water landscapes (4.8% decrease vs. 2.6% decrease with clumped tree cover distribution). However, the effect tree cover abundance on foraging efficiency was greater in high water than in low water landscapes (4.2% increase with increased tree cover abundance vs. 2.1% increase with increased tree cover abundance) (Table 4.2) (Figure 4.4).

### Total forage consumed

Water abundance had the greatest effect on total forage consumed (2.4% increase with increased water source density), as agents in high-water landscapes consumed more forage than agents in low-water landscapes. Tree cover abundance had the second greatest effect on forage consumed (1.7% decrease with increased tree cover abundance), followed by and forage distribution (.39% decrease with clumped forage distributions), and tree cover distribution (.05% increase with clumped tree cover distribution).

Contrary to my hypothesis, agents in low-water landscapes with high tree cover abundance consumed less forage than agents in low-water landscapes with low tree cover abundance (2.9% decrease with increased tree cover abundance). Tree cover distribution did not have as great of an effect on forage consumption in low-water landscapes (.008 % decrease with clumped tree cover distribution). Tree cover abundance and distribution did not have as great of an effect on forage consumption in high-water landscapes (.43% decrease and .09% increase with increased tree cover abundance and clumped tree cover distribution, respectively) (Table 4.2) (Figure 4.5).

### Distance traveled

Tree cover abundance had the greatest effect on distances traveled (5% decrease with increased tree cover abundance), followed by water source density (4.6% decrease with increased water source density), tree cover distribution (4.2% increase with clumped tree cover distribution), and forage distribution (3.9% decrease with clumped forage

distribution). Agents in landscapes with low tree cover abundance, low water source density, clumped tree cover distributions, and dispersed forage traveled the greatest distances (Table 4.1).

As expected, high tree cover abundance and dispersed tree cover distribution were both associated with a 5.4% decrease in distance traveled in low-water landscapes. However, I also found that high tree cover abundance and dispersed tree cover distribution were associated with a 4.6% decrease and 2.9% increase in distances traveled, respectively, with increased water source density (Table 4.2) (Figure 4.6).

### Home range size

Landscapes with high water source density, high tree cover abundance, dispersed forage, and dispersed tree cover had the largest home ranges (Table 4.1). Water source density had the greatest effect on home range size as expected (120% increase with increased water source density), followed by forage distribution (16.7% decrease with clumped forage distribution) tree cover abundance (13.5% increase with increased tree cover abundance), and tree cover distribution (5.8% decrease with clumped tree cover distribution).

Differences in home range size in low-water landscapes were associated with differences in forage distribution (16.1 % decrease with clumped forage distribution), tree cover abundance (13.3% increase with increased tree cover abundance), and tree cover distribution (11.1% decrease with clumped tree cover distribution).

I found that differences in home range size in high-water landscapes were also associated with differences in tree cover abundance (13.6% increase with increased tree cover abundance), forage distribution (16.9% decrease with clumped forage distribution), and tree cover distribution (3.3% decrease with clumped tree cover distribution). In both categories of water source density, landscapes with high tree cover abundance, dispersed tree cover distribution, and dispersed forage distribution had the largest home range size (Table 4.2) (Figure 4.7)

### Trip duration

Tree cover distribution was the factor that had the greatest effect on trip duration (11.1% decrease with clumped tree cover distribution), followed by tree cover abundance (7.9% increase with increased tree cover abundance), water source density (7% decrease with increased water source density), and forage distribution (2.8% decrease with clumped forage distribution) (Table 4.1). Figure 4.8 depicts examples of simulated trajectories in landscapes differing in tree cover distribution but having all other factors the same, and corresponding frequency distributions of trip durations.

Low tree cover abundances were associated with shorter trip durations; this pattern was present in both low and high-water landscapes. In low and high-water landscapes, high tree cover abundance and dispersed tree cover distributions were associated with greater trip durations (8.6% and 14.2% increase in trip duration when switching from low to high tree cover abundance and from clumped to dispersed tree cover distributions for low water landscapes, respectively, and 10.1% and 7.5% increase in trip duration when switching from low to high tree cover distributions in high water landscapes, respectively). Clumped to dispersed tree cover distributions were distribution was associated with a 5.3 % decrease in trip duration in low-water landscapes, while in

high-water landscapes, clumped forage distribution was associated with a 1.3% increase in trip duration (when compared to dispersed forage distributions) (Table 4.2).

### Time spent foraging

Water abundance had the greatest effect on time spent foraging (2.2% increase with increased water source density), followed by tree cover abundance (1.8% decrease with increased tree cover abundance), forage distribution (0.41% increase with clumped forage distributions), tree cover distribution (0.15% increase with clumped tree cover distribution) (Table 4.1).

Low tree cover abundance was associated with an increase in time spent foraging (3% increase with decreased tree cover abundance) in low-water landscapes, but tree cover distribution and forage distribution had negligible effects (0.19% and 0.87% increase in time spent foraging with clumped tree cover distributions and clumped forage distributions, respectively). The effects of tree cover abundance, tree cover distribution and forage distribution on time spent foraging in high-water landscapes was negligible for high-water source density landscapes (0.56% decrease with high tree cover abundance, 0.125% increase with clumped tree cover distribution, 0.04% decrease with clumped forage distribution) (Table 2) (Figure 4.9).

### *Time spent in shade*

Agents in landscapes with high tree cover abundance, low water source density, dispersed tree cover distribution, and dispersed forage distribution spent the longest time in the shade per day (Table 4.1).

Tree cover abundance had the greatest effect on time spent in the shade for both low and high-water landscapes, although the effect was greater in low-water landscapes (10.5%

increase vs 3.1% increase with increased tree cover abundance, respectively) (Table 4.2) (Figures 4.10).

### *Time spent drinking/wetting*

Tree cover distribution had the greatest effect on time spent drinking/wetting (12.1% increase with clumped tree cover distribution), followed by tree cover abundance (8.4% decrease with increased tree cover abundance), water source density (6.3 % increase with increased water source density), and forage distribution (2.8% increase with clumped forage distribution) (Table 4.1) (Figure 4.11).

Low tree cover abundance was associated with more time spent wetting and drinking in low-water landscapes (8.3% increase with decreased tree cover abundance). Surprisingly, I found that tree cover abundance had almost the same magnitude of effect on time spent wetting and drinking in high-water landscapes (8.4% increase with decreased tree cover). Tree cover distribution also had an effect on time spent wetting and drinking in low and high-water landscapes, as clumped tree cover was associated with increases in time spent wetting and drinking (17.4% and 7.2% increase with clumped tree cover distributions, respectively). Forage distribution had an appreciable effect on time spent wetting and drinking in low water landscapes (6% increase with clumped forage distribution) but had a negligible effect in high-water landscapes (.02% decrease with clumped forage distribution) (Table 4.2) (Figure 4.11).

### Sensitivity analysis

The direction of the changes in response variables associated with each factor generally matched between the initial model runs and the model runs with parameter changes. When they did not match, the difference was small (for example, 0.003 % increase vs 2 %

decrease). Importantly, this means that the main patterns produced by the model initially were also produced by the model when parameters were changed, suggesting that the model is relatively robust to parameter uncertainties. Increases in water source density was always associated with increases in home range size, decreases in distances traveled, and increases in foraging efficiency. Dispersed and high tree cover was always associated with increases in foraging efficency and trip durations. Clumped forage distributions were always associated with increases in foraging efficiency. In some cases, the factor that had the greatest impact on a response variable when the model was run with parameter changes was not the same factor that had the greatest impact on a response variable initially. Even then, the factor that had the greatest impact on a response variable when the model was run with parameter changes was usually the factor that had the second greatest impact on a response variable. Percent changes in foraging efficiency, forage consumed, distance traveled, home range size, trip duration, and time spent employing foraging, shade use, and wetting calculated for each landscape factor, for each parameter change are shown in Appendix Tables B.5-B.10.

### 4.7 Discussion

I simulated the behaviors and consequent movements of herbivore agents representing water-dependent herbivores in landscapes differing in forage distribution, tree cover abundance and distribution, and water source density. The agents prioritized behavioral thermoregulation and drinking water before foraging, and foraging efficiency was a direct result of the behavioral and movement decisions of the agents. Consequently, I was able to explore how landscape pattern beyond food availability influences movement patterns and foraging efficiency of water-dependent herbivores.

## 4.7.1 High water source density transforms herbivore agents into multiple-place foragers, decreasing distances traveled but increasing the area over which they range

Consistent with hypothesis 3, water source density had the greatest effect on foraging efficiency, exemplified by a 7.2% increase in foraging efficiency when switching from low to high-water source landscapes. However, the increase in foraging efficiency in high water landscapes was not associated with greater distances traveled, as I had expected. Rather, greater foraging efficiencies were due to agents traveling smaller distances in high-water landscapes compared to agents in low-water landscapes. This result can best be explained within the framework of central and multiple place foraging. In low-water landscapes, most agents acted like central place foragers, where the water source was the "central place" from which they dispersed to forage. When needing to employ wetting or drinking, the agents had no choice but to travel back to the central place, incurring travel costs. The pattern of travelling smaller distances when using multiple places compared to using one central place has been observed in real-world populations. For example, spider monkeys (Ateles geoffroyi) reduced travel costs by selecting multiple sleeping sites next to foraging areas rather than moving to and from one sleeping site (Chapman et al., 1989).

The greater distances traveled when water source density was low may have also been due to forage depletion that occurred near the water source that activity was concentrated around, driving agents to forage at longer distances from water. These results mirror the consequences of real-world piospheres (Derry & Dougill, 2008; Lange, 1969; Thrash & Derry, 1999) and are consistent with central-place foraging theory, which predicts that foragers move to farther resources after initially depleting food resources near the central place (Bakker et al., 2005; Orians & Pearson 1978). While I simulated initial piosphere conditions at the beginning of every simulation, such that forage levels decreased up to one km from water, forage depletion likely continued if agents focused their foraging efforts around one water source. I suspect that agents were eventually forced to select cells farther from water as the forage biomass of cells near water decreased. Measuring distances traveled from water through time as a function of forage depletion around water would be the most straightforward way to confirm this. Examples of herbivores travelling greater distances from water in order to reach areas with greater forage include goats in South Africa (Shrader et al., 2012b) and savanna elephants (Ndaimaniet al., 2017). When water sources were abundant, agents utilized multiple water sources, and no longer had to make long trips to a central water source. They spent more time foraging, which was generally characterized by shorter distances traveled per time step and greater consumption of forage.

While the selection of multiple water sources decreased the total distance traveled, it increased the area over which the individual ranged, supporting hypothesis 2 (Chapman & Chapman 1989). Our results on home range size agree with results from other studies exploring the influence of increased water availability on the movement of water-dependent herbivores. In keeping landscape factors constant while manipulating water source density, our comparisons are analogous to comparing home ranges in similar areas where artificial water sources have and have not been provided, or before and after in artificial water provisioning situations. Shannon et al., (2009) modeled the effects of

artificial water source removal on the presence of elephant movement paths and found that artificial water source removal would decrease the area over which elephants ranged by 79% (Shannon et al., 2009). Similarly, Purdon & van Aarde (2017) found that elephants using artificial water holes used a greater area of the landscape compared to elephants that did not use artificial water holes.

I recognize that this result seems counterintuitive to the notion that greater resource availability is generally associated with smaller home ranges. However, I did not model changes in forage availability directly, so simulated herbivores in both high-water and low-water source density landscapes experienced similar forage availabilities and were not necessarily forage-limited. A greater abundance of water effectively released simulated agents from having to remain in the vicinity of one water source due to waterdependency and increased the area of the landscape that was available for foraging, as was the case in low-water source density landscapes.

## 4.7.2 Low water source density highlights the effects of evaporative cooling on activity budgets

I expected that agents in low-water landscapes would have to rely on water when shade was not available, as would happen when tree cover was low in abundance or clumped in distribution. Time would then be spent traveling to and from water rather than foraging, eventually leading to reduced forage consumption and incurred travel costs. I expected the opposite would occur in low-water landscapes when high and relatively evenly dispersed tree cover was available, such that agents would spend more time foraging and thus consume more forage and have lower travel costs. Counterintuitively, agents in low-water landscapes with low abundances of tree cover spent more time foraging and consumed more forage than agents in low-water landscapes with high abundances of tree cover. This result highlights the benefits of using water for thermoregulation. Within the model (and in the real world), wetting behavior is much more efficient at lowering the perceived temperature compared to shade use behavior. In addition, the effects of wetting behavior are experienced for a longer period of time compared to the effects of shade use behavior (Lillywhite & Stein, 1987; Tulloch & Litchfield 1981). In the ABM, an agent employing wetting behavior will experience its effects for six hours, whereas an agent employing shade use only experiences the effects of this behavior for the following hour. Agents in landscapes with less tree cover had to rely on water for thermoregulation and employed behavioral thermoregulation less often than agents relying on shade use, essentially freeing up time to forage. This reflects the benefits of evaporative cooling over shade use behavior. Indeed, the benefits of using water for thermoregulation and similar effects on foraging have been described for swamp buffalo (Somparn et al., 2006), and suggested for cattle (Geraldo et al., 2012). If exposed to both trees and water sources, swamp buffalo preferred wallowing over using shade when temperatures were high. When using water sources for thermoregulation, swamp buffaloes were able to take advantage of the evaporative cooling benefits of wallowing and grazed for a longer period of time throughout 24 hours compared to swamp buffaloes that were in paddocks with only large trees (Somparn et al., 2006). I do note, however, that even though agents in landscapes with low tree cover abundances forced to employ wetting more frequently consumed for forage throughout the duration of the simulation, they also incurred greater traveling costs.
## 4.7.3 A role for tree cover characteristics in differentially influencing movement and foraging efficiency regardless of water source density

Tree cover distribution, and not tree cover abundance, had the greatest effect on trip durations, contrary to hypothesis 1. A clumped distribution of tree cover was associated with shorter trip durations more so than low tree cover abundance. As long as tree cover was dispersed, the agent had a greater likelihood of encountering shade and not having to return to water for wetting, even if tree cover itself was scarce.

Differences in tree cover characteristics were also associated with differences in trip durations and home range size in both low and high-water landscapes, although these differences were more pronounced overall in low-water landscapes, partially supporting hypothesis 4. Additionally, model results partially supported hypothesis 6: variation in trip duration and home range size among low and high-water landscapes with differences in tree cover characteristics was driven by differences in time spent wetting. Within the model, agents utilized close cells containing tree cover when a water source was not within their search radius. When tree cover was high in abundance and dispersed in distribution, there was a greater likelihood that herbivore agents encountered and used shade within their search radius rather than potentially having to travel back to a water source for wetting. High abundances and dispersed distributions of tree cover therefore altered spatial use by lessening the reliance of water-dependent herbivore agents on water sources for thermoregulation and allowing them to remain away from water for longer (increased trip duration) and to range over larger areas (increased home range size). In contrast, low and clumped tree cover effectively "tethered" simulated agents to water points, leading to frequent trips to water (decreased trip duration), and home ranges

centered on water sources (decreased home range size). These results corroborate observations made in natural systems. For instance, manipulating the placement of shade relative to water sources can "maximize range use" and lead to more uniform forage use across the landscape as cattle are able to move away from water (McIlvain & Shoop, 1971, Hunt et al., 2007). Manning et al., (2006, 2009), particularly highlight the potential role of dispersed/scattered trees in 'de-fragmenting' landscapes by facilitating "gradual boundary transitions" and increasing 'useable' habitat areas (Manning et al., 2006; Manning et al., 2009).

Differences in foraging efficiency due to differences in tree cover characteristics were also present and just as pronounced in high-water landscapes, rejecting hypothesis 5. The results of our model suggest that tree cover characteristics drive differences in foraging efficiency by influencing distances traveled more than forage consumption, rejecting hypothesis 7. High abundances and dispersed distributions of tree cover led to increases in foraging efficiency driven by decreases in distances traveled, while low abundances and clumped distributions of tree cover led to decreases in foraging efficiency driven by increases in distances traveled. The time spent wetting and drinking increased as shade resources became less readily available, and agents relied on water to respond to thermal stress. In low-water landscapes, low and clumped tree cover also prompted frequent returns to water when shade was too far for agents to easily reach, and this may have contributed to greater increases in distances traveled compared to high-water landscapes.

To our knowledge, the influence of shade availability and distribution on distances traveled by water-dependent herbivores remains largely unexplored but results from the model indicate that the presence of shade away from water prevents herbivores from making frequent, short trips to water to employ behavioral thermoregulation. Rozen-Rechels et al., (2020) suggested such a role for tree cover in their study exploring the effects of temperature on the onset and duration of elephant foraging trips. The authors posited that shade may potentially act as a heat "buffer" and allows elephants to avoid thermal stress as they make their way back to water (Rozen-Rechels et al., 2020). Frank et al., (2012) also found that cattle in arid central Australia intensively used woodland when away from water, likely because high temperatures prohibited returns to water sources when cattle were returning from nocturnal grazing grounds (Frank et al., 2012). The results of our model further show that, specifically, dispersed distributions of tree cover are more efficient at increasing the time spent away from water by increasing the probability of being encountered by herbivores and being used as shade, stressing the importance of considering resource configuration (and not just abundance) in influencing animal movement.

### 4.7.4 Clumped forage distributions increased foraging efficiency and decreased home range sizes in low and high-water landscapes

I did not intentionally manipulate the forage abundance of layers to create landscapes with "low" and "high" forage abundances; rather, all of the forage layers had similar and relatively high abundances of food at the beginning of the simulations. There were two reasons for this. First, I was more interested in exploring the influence of water and tree cover characteristics on movement and foraging efficiency and found it sufficient to include differences in forage distribution as representing differences in forage characteristics among landscapes. Second, in keeping the forage abundances similar among landscapes, I was able to use the same simple optimal foraging rule to simulate the foraging of agents in both dispersed and clumped forage landscapes. This is because when food is not scarce, as in our forage layers, individuals should easily encounter food resources and thus the foraging strategy used should not be as consequential as when food is not as readily available (Gross et al., 1995). Thus, I did not expect that differences in forage distribution would lead to great differences in movement patterns and foraging efficiency for simulated herbivores. Contrary to my expectations, forage distribution had effects on foraging efficiency and home range size in both low and high-water landscapes that were comparable in magnitude to the effects of tree cover characteristics.

Effects of forage distribution on foraging efficiency were due mainly to effects on distances traveled, as herbivores in landscapes with clumped forage distributions traveled smaller distances than herbivores in landscapes with dispersed forage distributions. In natural systems, herbivores can achieve greater foraging efficiency when forage resources are clumped by using an area-restricted searching strategy, increasing the frequency of turns and decreasing step lengths in order to remain in profitable areas (Benhamou, 1992; De Knegt et al., 2007). While I did not explicitly simulate changes in turning angles when forage biomass within the search radius increased or decreased, I did allow the agents to "rank" the cells within the search radius by their forage level and distance to the agent. Cells with higher forage biomass closer to the agent would have a higher likelihood of being selected. When forage was clumped in distribution, cells with high forage levels were closer to each other compared to when forage was dispersed in distribution, and consequently, there was a higher likelihood of agents not having to travel as far to reach a suitable cell for foraging. Forage biomass also continuously decreased as the simulation progressed to reflect vegetation die-off in the dry season. By

the end of a simulation, clumped forage landscapes were characterized by a few large patches of cells with no forage biomass, while dispersed forage landscapes exhibited thousands of very small patches of cells with no forage dispersed with cells of higher forage (Figure 4.12 A). As time progressed, cells with higher "ranks" generally remained close together in clumped forage landscapes, whereas in dispersed forage landscapes, cells with higher "ranks" were farther from the agent as cells with no forage were more widely distributed (Figure 4.12 B). I found a general pattern that corroborated the observations made in Figure 4.13 B: when forage is dispersed, the average distance between highly ranked cells and the agent slightly increases as time progresses, correlating with a slight increase in distances traveled by the agent. When forage is clumped, the distances traveled by the agent and the average distance between the highly ranked search radius cells and the agent remain relatively constant through time (Figure 4.13).

This explains why increased foraging efficiency in clumped forage landscapes was associated with smaller total distance traveled throughout entire simulations compared to dispersed forage landscapes. This may also explain why dispersed forage distributions were associated with larger home ranges. As forage biomass within the landscapes decrease through time, the agent makes greater movements, and extends its range. African buffalo have been found to increase their home ranges when forage levels decrease over time (Ryan et al., 2006).

Even though I made an effort to keep the forage abundances of each landscape similar, the inclusion of piospheres within the model led to high-water landscapes with slightly less forage than low-water landscapes, and dispersed forage landscapes with slightly less forage than clumped forage landscapes (see Figure B.1 in the Appendix). While the differences in mean forage abundance between low and high-water and clumped and dispersed forage landscapes were not great, I was aware that this might cause agents in high-water and dispersed forage landscapes to consume less forage than agents in low-water and clumped forage landscapes, which would call into question validity of the results. This was not the case, however, as agents in high-water landscapes consumed more forage than agents in low-water landscapes, and there was a less than 1% difference in forage consumption between agents in dispersed forage and clumped forage landscapes.

#### 4.7.5 Management implications and implications on herbivore fitness

The results of the ABM point to water source density having the greatest effect on the spatial use of water-dependent herbivores when forage availability is not necessarily limited, which has implications for the usefulness of water provisioning strategies in managing herbivore distributions (Chamaillé -Jammes et al., 2007a; Smit et al., 2007). Switching from low to high water source density resulted in a 120% increase in the home range size of agents, suggesting that the manipulation of surface water availability influences the home range size of herbivores. Our results thus corroborate those of other empirical and theoretical studies suggesting that water provision allows herbivores to expand their range and utilize areas that may have not been available to them had water been scarce (Redfern et al., 2005; Purdon & van Aarde 2017; Loarie et al., 2009a). Switching from low to high water source density also resulted in increased foraging efficiencies driven by agents traveling smaller total distances and consuming more forage. An increase in the range of individuals due to water provisioning can eventually

lead to increased foraging impact across the landscape (Purdon & van Aarde, 2017a; Smit et al., 2007), and greater forage depletion overall (Owen-Smith, 1996; Valls-fox et al., 2018). Consequently, herbivore populations may experience starvation-induced mortality during droughts when forage is already scarce (Walker et al., 1987). Thus, while increased waterhole abundance may be associated with increases in foraging efficiency (and individual fitness) in the short-term, the longer-term consequences on populations may not be as positive.

Differences in tree cover characteristics were associated with differences in movement, including distances traveled, trip duration, and home range size, and activity budgets. These differences were, in general, more pronounced in low water compared to highwater landscapes, but nonetheless suggest that shade may also play a role in altering herbivore spatial use and behavior. Specifically, our model results indicate that tree cover loss or changes in the distribution of tree cover such that tree cover occurs in clumps may decrease home range size and cause herbivores to spend more time employing wetting behavior. Consequently, the central place effects of water sources may be amplified, particularly when water is already scarce. This has implications for future effects of tree cover changes on the spatial use of water-dependent herbivores in African savannas, where land-use change has been identified as a threat to tree cover persistence (Aleman et al., 2016). For example, the resulting landscape fragmentation from land-use change has been associated with decreases in wooded areas in Zimbabwe (Kamusoko & Aniya, 2007). Additionally, our results emphasize the need to explicitly include thermal cover in spatially-explicit models of foraging and movement, an uncommon yet important practice for adequate conservation planning of water-dependent herbivores sensitive to high temperatures (Elmore et al., 2017).

Foraging efficiency is a determinant of individual fitness (Bailey et al., 1996; Hainsworth, 1974; Nagaoka, 2002), influencing body condition and size (Belovsky, 1978; Giles et al., 2020), and reproductive success (White, 1983). Our results showed that variation in foraging efficiency among agents in different landscapes was influenced by differences in water and shade abundance and distribution. High environmental temperatures drive herbivores to use behavioral thermoregulation to avoid hyperthermia and thermal discomfort (Cunningham et al., 2021; Hall et al., 2016; Plessis et al., 2012). Several studies have documented the link between high environmental temperatures and lower foraging efficiency for endotherms, including birds (Van de ven et al., 2019; Plessis et al., 2012), and wild pigs (Choquenot & Ruscoe, 2003). Lower foraging efficiency is usually attributed to missed opportunity costs related to decreased forage consumption due to the increased employment of thermoregulatory behaviors when temperatures are high (Cunningham et al., 2015; Hetem et al., 2012). Our results point to a different way in which the employment of behavioral thermoregulation may decrease foraging efficiency. Depending on the spatial characteristics of shade, foraging efficiency in our model was reduced due to increases in distances traveled. This was true even in landscapes where water sources were high in abundance, and where one would expect that differences in shade would not influence distances traveled due to the abundance of water.

In landscapes where the availability of tree cover was low and clumped, agents primarily used water sources for behavioral thermoregulation and continuously returned to water for wetting. These continual returns to water by the agent contributed to the greater distances traveled and subsequent lower foraging efficiencies, suggesting that the energetic costs of behavioral thermoregulation increase when shade is not as available, and individuals must move more to access it. At least two studies have documented herbivores spending more time at water sources when shade was scarce or not available (Mader et al., 1997; Schütz et al., 2010); however, whether distances traveled were influenced by the scarcity of shade remains to be further tested. Nonetheless, it is apparent that tree cover plays a critical role in influencing foraging efficiency, even when the availability of surface water is high.

#### Concluding thoughts

In this chapter, I used an ABM developed for elephant movement to explore how spatial variation in critical resource distribution can lead to spatial differences in grazer movement and foraging efficiency. I found that spatial differences in water source density, tree cover characteristics, and forage distribution led to differences in home range size, activity budgets, trip durations, and foraging efficiency among simulated herbivores in different artificial landscapes.

#### **CHAPTER 5**

#### **Conclusions and future directions**

#### 5.1 Thesis overview

The first objective of this thesis was to identify spatiotemporal patterns emerging from movement data of elephants in southern Africa. In Chapter 2, I discussed the utility of pattern-oriented modeling in guiding the testing and validation of ABMs, introduced some common movement characteristics, and summarized each movement characteristic as it related to elephant movement and patterns found in the literature. I identified twelve patterns highlighting differences in spatial use between wet and dry seasons and between the two parks and discussed potential factors shaping those patterns.

In Chapter 3, I developed a spatially-explicit ABM to simulate the movement and spatial use of elephants in CNP and KNP. I linked the internal and external drivers of elephant movement through hierarchical behavior-based movement rules where the higher priorities were to respond behaviorally to ambient temperature and the need to drink water, and foraging became an option once those needs were met. The same movement characteristics calculated in Chapter 2, along with activity budgets, were allowed to emerge from the conditions experienced by the ABM agent. Simulated and empirical home range sizes differed statistically between parks and between seasons; however, the direction of the seasonal and park effects generally matched between simulated and empirical home range sizes.

The ABM was also successful at reproducing some differences in diel displacement distances and net daily displacement distances between seasons, particularly for KNP,

99

and in maximum distances traveled from a permanent water source. The temporal patterns of movement of the elephant agents were also similar to those observed in real elephants. I also conducted a sensitivity analysis and identified the parameter changes that had the greatest influence on model outputs. Movement characteristics were most sensitive to : 1) increases in the probability of employing 'drinking' behavior at any given time since the agent last visited a water source, 2) increases and decreases in the parameters determining the turning angles when the agent foraged, and 3) decreases in the temperature threshold for employing behavioral thermoregulation. Finally, I discussed some potential reasons for discrepancies between the model outputs and the empirical data.

In Chapter 4, I used the ABM developed for elephants in Chapter 3 to explore how spatial differences in critical resources translate into differences in spatial use and foraging efficiency of water-dependent herbivores in the limiting dry season. I created 16 artificial landscapes to capture spatial differences in forage, water, and tree cover using a full factorial approach, and allowed movement characteristics and foraging efficiencies to emerge from interactions between the simulated grazer and the landscape. I calculated foraging efficiency and movement characteristics such as home range size and foraging trip duration, as well as activity budgets, for each trajectory. Model results were corroborated by those from empirical studies stressing the importance of surface water availability in influencing spatial use patterns and foraging efficiency for waterdependent herbivores within savannas. Additionally, model results pointed to a role for tree cover influencing movement and foraging efficiency regardless of water source density throughout the landscape. 5.2 Forage abundance and social interactions: fitting in the missing pieces to understanding spatial variation in movement and foraging efficiency of large herbivores

I recognized that a vast majority of studies exploring movement in relation to resource variation have focused on the influence of forage abundance/availability, and so I focused on exploring the influence of water and tree cover on the spatial variation of large herbivore movement for this dissertation. As a result, I did not include landscapes with "low" and "high" forage abundance, but only simulated decreases in forage abundance as a simulation progressed. However, to further gain a more complete understanding of how movement varies through space, spatial differences in forage abundance must be incorporated into the model along with spatial differences in tree cover and water characteristics. In the model, forage abundance was kept constant from one artificial landscape to the next and was not necessarily limited (except within piospheres). Forage abundance in real-world savannas, however, is linked to rainfall (Zhang et al., 2021) and is a limiting resource in landscapes with lower annual rainfall (Redfern et al., 2003). Realistically, as herbivores in dryer savannas also experience lower forage abundances, simulated agents in landscapes with low water source densities should have also experienced lower forage abundances. Forage abundance interacts with surface water availability to drive movement, and for many large herbivores, limited forage availability in conjunction with scarce surface water availability translates to larger home ranges and greater movement as herbivores must travel greater distances to obtain both critical resources (Owen-Smith 2013; Ryan et al., 2006; Young et al., 2009). The link between foraging efficiency, movement, including distances traveled, trip duration, and home

101

range size, and activity budgets, will likely change when forage abundance is incorporated into the model.

In addition to incorporating differences in forage abundance into the model, simulating multiple agents would add another layer of biological realism to the model. Previous studies have revealed the impact of social factors on the movement characteristics of large herbivores, including wildebeest (Mduma et al., 1999), buffalo (Sinclair 1974; Spaan et al., 2018), and elephants (Wittemyer et al., 2007; Wittemyer et al., 2008). The ABM does not currently simulate the movement of more than one agent, and thus spatial use patterns produced by the model cannot reflect the influence of socioecological factors, including socioecological factors into the model would be most important for simulating movement where resources are the most limiting, such as in areas where forage or water are scarce. The most straightforward way to include social interactions in the model is to first simulate the movement of more than one agent. Simulating the behavior and movement of multiple agents may result in outcomes different than those of the current ABM.

First, crowding may drive dispersal movement if resources become limited (Matthysen, 2005). Crowding is likely to occur around water points if surface water availability is scarce and increases in grazing and trampling near the vicinity of water may lead to more intense piosphere effects (Valeix et al., 2007; Chamaillé -James et al., 2008). Conceptually, foraging pressure from multiple agents would most likely lead to depletion of food resources around water sources, and agents would then alter their movement in response to decreases in local food availability. Consequently, a low abundance of water

may lead to increases in home range size (rather than decreases as produced by the ABM) compared to landscapes with high water source densities. Simulating the movement of multiple agents through time may thus alter the relationship between water source density, movement, activity budgets, and foraging efficiency depicted by the model. Second, increases in population density may induce negative density-dependent habitat selection (Avgar & Betini, 2020; Morris, 1988; van Beest et al., 2014), where individuals become less selective in the habitats they use due to increased competition. Elephants, for example, have been observed to exhibit density-dependent habitat selection, likely as a response to resource competition. At lower densities, elephants in KNP selected for high woody cover; however, as densities increased, selection for high woody cover weakened, suggesting that elephants were "forced" to utilize areas of lower woody cover at higher densities. Similarly, MacFayden et al., (2018) found that bull and female elephants in KNP have been moving into any available spaces within the park and becoming less segregated, a response to an increasing population. Due to increased population density, waterbuck in Mozambique's Gorongoza National Park expanded their selection of habitat to include poorer-quality savannas, rather than solely select for higher-quality floodplains (Becker et al., 2021). Density-dependent habitat selection may impact foraging efficiency if individuals spend more time traveling to resources or if areas with less preferred resources lead to decreased forage consumption. Within the current model, the rules dictating the agent's behavior reflect potential decision-making processes in which it selects for the highest quality resources available on the landscape. It is therefore not currently possible to allow density-dependent habitat selection. However, modifying the cell selection rules so that agents can select lower quality resources (e.g., cells with low

forage biomass) would allow for exploration of whether and how density-dependent habitat selection alters the relationship between resource availabilities, movement, and foraging efficiency.

## 5.3 Limitations of using remote sensing products when modeling elephant movement

#### 5.3.1 Foraging and EVI

Within the ABM developed in Chapter 3, foraging movements were driven by the EVI values underlying the landscape cells. EVI is a remotely sense vegetation index measuring the overall "greenness" underlying a cell and has been used extensively to represent vegetation quality and quantity for a given area. For example, at larger scales (250 m and 500 m), elephants do prefer areas with greener than average vegetation (Loarie et al., 2009b), suggesting that "greenness" indicates "nutritionally superior" vegetation at such scales.

Grass growth rate is more closely linked to rainfall than the growth rate of woody plants (Archibald & Scholes, 2007). Consequently, many woody species generally remain green for a longer period of time than do grasses when surface water availability decreases in the dry season. At this time, grasses begin to senesce and browse contains a much higher concentration of protein (O'Connor et al., 2007), and elephants' diet consists primarily of the relatively higher quality browse during the dry season. I thus assumed that the "greenness" underlying a pixel during the dry season was most likely due to the presence of browse, and because elephants primarily consume browse during the dry season, I also

assumed that the "greenness" underlying a cell was directly positively associated with the likelihood that elephants would select the cell for foraging.

There is one problem with making the sweeping assumption that elephants will select cells with higher greenness during the dry season. Elephants do not feed on all woody species equally. Some woody species produce secondary metabolites, chemical compounds that inhibit digestion or are toxic to herbivores when consumed (Jachmann, 1989; Owen-Smith & Chafota, 2012). A study has found that the presence of secondary metabolites in vegetation, including tannins and other phenolics, deters elephants (Holdo, 2003) and thus may influence forage selection. In Chobe National Park, for example, elephants did not consume the leaves of *Combretum* spp., woody species with high contents of polyphenols (Owen-Smith & Chafota, 2012). In South Africa's Ithala Game Reserve, elephants preferred woody plant species with high nutritional quality in relation to their concentration of tannins, rather than outright avoiding species with secondary metabolites (Shrader et al., 2012a). Recently, Shmitt et al., (2020) found that elephants avoided plants that emitted high levels of volatile secondary metabolites, including monoterpenes, a compound that may be more toxic to herbivores than tannins (Schmitt et al., 2020). If woody species in CNP and KNP produced unpalatable secondary metabolites yet contributed to the "greenness" of a cell, model agents were likely to select the cell when they should have avoided it.

For our agents to make more realistic decisions when selecting cells for foraging, a raster representing palatability associated with the concentration of secondary metabolites of species could be included. Cell selection could then involve identifying cells with high greenness that are also palatable. This would be difficult as there is incomplete

knowledge of the palatability and secondary metabolite concentrations of every single vegetation type in CNP and KNP during the wet and dry season.

It is worth considering that that there may be other satellite-based indicators better suited to drive fine-scale foraging of elephant movement compared to EVI within the model. These indicators include alternative vegetation indices less widely used in ecological studies, like leaf area index (LAI) and fraction of photosynthetically active radiation (FPAR). The concentration of nitrogen present in vegetation is associated with the quality of forage. Some indices, including EVI and NDVI, saturate at high levels of greenness and are thus not well-suited to capturing small changes in the nitrogen concentration of foliage (Ramoelo et al., 2011; Ramoelo et al., 2018). Even though FPAR is correlated with NDVI and EVI, it better predicts dry forage and herbaceous biomass (Tsalyuk et al., 2019), particularly in dry vegetation (Tsalyuk et al., 2015) as NDVI may not capture the little photosynthetic activity of dry vegetation. Studies have also incorporated other spectral bands when estimating foliar and canopy nitrogen concentration. Ramoelo et al., (2012) integrated the red-edge bands of the Rapideye sensor into traditional vegetation indices to map foliar and canopy nitrogen of KNP and surrounding areas. The authors found that the indices using the red-edge band had greater accuracy in estimating foliage nitrogen compared to indices computed without the red-edge band.

#### 5.3.2 Foraging and changes in greenness

Herbivores frequently change their movement patterns in response to spatiotemporal changes in their environments, in particular, to changes in forage resources (Merkle et al., 2016; Van Moorter et al., 2013). Studies using NDVI, a vegetation index similar to EVI, as a proxy for forage quality and quantity have shown that elephants respond to changes in vegetation greenness at different scales. Bohrer et al., (2014) found that elephants in Kenya responded to changes in NDVI, measured at 16-day intervals, by altering their movement patterns such that they "tracked" the phenological changes in vegetation (Bohrer et al., 2014). When there was a flush of vegetation in the lower regions of Mt. Marsabit, elephants increased their speed to reach those areas.

It was thus important to somehow reproduce these changes within our model to accurately model influences on elephant movement. To accomplish this, I first had to determine the extent of "greenness change" that occurred during the time span of the trajectories I used. I decided to calculate the percentage of landscape cells that increased in greenness from the beginning of a trajectory to the end of a trajectory, as a measure of greenness change (throughout a 14-day span). I assumed that a lower percent of landscape cells would increase in greenness during the dry season, compared to the wet season, as lower rainfall causes much of the vegetation to senesce. I created a raster corresponding to initial EVI conditions in the landscape at the time of each empirical trajectory from Landsat 8 Operation Land Imager (OLI) images (U.S. Geological Survey, 2016) by merging tiles with similar acquisition dates in order to cover the entirety of the model landscapes. To determine the percentage of the landscape that increased in greenness during a 16-day period for each month in the wet and dry seasons, I utilized a time-series of 16-day Moderate Resolution Imaging Spectroradiometer (MODIS 13Q1 product) EVI datasets for the years 2012-2014, which achieves cloud-free coverage by selecting the higher quality, cloud-free pixels during the time period. I then used the calculated percentage of the landscape that increased in greenness during a 16day period to determine the number of cells that would have to increase in EVI every

time step to reflect the percentage by the end of a simulation. The greenness level of any cell thus changed throughout the simulation period by a small amount, reflecting the vegetation changes that occurred throughout the wet and dry seasons.

There were three potential caveats associated with the way that I calculated changes in greenness and represented this change within the model. First, I used remote sensing imagery of courser resolution than the rasters used within the model to calculate percent change in greenness. Landsat 8 Operation Land Imager (OLI) images have a resolution of 30 m, which corresponds to the resolution of our landscape rasters. Ideally, I would have used Landsat OLI images to calculate greenness change through time rather than using MODIS 13Q1 images, which have a courser resolution of approximately 250 m. However, much of the wet-season Landsat images were riddled with cloud cover and change estimates would not have been accurate. Thus, I applied the greenness change estimates derived from MODIS images to initial Landsat EVI images/rasters in the model. Whether MODIS-derived greenness change can be scaled down to the resolution of Landsat images is beyond the scope of the dissertation. Obtaining cloud-free wet season Landsat imagery would be the most straightforward solution. Cloud and cloudshadow removal techniques, such as using auxiliary data as reference images, would potentially make this possible (Cao et al., 2020).

Second, I used one EVI raster to represent initial EVI conditions for the wet season. Ideally, I would have also utilized one raster corresponding to initial EVI conditions at the beginning of each simulated trajectory; however, cloud cover made this impossible to achieve for the wet season months in both parks. Consequently, I selected one raster with minimal cloud cover to represent initial EVI conditions for all wet season simulations in

each respective park. Obtaining cloud cover-free rasters representing initial EVI conditions for the dry season was more feasible, and I utilized a separate raster representing initial EVI conditions for most months in the dry season for both parks. Finally, when updating the greenness of landscape cells for each time step, I increased the EVI of random cells throughout the landscape. This is not consistent with real-world savannas, where there is variability in the phenology of vegetation and changes in greenness do not occur in a spatially random manner. For example, Whitecross et al., (2016) found that, during the dry season, T. sericea trees "green[ed]-up" faster than Burkea africana trees (Whitecross et al., 2017). One way to solve this problem within a GIS is to overlay a shapefile layer of vegetation type with MODIS 13Q1 imagery, calculate changes in greenness for each cell, and determine whether these changes are overrepresented in one vegetation type or another. The shapefile layer can then be rasterized and used as input within the model so that the EVI of cells with underlying vegetation types undergoing greater changes in greenness is updated over the EVI of other cells.

#### 5.3.3 Shade use and tree cover datasets

I assumed elephant agents seeking shade would select cells with higher values of tree cover and greenness, as higher values of tree cover reflect greater shade availability for elephants. This simulated behavior was meant to mirror the behavior of real-world elephants, which have also been found to select areas with high tree cover (Harris et al., 2008; Hoare, 1999; Kinahan et al., 2007; Roever et al., 2012). I used (Hansen et al., 2013) Global Forest Change's tree cover dataset to represent percent tree cover underlying each cell, in which tree cover was defined as canopy closure for vegetation

taller than five meters. Tree cover is generally estimated for the wet season; however, I used the same dataset to represent percent tree cover for both the wet season and the dry season. Many savanna tree species used by elephants for shade, including *Terminalia sericea* and *Combretum apiculatum*, lose their leaves during the dry season (February & Higgins, 2016), and as such, wet season tree cover estimates may not provide an accurate representation of shade availability for elephants during the dry season. I assumed that, even when trees lack leaves, it is possible that their branches can still provide shade during the hot dry season. Thus, if a higher tree cover percentage underlying a landscape cell (as defined by the data set) provides greater amounts of shade to elephants compared to a lower tree cover should have more branches and provide a greater amount of shade than a cell with a lower tree cover percentage, during the dry season. Nonetheless, remotely sensed dry season estimates of tree cover for savannas would be ideal for representing shade availability for elephants during the dry season.

#### 5.4 Potential model applications

In this dissertation, application of the ABM developed for elephant spatial use in Chapter 3 was limited to that of Chapter 4, where the model was extended to explore how differences in critical resource distributions influenced the movement and foraging efficiency of water-dependent herbivores. There is potential, however, to extend the application of the model to explore how scenarios of environmental change might influence savanna herbivores spatial use. Below I discuss two such potential applications.

#### 5.4.1 Predicting responses to climate change

Climate change across southern Africa entails future changes in temperature and precipitation regimes, attributed mainly to increasing carbon dioxide levels (Solomon et al., 2009). Over the last century alone, southern Africa has experienced temperature increases of over 0.5 degrees Celsius (Kandji et al., 2006). In the near future, much of Africa, including Botswana, is expected to experience warming temperatures in all emissions scenarios (compared to 1980-1999) (Christensen, 2007). For parts of southern Africa, drying of large regions associated with decreased rainfall reflects changes in precipitation regimes. El Niño-related extreme climatic events, such as intense droughts are expected to contribute to the drying of the southern African region in the future (Kandji et al., 2006).

Elevated levels of CO<sub>2</sub> and changes in rainfall have implications for the tree cover-grass dynamics that characterize savanna ecosystems. Several studies acknowledge that rainfall is a limiting factor for woody cover in dryer savannas (Sankaran et al., 2005), whereas increases in CO<sub>2</sub> favor thickening of woody cover in savannas by promoting increases in tree growth rates (Bond & Midgley, 2012). Predicting how climate change will influence spatial changes in grass-tree dynamics is difficult because of the confounding effects of disturbance regimes, namely fire and herbivory (Buitenwerf et al, 2012; Sankaran et al., 2005). Global climate change is predicted to bring about increased fires to southern Africa, which act to decrease the number of trees reaching larger size classes (Scheiter & Higgins, 2009; Strydom & Savage, 2016). Similarly, herbivory by large megafauna can have negative impacts on trees (Mosugelo et al., 2002). As such, while future increases in CO<sub>2</sub> and changes in rainfall may promote increases or decreases in woody cover, the extent of this change is modulated by the impact of fire and herbivory which act to suppress woody encroachment in most savannas.

Environmental temperature, tree cover, and surface water availability all influence the spatial use of many savanna herbivores (Kinahan et al., 2007; Mole et al., 2016; Roever et al., 2012). Consequently, it is likely that increasing temperatures, shifts in tree covergrass proportions, and the increasing dryness of many of Africa's savannas, all of which are associated with future climate change, have the potential to influence future movement patterns of elephants. Utilizing the ABM described in Chapter 3, it is possible to explore the following question: How might potential landscape changes associated with future global climate change influence herbivore movement patterns and space use?

Changes in the landscape that will potentially occur under future scenarios of climate change can be represented through artificial landscapes. The International Panel on Climate Change (IPCC) regularly reports scenarios associated with possible futures shaped by different greenhouse emission rates. Several studies have used these scenarios to explore the responses of species to changes in environmental variables associated with global climate change, including changes in temperature and surface water availability. For example, Mpakairi et al., (2020) explored changes in suitable habitat for elephants in response to the most extreme scenario projected for 2050, which included increased temperatures and decreased surface water availability. The IPCC scenarios can thus be used to build artificial landscapes and environments reflecting the environments that each scenario predicts. Increases in temperature representing "optimistic" scenarios, intermediate scenarios, and the "pessimistic" scenarios can be simulated from current

112

daily temperatures obtained from meteorological data. Increases and decreases to tree cover can be achieved by increasing or decreasing current tree cover spatial layers. Decreases in precipitation can be reflected as two degrees of water source desiccation: 1) complete desiccation (removal of all seasonal pans and ephemeral rivers from water source spatial layers, leaving the artificial water holes and permanent rivers), and 2) partial desiccation (removal of ephemeral rivers from water source spatial layers, leaving artificial water holes, seasonal pans, and permanent rivers). Naturally, changes in precipitation will also lead to changes in landscape greenness, in which areas that experience decreases in precipitation may experience decreases in greenness.

Finally, a full factorial combination of changes in 1) temperature, 2) tree cover, 3) water availability, and 4) greenness can be implemented within the ABM. Outputs for all simulations can be compared to outputs from simulations run on current environmental conditions.

#### 5.4.2 Predicting responses to water point closure

In many national parks and reserves across southern Africa, surface water is supplemented by artificial water sources, which circumvents the detrimental effects of water shortage during the dry season (Epaphras et al., 2008). Several studies have revealed that artificial water holes influence herbivore distribution and subsequent densities, and well as dry season ranging extent (Chamaillé-Jammes et al., 2007b; Loarie et al., 2009a). Provisioning supplementary water supply for herbivore populations during the dry season also has several drawbacks, such as the increase in the transformation of vegetation cover in the areas surrounding water points (Chamaillé-Jammes et al., 2007a; Gandiwa et al., 2012). In KNP, the abundance of artificial water points increased to approximately 300 units, and then decreased (Brits et al., 2002; Redfern et al., 2003). Because of the high density of artificial water points, most of KNP's area is within a few kilometers of water (Redfern et al., 2003). Managing surface water availability by manipulating the abundance of artificial water points has been previously proposed as a method to manage the distribution of herbivores (Owen-Smith et al., 2006), and possibly avoid increased herbivore-induced negative impacts. Owen-Smith et al., (2006) acknowledged that the spacing and position of water points relative to other water points (artificial and natural) is just as important for managing herbivore distributions as the abundance of water points in an area (Owen-Smith, 1996).

Because surface water availability is a key determinant of spatial use in savannas, altering the number and spatial distribution of artificial water points may influence the movement patterns and spatial distribution of populations in large areas, such as KNP. Utilizing the ABM described in Chapter 3, it is possible to explore the following question: How might water point closure influence savanna herbivore movement patterns and spatial use?

Virtually "closing" water points can be achieved by removing points representing artificial water holes in a spatial layer within a GIS during the wet and dry season in KNP. Model outputs of interest would include movement characteristics and activity budgets, and outputs of two sets of simulations representing the wet and dry season can be compared to baseline simulations where the distribution of artificial water sources remains at the present distribution. The two sets of simulations would represent the following conditions: 1. During the wet season, when all natural water sources are expected to be filled.

2. During the dry season, when it is assumed that ephemeral rivers have desiccated, and the only permanent sources of water are the open artificial water holes and main rivers. Model results would shed light on how reduced surface water availability would differentially affect herbivore spatial use in the wet and dry season.

#### **5.5 Future directions**

Below I briefly discuss future directions. I relate the first specifically to modeling elephant movement and spatial use. The second applies to large herbivores in general.

#### 5.4.1 Testing and validating the ABM for other protected areas

Even though I tested and validated the ABM for elephants in two protected areas differing in the spatiotemporal characteristics and patterns of critical resources and temperature, I would have ideally selected a third area for validation where elephants experience much different environmental conditions than elephants in KNP and CNP. This would further test whether the model can be applied to elephant populations inhabiting a wide range of environments and spatial context.

For example, Etosha National Park in Namibia has a lower 20-year mean annal rainfall than both KNP and CNP (Shrader et al., 2010), and thus, elephants may contend with more limited water and food availabilities in this area compared to elephants in CNP and KNP. Elephants in the very arid Namib dessert experience even less rainfall. Indeed, the home ranges of elephants in these regions are considerably larger than the home ranges of elephants in other regions (Viljoen, 1989), suggesting that the spatial distribution and availability of resources differs considerably from that in CNP and KNP. I understand that there is often insufficient empirical data to compare ABM outputs with data from multiple populations in different conditions, but when the opportunity arises and such data is available, it is imperative to do so in order to ascertain the structural realism of the model and its domain of applicability. Perhaps more importantly, validating the model with data on populations from different geographical locations would shed light on whether the model should be utilized to make predictions to new scenarios. Testing and validating the model for elephants in more arid (or even wetter) areas would further increase confidence in the model's ability to capture the mechanisms of movement.

# 5.4.4 Combining movement models with energy budgets to explore the influence of movement on population dynamics

For this dissertation, I was primarily interested in assessing the utility of a resource-based ABM in reproducing elephant movement patterns, and in exploring hypotheses related to the influence of organism-resource interactions on movement and foraging efficiency. Many movement ABMs simulating more than one agent and with temporal extents longer than two weeks take a step further and track energy intake and expenditure through the duration of the simulation to explore how responses to fluctuations in food availability influence population dynamics.

To keep track of how energy is used and allocated by agents, ABMs model energy budgets, generally assuming that animals use the energy gained through foraging for (in order of priority when there is enough energy intake) maintenance, growth, and reproduction or storage (Sibly & Calow 1986; Karasov & Martinez del Rio 2007; Sibly et al., 2013). Sibly et al., (2013) proposed that allocating food for maintenance is a priority when forage resources decline, and when forage resources are abundant, excess energy acquired is stored in reserves as fat and carbohydrates (Sibly et al., 2013). Locomotion to reach food resources then represents energy costs.

To incorporate energetics in the ABM, multiple agents with their own energy budgets must first be initialized on the landscape. Agents maintain daily growth rates if energy is sufficient, and those of reproductive age can reproduce and contribute to population growth. Agents with depleted energy reserves die and contribute to population decline. Movement responses to the spatiotemporal characteristics of critical resources are reflected in the energy budgets, and ultimately, demographic rates and population dynamics. For example, agents may respond to dry season decreases in forage by moving long distances between water and foraging areas, which may lead to energy expenditure and death of agent, and potential population decrease if the same occurs to multiple agents.

Model outputs, which can include birth and death rates, and population size, can be compared with empirical data to determine whether the outputs fit observed population dynamics data. A validated model could then be used to explore the effects that changing availabilities and distributions of critical resources, such as decreases in surface water availability and forage, may have on spatial use and subsequent population distribution and density (Nathan et al., 2006).

#### 5.6 Concluding remarks

Fine-scale data on the location of individual animals combined with statistical models facilitate the understanding of movement patterns and spatial use for many wildlife species (Hooten & Johnson, 2017; Langrock & Patterson, 2016; Leos-barajas et al., 2017; Moorcroft, 2012; Patterson et al., 2008; Semeniuk et al., 2011). In the face of a changing environment, there is impetus to shift focus to developing models to simulate realistic animal movement to make predictions and to provide a greater conceptual understanding of animal movement.

The strength of the ABM approach in simulating animal movement lies in its flexibility. There is no limit to the number of factors influencing the movement process that can be incorporated into an ABM, and there are countless ways to represent how external and internal information is integrated into the decision-making process that drives movement. In this dissertation, I have shown that agent-based modeling is a powerful alternative to traditional movement simulation techniques by developing a resource-driven model with simple, hierarchical behavior-based rules that is capable of simulating realistic movement of elephants. By identifying seasonal and intraspecific differences in movement patterns of elephants from different geographical locations, I have illustrated the importance of identifying multiple patterns to validate model outputs and to gain confidence about the model's structural realism (Grimm & Railsback 2012).

The fitness-related rules governing decision-making in the ABM reflect how large herbivores in general modify their decisions and adjust their behaviors in response to both biotic and abiotic factors. Consequently, I was able to use the model to shed light into the processes underlying differences in spatial use patterns and foraging efficiency of

### Figures



**Figure 2.1:** Cartogram depicting wet and dry season water sources for one of our study areas in northern Botswana, including CNP and surrounding protected areas. The gray outline represents the specific areas included in the model.



**Figure 2.2:** Cartogram depicting wet and dry season water sources for one of our study areas in South Africa, KNP.



**.Figure 2.3:** 95% contour isopleths of utilization distributions (home ranges) for CNP's wet season (dark green), and CNP's dry season (yellow green) determined by dynamic Brownian Bridge movement models. The utilization distributions for the wet and dry season represent a total of 29 and 16 home ranges, respectively, from four cows
























**Figure 3.4:** Boxplots of A) home range sizes, B) diel displacement distances, C) net daily displacement distances, and D) maximum distances traveled from permanent water calculated for empirical and simulated data (n = 80 trajectories for KNP's wet season, 71 trajectories for KNP's dry season, 29 trajectories

for CNP's wet season, and 16 trajectories for CNP's dry season). Data points corresponding to simulations represent a mean of the data collected over ten runs. The bold horizontal lines indicate medians, the top and bottom edges of the boxes indicate the upper 25<sup>th</sup> and lower 75<sup>th</sup> percentile, respectively. The whiskers indicate the maximum and minimum, and the black dots indicate outliers.



**Figure 4.1:** Forage layers with a clumped forage distribution (left), and a dispersed forage distribution (right). Clumped and dispersed forage landscapes have approximately similar means, sums, and standard deviations, but differ in the range of autocorrelation of cells. Cells with higher vegetation biomass are in white, while cells with lower vegetation biomass are in black.











**Figure 4.6:** Boxplots of total distance traveled calculated for landscapes with clumped forage distributions (left facets), and dispersed forage distributions (right facets), and tree cover characteristics (n=100 simulations for each landscape). The bold horizontal lines indicate median values, the top and bottom edges of the boxes indicate the upper 25th and lower 75th percentile, respectively. Whiskers indicate the maximum and minimum values, and the black dots indicate outliers. Outliers are data outside 1.5 times the interquartile range above and below the upper and lower quartile, respectively



**Figure 4.7:** A) Boxplots of home range sizes calculated for landscapes with clumped forage distributions (left facets), and dispersed forage distributions (right facets), and tree cover characteristics (n=100 simulations for each landscape), for both low and high-water landscapes. The bold horizontal lines indicate median values, the top and bottom edges of the boxes indicate the upper 25th and lower 75th percentile, respectively. Whiskers indicate the maximum and minimum values, and the black dots indicate outliers. Outliers are data outside 1.5 times the interquartile range above and below the upper and lower quartile, respectively. B) Examples of home ranges for simulated trajectories in high water landscapes with clumped forage distributions. C) Examples of home ranges for simulated trajectories in low water landscapes with clumped forage distributions. For both B and C, the blue dots represent water sources, the red polygons represent the 95% isopleths for each home range, and the black lines within the polygons represent the corresponding trajectory.



**Figure 4.8:** Simulated trajectories of an agent in landscapes with low water, clumped forage, low tree cover, and either A) dispersed tree cover, or B) clumped tree cover. Green cells represent the presence of tree cover. Both trajectories converge on one water point, and the color of the path represents the duration of the respective trip. Darker blue paths represent longer trip durations from water. Frequency distributions for both simulated trajectories are depicted in C.



**Figure 4.9:** Boxplots of average time spent foraging per day for landscapes with clumped forage distributions (left facets), and dispersed forage distributions (right facets), and tree cover characteristics (n=100 simulations for each landscape). The bold horizontal lines indicate median values, the top and bottom edges of the boxes indicate the upper 25th and lower 75th percentile, respectively. Whiskers indicate the maximum and minimum values, and the black dots indicate outliers. Outliers are data outside 1.5 times the interquartile range above and below the upper and lower quartile, respectively.



**Figure 4.10:** Boxplots of average time spent in shade per day for landscapes with clumped forage distributions (left facets), and dispersed forage distributions (right facets), and tree cover characteristics (n=100 simulations for each landscape). The bold horizontal lines indicate median values, the top and bottom edges of the boxes indicate the upper 25th and lower 75th percentile, respectively. Whiskers indicate the maximum and minimum values, and the black dots indicate outliers. Outliers are data outside 1.5 times the interquartile range above and below the upper and lower quartile, respectively.









**Figure 4.13:** A) Average distance between high ranked cells in the search radius and the agent, (calculated over a sliding window of 10 data points) through an entire run of only the foraging submodel. B) Moving average of distances traveled, (calculated over a sliding window of 10 data points) through an entire run of only the foraging submodel

## Tables

Home range size
1. Larger home range sizes in the wet season compared to the dry season
2. Larger home range sizes in CNP compared to KNP
Diel displacement distance
3. No difference in diel displacement distances in CNP's wet season compared to CNP's dry season
4. Greater diel displacement distances in KNP's wet season compared to KNP's dry season
5. Greater diel displacement distances in CNP's wet season compared to KNP's wet season
6. Greater diel displacement distances in CNP's dry season compared to KNP's dry season
Net daily displacement distance
8. Greater net daily displacement distances in the wet season compared to the dry season
9. Greater net daily displacement distances in CNP compared to KNP
Maximum distance traveled from a permanent water source
9. Greater distances traveled from permanent water sources in CNP's wet season compared to CNP's dry season
10. Greater distances traveled from permanent water sources in KNP's wet season compared to KNP's dry season
11. Greater distances traveled from permanent water sources in CNP's wet season compared to KNP's wet season
12. No difference in distances traveled from permanent water sources in CNP's dry season compared to KNP's dry season

 Table 2.1: Twelve patterns present in the empirical data.

145

Entity	Variable name	Description	Possible values
Agent	State	Sensitivity to	-0.1 or -0.2
	Denitien (men 1	environmental	
	Position (x and	temperature	
	y)	The agent's position on	
		the landscape	
	T_water		1 – undefined hours
	Deherrien	Amount of time elapsed	
	Benavior	visited a water source	
	Perceived temp	visited a water source	Foraging, drinking,
	<b>r</b>	The behavior the agent is	wetting, shade use
		employing	Ċ,
			Current temperature or
		Temperature the agent	lower
		experiences (due to	
		thermoregulatory	
Cells	Greenness	Indicates the EVI that	0 1
Cells	Greenness	underlies the cell	0 - 1
	Tree cover		
		Indicates the percentage	
	Water	of tree cover that	0 - 100 %
		underlies the cell	
			0 (absent) or 1 (present)
		Indicates whether a	
		water source underlies	
Environment		Current environmental	5 – 44 Celsius
Liiviioiiiieiit	Current_temp	temperature	
	V	1	
	vegetation	Number of cells that	
	change	increase in greenness	5500 – 180000 cells
		every time step	

**Table 3.1**: Variables used within the model, their descriptions, associated entities and possible values

Parameter	Parameter value or parameter range	Supporting references				
Thermoregulatory behavior						
Distance traveled for shade use	Maximum = 30 cells (speed of .9 km/h)	High temperatures influence locomotion and heat storage (Rowe et al., 2013). Elephants will most likely not travel as far to reach shade.				
Coefficient used in logistic equation to determine the probability of thermoregulation	Varies according to the agent's state: State 1: -0.2, or State 2: -0.1 $P_{thermoregulation} = \frac{1}{1 + e^{state(Temp_{current} - Temp_{threshold})}}$	Higher temperatures increase the probability returning to water (Purdon, 2015), and employing wetting and shade use (Mole et al., 2016).Calves may be more susceptible to heat stress (Mumby et al., 2013)				
Degrees by which perceived temperature is lowered after wetting or shade use	Wetting: 10 degrees lower than actual temperature Shade use: 3 degrees lower than actual temperature	Elephants experienced a temperature difference of 3.5 and 8.5 degrees C after shade use and wetting, respectively (Mole, 2015)				
Probability of moving to water when thermoregulating	<ul><li>75% probability of moving to water if within 30 cell radius</li><li>25% probability of moving to water if within 60 cell radius</li></ul>	Water is used for thermoregulation and to replenish water reserves (Thaker et al., 2019)				
Duration of lower temperature experienced after wetting	4 hours, temperature gradually increases to the current environmental temperature	African elephant skin retains water and mud; thermoregulatory benefits of wetting behavior last for hours (Lillywhite & Stein, 1987)				
Drinking						
Distance traveled for	Maximum=60 cells (speed of 1.8 km/h)	Maximum speed traveling to water was ~				

drinking		3 km/h (Chamaillé- Jammes et al., 2013)
Coefficient used in logistic equation to determine the probability of drinking at a given time since the agent last visited a water source $((t_{water}))$	-0.1 in: <i>P</i> drinking $(t_{water}) = \frac{1}{1+e^{-0.1(T_{water}-50)}}$ T <sub>water</sub> is the cumulative time since the agent last visited water weighted by the current perceived temperature	Elephants return to water sources every 12 to 36 hours ( Chamaillé- Jammes et al., 2013, Purdon et al., 2017)
Parameter representing when the temperature at which the probability of switching to drinking rises to $\frac{1}{2}$ .	$50 \text{ in: } P \text{ drinking } (t_{water}) = \frac{1}{1 + e^{-0.1(T_{water} - 50)}}$ T <sub>water</sub> is the cumulative time since the agent last visited water weighted by the current perceived temperature	Elephants return to water sources every 12 to 36 hours ( Chamaillé- Jammes et al., 2013, Purdon et al., 2017)
Foraging		
Distance traveled for foraging	Varies according to the agent's state: State 1: Maximum of 30 cells (speed of .9 km/h) State 2: Maximum of 60 cells (speed of 1.8 km/h)	Foraging 'mode' described as maximum movement of ~ 750 m/30 min (Supplementary information, Polansky et al 2015). Family groups with calves had a lower likelihood of walking, compared to family groups with no calves (Mole et al., 2016).

**Table 3.2:** Model parameters and relevent values or ranges used in the ABM, along with supporting references

Behavior	Cell selection strategy	Supporting references
Shade use	Move to closer cells having higher percent	Generally, female
	tree cover and vegetation greenness	elephants select areas
		with high tree cover
		(Roever et al., 2013)
Wetting	Move to the closest cell containing water	Elephants usually travel
		to the closest water
		source (Chamaillé-
		Jammes et al., 2013,
		Polansky et al., 2013)
Drinking	Move to the closest cell containing water, or	Elephants usually travel
	to the cell within the search radius closest to	to the closest water
	the nearest water source	source (Chamaillé-
		Jammes et al., 2013,
		Polansky et al., 2013)
Foraging	Identify search radius cells with EVI values	Elephants avoid less
(if the	greater than or equal to the running average	green vegetation and
average	EVI of previously visited areas, and the EVI	favor greener than
EVI of the	of these cells is divided by their distance to	average landscapes
search	the agent's position. Calculate the angle	(Loarie et al., 2009b).
radius is	formed between the current direction the	Foraging movements can
greater	agent was neading, and every cell with the	be characterized as an
than or	nignest resultant values as determined above.	area-restricted search,
equal to	Generale 10 000 random numbers	with higher turning
visited	( running_angle_distribution ) representing	(Renhamou 1002) In
	distribution is skewed to generate larger	(Definition, 1992). In
cens)	numbers, representing more tortuous	elephants turn more
	movement:	(Duffy et al. 2011)
	movement.	(Durry et al., 2011)
	Turning angle=5	
	Turning angle distribution=round((1+(180-	
	$1)*nower(rand(1 \ 10000) \ x)))$	
	random value=round(randsample(X 1) 2)	
	Select a random number ("random value")	
	from this distribution, and identify a cell	
	characterized by the same turning angle.	
	Move to this cell.	
Foraging	Identify the search radius cells with EVI	In unfavorable habitats.
(if the	values greater than or equal to the running	elephant movement can
average	average EVI of previously visited areas.	be characterized as
EVI of the	Identify the furthest of these cells. Calculate	having small turning
search	the angle formed between the current	angles and being

radius is	direction the agent was heading and every	straighter (Duffy Dai
		Stranginer (Dully, Dal,
less than	cell with the highest resultant values as	Shannon, Slotow, &
previously	determined above. Generate 10 000 random	Page, 2011)
visited	numbers ("Turning angle distribution")	
cells)	representing turning angles in which the	
censy	representing turning angles, in which the	
	resulting distribution is skewed to generate	
	smaller numbers, representing less tortuous	
	movement:	
	Turning angle=15	
	Turning angle distribution=round((1+(180-	
	1)*nowor(nond(1,10000), y)))	
	$1)^{1} power(rand(1,10000),X)))$	
	random_value=round(randsample(X,1),2)	
	Select a random number ("random_value")	
	from this distribution, and identify a cell	
	characterized by the same turning angle.	
	Move to this cell.	

**Table 3.3:** Agent behaviors and their corresponding cell selection strategies and supporting references

Patterns present in empirical movement data	Patterns reproduced by the ABM				
Home range size					
1. Larger home ranges in the	Larger home range sizes in the				
wet season compared to the	wet season compared to the dry				
dry season.	season, but only when comparing				
	within parks				
2. Larger home ranges in CNP	Larger home range sizes in CNP				
compared to KNP	compared to KNP's dry season,				
	but not KNP's wet season				
Diel displacement distance (DDD)					
3. No difference in DDD in	No difference in DDD in CNP's				
CNP's wet season compared to	wet season compared to CNP's				
CNP's dry season	dry season				
4. Greater DDD in KNP's wet	Greater DDD in KNP's wet				
season compared to KNP's dry	season compared to KNP's dry				
season	season				
5. Greater DDD in CNP's wet	No difference in DDD in CNP's				
season compared to KNP's wet	wet season compared to KNP's				
season	wet season				
6. Greater DDD in CNP's dry	Greater DDD in CNP's dry				
season compared to KNP's dry	season compared to KNP's dry				
season	season				
Net daily displacement distance (NDD)					
7. Greater NDD in the wet	Greater NDD in the wet season				
season compared to the dry	compared to the dry season, but				
season	only when comparing within				
	parks				
8. Greater NDD in CNP	Greater net NDD in CNP				
compared to KNP	compared to KNP's dry season,				
	but not KNP's wet season				
Maximum distance traveled from a permanent water source					
9. Greater distances traveled	Greater distances traveled				
from permanent water sources	from permanent water sources				
in CNP's wet season	in CNP's wet season compared				
compared to CNP's dry season	to CNP's dry season				
10. Greater distances traveled	Greater distances traveled				
from permanent water sources	from permanent water sources				

in KNP's wet season compared	in KNP's wet season compared
to KNP's dry season	to KNP's dry season
11. Greater distances traveled	Greater distances traveled
from permanent water sources	from permanent water sources
in CNP's wet season compared	in CNP's wet season compared
	=
to KNP's wet season	to KNP's wet season
to KNP's wet season 12. No difference in distances	to KNP's wet season Greater distances traveled from
to KNP's wet season 12. No difference in distances traveled from permanent water	to KNP's wet season Greater distances traveled from permanent water sources in
to KNP's wet season 12. No difference in distances traveled from permanent water sources in CNP's dry season	to KNP's wet season Greater distances traveled from permanent water sources in CNP's dry season compared to

**Table 3.4**: Patterns present in the empirical movement data for both CNP and KNP, and those produced by the ABM. Bolded patterns represent those that fully matched the respective pattern in the empirical data.

Home range size	<b>P-Value</b>	Effect size
Sims	.595	042
Season*Sims	.022	361
Park*Sims	.008	.495
Season*Park*Sims	.003	-1.132
Diel displacement distance		
Sims	6.78E05	.297
Season*Sims	.136	210
Park*Sims	3.33E11	1.128
Season*Park*Sims	.883	.05
Net daily displacement distance		
Sims	.0004	285
Season*Sims	.026	354
Park*Sims	5.66E05	.755
Season*Park*Sims	.0002	-1.39
Max distance traveled from permanent water source		
Sims	.001	161
Season*Sims	.03	213
Park*Sims	.352	.108
Season*Park*Sims	.439	186

**Table 3.5**: Model validation results. P-values and effect sizes for models comparing empirical and simulated movement patterns across different ecological contexts.

Patterns present in the literature	Patterns reproduced by the ABM					
Mean time spent employing thermoregulatory behaviors $(\pm SD)$						
Approximately 30% of the time spent in shade during observation periods (Mole et al., 2016) Approximately 33% and 1% of the time spent in shade and in water, respectively, during the hot season observation periods (Guy 1976) Approximately 17% and 4.3% of the time spent in shade and in water, respectively, during the cold season observation periods (Guy 1976)	24.6 $\pm$ 0.1% in CNP during the wet season 24.2 $\pm$ 0.1% in CNP during the dry season 24.2 $\pm$ 0.1% in KNP during the wet season 19.9 $\pm$ 0.1% in KNP during the dry season					
Links between environmental temperature and thermoregulatory behaviors						
As temperatures increase, there was an increase in the time spent in the shade (Mole et al., 2016) Elephants spent the most amount of time resting in the shade in the middle of the day (Guy 1976)	On average, agents spent the most amount of time employing behavioral thermoregulation in the afternoon hours					
Mean number of hours spent for ging per day $(\pm SD)$						
Approximately 12-14 hours (Guy 1976) Approximately 16-18 hours (Wyatt & Eldringham 1974) Approximately 60-90% of the observation period (Mole et al., 2016)	$17.6 \pm 1.7$ hours in CNP during the wet season $17.6 \pm 2.2$ hours in CNP during the dry season $17.6 \pm 1.8$ hours in KNP during the wet season $19.1 \pm 1.8$ hours in KNP during the dry season					
Links between environmental temperature and foraging						
Elephants reduced the time spent feeding in the middle of the day, likely because of an increase in environmental temperature during these hours (Shannon et al., 2008)	On average, agents spent the least amount of time foraging in the afternoon hours					

**Table 3.6**: Patterns associated with activity budgets present in the relevent literature, and those produced by the model

		Tree cover	Forage	Tree cover
	Water	distribution	distribution	abundance
	abundance	(dispersed	(dispersed	(low to
	(low to high)	to clumped)	to clumped)	high)
Foraging efficiency	7.2	3.8	3.7	3.2
Forage consumed	2.4	0.05	0.39	1.7
Distance traveled	4.6	4.2	3.9	5
Home range size	120	5.8	16.7	13.5
Trip duration	7	11.1	2.8	7.9
Time spent foraging	2.2	0.15	0.41	1.8
Time spent in shade	2.5	2.3	1.8	6.7
Time spent wetting/drinking	6.3	12.1	2.8	8.4

**Table 4.1:** Percent changes in foraging efficiency, forage consumed, distance traveled, home range size, trip duration, and time spent employing foraging, shade use, and wetting and drinking for each landscape factor. Percent changes attributed to each factor were averaged across landscapes with all different combinations of the other three landscape factors. Blue cells indicate a percent increase and red cells indicate a percent decrease. The direction of the change is described under each landscape factor (e.g., foraging efficiency is associated with a 7.2 percent increase when we shift from considering a low-water landscape to a high-water landscape).

	Low water landscapes			High water landscapes		
	Tree cover	Tree cover   Tree cover   Forage 7		Tree cover	Tree cover	Forage
	abundance	distribution	distribution	abundance	distribution	distribution
	(low to	(dispersed	(dispersed	(low to	(dispersed	(dispersed
	high)	to clumped)	to clumped)	high)	to clumped)	to clumped)
Foraging efficiency	2.1	4.8	3.3	4.2	2.6	4
Forage consumed	2.9	0.008	0.3	0.43	0.09	0.48
Distance traveled	5.4	5.4	3.4	4.6	2.9	4.4
Home range size	13.3	11.1	16.1	13.6	3.3	16.9
Trip duration	8.6	14.2	5.3	10.1	7.5	1.3
Time spent foraging	3	0.19	0.87	0.56	0.12	0.04
Time spent in shade	10.5	2.7	3.1	3.1	2	0.38
Time spent wetting/drinking	8.3	17.4	6	8.4	7.2	0.02

**Table 4.2:** 

Percent changes in foraging efficiency, forage consumed, distance traveled, home range size, trip duration and time spent employing foraging, shade use, and wetting and drinking due to tree cover abundance and distribution, assessed separately for low- and high-water landscapes. Percent changes attributed to each factor were averaged across landscapes with all different combinations of the other two landscape factors. Blue cells indicate a percent increase and red cells indicate a percent decrease. The direction of the change is described under each landscape factor (e.g., foraging efficiency is associated with a 2.1 percent increase when we shift from considering a low tree cover landscape to a high tree cover landscape, assuming water availability remains low)

Hypotheses	Supported?	Results	
Which factor has the greatest effect on movement and foraging efficiency?			
H1. Tree cover abundance has the	Partially	H1. Tree cover distribution had the greatest effect	
greatest effect on trip duration		on trip duration	
• High tree cover		• Dispersed tree cover distribution was	
abundance will be	Yes	associated with longer trip durations	
associated with longer trip		(as was high tree cover abundance)	
durations	D (* 11	H2. Water abundance had the greatest effect on	
H2. Water abundance has the	Partially	home range size	
greatest effect on home range size		<ul> <li>High water source density was</li> </ul>	
• High water source density		associated with greater home range	
will be associated with		sizes	
greater home range sizes		H3. Water abundance had the greatest effect on	
H3. Water abundance has the		foraging efficiency	
greatest effect on foraging efficiency		• In high-water landscapes, herbivores	
• In high-water landscapes,		consumed more forage but traveled	
herbivores will be able to		smaller distances	
travel greater distances and			
consume more forage			
Can tree cover characteristics affect foraging efficiency and movement differently in low water vs high water			
	landscapes?		
H4. Differences in trip durations and	Partially	H4. Differences in trip durations and home range	
nome range size due to differences in		size due to differences in tree cover distribution	
more pronounced in low water		(but not tree cover abundance) were more	
landscapes		pronounced in low-water landscapes.	
H5 Differences in foraging	No	H5 Differences in foraging efficiency due to	
efficiency due to differences in tree	110	differences in tree cover characteristics were also	
cover characteristics will be more		present and just as pronounced in high-water	
pronounced in low-water landscapes		landscapes	
		*	

If so, what drives these differences?		
<ul> <li>H6. Variation in trip duration and home range size among low-water landscapes with differences in tree cover characteristics will be driven by differences in time spent wetting.</li> <li>In low water landscapes, trip durations will be shorter and home range sizes will be smaller when tree cover is low and clumped and agents must constantly return to water for wetting</li> <li>In high water landscapes, trip durations and home range sizes will be similar regardless of tree cover characteristics</li> </ul>	Partially	<ul> <li>H6. Variation in trip duration and home range size among low <i>and</i> high-water landscapes with differences in tree cover characteristics was driven by differences in time spent wetting.</li> <li>In low water landscapes, trip durations were shorter and home range sizes were smaller when tree cover was low and clumped and agents constantly returned to water for wetting</li> <li>In high water landscapes, trip durations were shorter and home range sizes were smaller when tree cover was low and clumped and agents constantly returned to water for wetting</li> <li>In high water landscapes, trip durations were shorter and home range sizes were smaller when tree cover was low and clumped and agents constantly returned to water for wetting</li> </ul>
<ul> <li>H7. Variation in foraging efficiency among low-water landscapes with differences in tree cover characteristics will be driven by differences in forage consumption.</li> <li>When tree cover is low and clumped, agents will consume less forage due to less time spent foraging at the expense of traveling to and from water.</li> </ul>	No	<ul> <li>H7. Variation in foraging efficiency among low- water landscapes with differences in tree cover characteristics were driven primarily by differences in distances traveled</li> <li>When tree cover was low and clumped, agents consumed more forage, and spent more time foraging, but traveled greater distances.</li> </ul>

**Table 4.3**: Hypotheses, whether the hypotheses were supported, and the model's results

## Works cited

- Aarts, G., Mackenzie, M., Mcconnell, B., Fedak, M., & Matthiopoulos, J. (2009). Estimating space-use and habitat preference from wildlife telemetry data Estimating space-use and habitat preference from wildlife telemetry data. *Ecography*, 31, 140-160. https://doi.org/10.1111/j.2007.0906-7590.05236.x
- Aben, J., Strubbe, D., Adriaensen, F., Palmer, S. C. F., Travis, J. M. J., Lens, L., & Matthysen, E. (2014). Simple individual-based models effectively represent Afrotropical forest bird movement in complex landscapes. *Journal of Applied Ecology*, 51(3), 693–702. https://doi.org/10.1111/1365-2664.12224
- Abrahms, B., Aikens, E. O., Armstrong, J. B., Deacy, W. W., Kauffman, M. J., & Merkle, J. A. (2021). Emerging perspectives on resource tracking and animal movement ecology. *Trends in Ecology & Evolution*, 36(4), 308–320. https://doi.org/10.1016/j.tree.2020.10.018
- Ahearn, S. C., Dodge, S., Simcharoen, A., Xavier, G., & Smith, J. L. D. (2016). A context-sensitive correlated random walk: A new simulation model for movement. *Internation Journal of Geographical Information Science*, 1224887. https://doi.org/10.1080/13658816.2016.1224887
- Aleman, J. C., Blarques, O., & Staver, C. A. (2016). Land-use change outweighs projected effects of changing rainfall on tree cover in sub-Saharan Africa. *Global Change Biology*, 1, 1–13. https://doi.org/10.1111/gcb.13299
- Alston, J. M., Joyce, M. J., Merkle, J. A., & Moen, R. A. (2020). Temperature shapes movement and habitat selection by a heat-sensitive ungulate. *Landscape Ecology*, 35(9), 1961–1973. https://doi.org/10.1007/s10980-020-01072-y
- Alwij, J. M. K., De Boer, W. F., Mucina, L., Prins, H. H. T., Skarpe, C., & Winterbach, C. (2010). Tree cover and biomass increase in a southern African savanna despite growing elephant population. *Ecological Applications*, 20(1), 222–233.
- Amoroso, C. R. (2020). Water availability impacts habitat use by red-fronted lemurs ( Eulemur rufifrons ): An Experimental and Observational Study. *International Journal of Primatology*, 61–80.
- Archibald, S., & Scholes, R. J. (2007). Leaf green-up in a semi-arid African savanna separating tree and grass responses to environmental cues. *Journal of Vegetation Science*, 18(4), 583. https://doi.org/10.1658/1100-9233(2007)18[583:lgiasa]2.0.co;2
- Augustine, D. J. (2012). Spatial heterogeneity in the herbaceous layer of a semi-arid savanna ecosystem, *Plant Ecology*, 319–332.
- Avgar, T., & Betini, G. S. (2020). Habitat selection patterns are density dependent under the ideal free distribution. *Journal of Animal Ecology*, 2777–2787. https://doi.org/10.1111/1365-2656.13352

- Bailey, D. W., Gross, J. E., Laca, E. a., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., & Sims, P. L. (1996). Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management*, 49(5), 386. https://doi.org/10.2307/4002919
- Bakker, E. S., Reiffers, R. C., Olff, H., & Gleichman, J. M. (2005). Experimental manipulation of predation risk and food quality: Effect on grazing behaviour in a central-place foraging herbivore. *Oecologia*, 146(1), 157–167. https://doi.org/10.1007/s00442-005-0180-7
- Bartumeus, F., Da Luz, M. G. E., Viswanathan, G. M., & Catalan, J. (2005). Animal search strategies: A quantitative random-walk analysis. *Ecology*, 86(11), 3078– 3087. https://doi.org/10.1890/04-1806
- Bastille-rousseau, G., Wall, J., Douglas-hamilton, I., Lesowapir, B., Loloju, B., Mwangi, N., ... Svenning, J. C. (2020). Landscape-scale habitat response of African elephants shows strong selection for foraging opportunities in a human dominated ecosystem. *Ecography*, 43, 149–160. https://doi.org/10.1111/ecog.04240
- Becker, J. A., Hutchinson, M. C., Potter, A. B., Park, S., Guyton, J. A., Abernathy, K., ... Long, R. A. (2021). Ecological and behavioral mechanisms of density-dependent habitat expansion in a recovering African ungulate population. *Ecological Monographs*, 1–20. https://doi.org/10.1002/ecm.1476
- Beest, F. M. Van, Rivrud, I. M., Loe, L. E., Milner, J. M., & Mysterud, A. (2011). What determines variation in home range size across spatiotemporal scales in a large browsing herbivore ? *Journal of Animal Ecology*, *80*, 771–785. https://doi.org/10.1111/j.1365-2656.2011.01829.x
- Belovsky, G. E. (1978). Diet optimization in a generalist herbivore: The Moose. *Theoretical Population Biology*, *134*, 105–134.
- Benhamou, S. (1992). Efficiency of area-concentrated searching behaviour in a continuous patchy environment. *Journal of Theoretical Biology*, *159*, 67–81.
- Bergman, C. M., Schaefer, J. A., & Luttich, S. N. (2000). Caribou movement as a correlated random walk. *Oecologia*, *123*(3), 364–374.
- Birkett, P. J., Vanak, A. T., Muggeo, V. M. R., Ferreira, S. M., & Slotow, R. (2012). Animal Perception of Seasonal Thresholds : Changes in elephant movement in relation to rainfall patterns, *PLoS One*, 7(6). https://doi.org/10.1371/journal.pone.0038363
- Boggs, G. S. (2010). International Journal of Applied Earth Observation and Geoinformation Assessment of SPOT 5 and QuickBird remotely sensed imagery for mapping tree cover in savannas. *International Journal of Applied Earth Observation* and Geoinformation 12, 217–224. https://doi.org/10.1016/j.jag.2009.11.001

- Bohrer, G., Beck, P. S., Ngene, S. M., Skidmore, A. K., & Douglas-Hamilton, I. (2014). Elephant movement closely tracks precipitation-driven vegetation dynamics in a Kenyan forest-savanna landscape. *Movement Ecology*, 2(1), 2. https://doi.org/10.1186/2051-3933-2-
- Bond, W. J., & Midgley, G. F. (2012). Carbon dioxide and the uneasy interactions of trees and savannah grasses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1588), 601–612. https://doi.org/10.1098/rstb.2011.0182
- Boult, V. L., Moss, C., Sibly, R. M., Quaife, T., Fishlock, V., & Lee, P. C. (2018a). Modeling large herbivore movement decisions : Beyond food availability as a predictor of ranging patterns, *African Journal of Ecology*, 1–10. https://doi.org/10.1111/aje.12553
- Boult, V. L., Quaife, T., Fishlock, V., Moss, C. J., Lee, P. C., & Sibly, R. M. (2018b). Individual-based modelling of elephant population dynamics using remote sensing to estimate food availability. *Ecological Modelling*, 387(September), 187–195. https://doi.org/10.1016/j.ecolmodel.2018.09.010
- Boyer, D., & Walsh, P. D. (2010). Modelling the mobility of living organisms in heterogeneous landscapes: Does memory improve foraging success? *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 368(1933), 5645–5659. https://doi.org/10.1098/rsta.2010.0275
- Boyers, M., Parrini, F., Owen-smith, N., Erasmus, B. F. N., & Hetem, R. S. (2019). Themed Issue Article : Conservation of southern hemisphere mammals in a changing world how free-ranging ungulates with differing water dependencies cope with seasonal variation in temperature and aridity. *Conservation Physiology*, 7(1), 1–12. https://doi.org/10.1093/conphys/coz064
- Bracis, C., Mueller, T., & Bracis, C. (2017). Memory, not just perception, plays an important role in terrestrial mammalian migration. *Proceedings Royal Society B*, 284.
- Brennan, A., Shapiro, A. C., Beytell, P., Aschenborn, O., Preez, P. Du, & Kilian, J. W. (2020). Mapping and assessing the impact of small-scale ephemeral water sources on wildlife in an African seasonal savannah. *Ecological Applications*, 30(8), 1–12. https://doi.org/10.1002/eap.2203
- Brits, J., van Rooyen, M. W., & van Rooyen, N. (2002). Ecological impactof large herbivores on the woody vegetation at seleted watering points on the eastern basaltic soils in the Kruger National Park. *African Journal of Ecology*, *40*, 53–60.
- Buchholtz, E., Fitzgerald, L., Songhurst, A., & Mcculloch, G. (2019). Overlapping landscape utilization by elephants and people in the Western Okavango Panhandle : implications for conflict and conservation. *Landscape Ecology*, 34(6), 1411–1423. https://doi.org/10.1007/s10980-019-00856-1
- Buitenwerf, R., Bond, W. J., Stevens, N., & Trollope, W. S. W. (2012). Increased tree densities in South African savannas: >50 years of data suggests CO 2 as a driver. *Global Change Biology*, 18(2), 675–684. https://doi.org/10.1111/j.1365-2486.2011.02561.x
- Cain, J. W., Owen-Smith, N., & Macandza, V. A. (2012). The costs of drinking: Comparative water dependency of sable antelope and zebra. *Journal of Zoology*, 286(1), 58–67. https://doi.org/10.1111/j.1469-7998.2011.00848.x
- Cao, R., Chen, Y., Chen, J., Zhu, X., & Shen, M. (2020). Thick cloud removal in Landsat images based on autoregression of Landsat time-series data. *Remote Sensing of Environment*, 249(April 2019), 112001. https://doi.org/10.1016/j.rse.2020.112001
- Carter, N., Levin, S., Barlow, A., & Grimm, V. (2015). Modeling tiger population and territory dynamics using an agent-based approach. *Ecological Modelling*, 312, 347– 362. https://doi.org/10.1016/j.ecolmodel.2015.06.008
- Caylor, K. ., Shugart, H. ., Dowty, P. ., & Smith, T. . (2003). Tree spacing along the Kalahari transect in southern Africa. *Journal of Arid Environments*, 54(2), 281–296. https://doi.org/10.1006/jare.2002.1090
- Chamaillé-Jammes, S., Fritz, H., & Madzikanda, H. (2009). Piosphere contribution to landscape heterogeneity: A case study of remote-sensed woody cover in a high elephant density landscape. *Ecography*, 32(5), 871–880. https://doi.org/10.1111/j.1600-0587.2009.05785.x
- Chamaillé-jammes, S., Fritz, H., & Murindagomo, F. (2007a). Climate-driven fluctuations in surface-water availability and the buffering role of artificial pumping in an African savanna : Potential implication for herbivore dynamics, *Austral Ecology*, 740–748. https://doi.org/10.1111/j.1442-9993.2007.01761.x
- Chamaillé-Jammes, S., Fritz, H., Valeix, M., Murindagomo, F., & Clobert, J. (2008). Resource variability, aggregation and direct density dependence in an open context: The local regulation of an African elephant population. *Journal of Animal Ecology*, 77(1), 135–144. https://doi.org/10.1111/j.1365-2656.2007.01307.x
- Chamaillé-Jammes, S., Mtare, G., Makuwe, E., & Fritz, H. (2013). African elephants adjust speed in response to surface-water constraint on foraging during the dryseason. *PLoS ONE*, 8(3). https://doi.org/10.1371/journal.pone.0059164
- Chamaillé-Jammes, S., Valeix, M., & Fritz, H. (2007b). Managing heterogeneity in elephant distribution: Interactions between elephant population density and surfacewater availability. *Journal of Applied Ecology*, 44(3), 625–633. https://doi.org/10.1111/j.1365-2664.2007.01300.x
- Chapman, C. A., Chapman, L. J., & Mclaughlin, R. L. (1989). Multiple central place foraging by spider monkeys : travel consequences of using many sleeping sites. *Oecologia*, https://doi.org/10.1007/BF00378668

- Choquenot, D., & Ruscoe, W. A. (2003b). Landscape complementation and food limitation of large herbivores: Habitat-related constraints on the foraging efficiency of wild pigs. *Journal of Animal Ecology*, 72(1), 14–26. https://doi.org/10.1046/j.1365-2656.2003.00676.x
- Christensen. (2007). Regional Climate Projections. *Climate Change 2007: The Physical Science Basis*, 27(2007), 847–940. https://doi.org/10.1080/07341510601092191
- Codling, E. A., Plank, M. J., & Benhamou, S. (2008). Random walk models in biology. *Journal of the Royal Society Interface*, 5(25), 813–834. https://doi.org/10.1098/rsif.2008.0014
- Codron, J., Lee-Thorp, J. A., Sponheimer, M., Codron, D., Grant, R. C., & de Ruiter, D. J. (2006a). Elephant (Loxodonta africana) diets in Kruger National Park, South Africa: spatial and landscape differences. *Journal of Mammalogy*, 87(1), 27–34.
- Cook, R. M., Henley, M. ., & Parrini, F. (2015). Elephant movement patterns in relation to human inhabitants in and around the Great Limpopo. *Koedoe*, *57*(1). https://doi.org/10.4102/koedoe.v57i1.1298
- Cunningham, S. J., Gardner, J. L., & Martin, R. O. (2021). Opportunity costs and the response of birds and mammals to climate warming. *Frontiers in Ecology and the Environment*, *19*(5), 300–307. https://doi.org/10.1002/fee.2324
- Cunningham, S. J., Martin, R. O., & Hockey, P. A. R. (2015). Can behaviour buffer the impacts of climate change on an arid-zone bird ? *Frontiers in Ecology and the Environment*, 6525. https://doi.org/10.2989/00306525.2015.1016469
- de Beer, Y., & van Aarde, R. J. (2008). Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas? *Journal of Arid Environments*, 72, 2017–2025. https://doi.org/10.1016/j.jaridenv.2008.07.002
- De Knegt, H. J., Hengeveld, G. M., Van Langevelde, F., De Boer, W. F., & Kirkman, K. P. (2007). Patch density determines movement patterns and foraging efficiency of large herbivores. *Behavioral Ecology*, 18(6), 1065–1072. https://doi.org/10.1093/beheco/arm080
- De Leeuw, J., Waweru, M. N., Okello, O. O., Maloba, M., Nguru, P., Said, M. Y., ... Reid, R. S. (2001). Distribution and diversity of wildlife in northern Kenya in relation to livestock and permanent water points. *Biological Conservation*, 100(3), 297–306. https://doi.org/10.1016/S0006-3207(01)00034-9
- DeAngelis, D. L., & Diaz, S. G. (2019). Decision-making in agent-based modeling : a current review and future prospectus. *Frontiers in Ecology and Evolution*, 1–15. https://doi.org/10.3389/fevo.2018.00237

- DeAngelis, D. L., & Grimm, V. (2014). Individual-based models in ecology after four decades. *F1000prime Reports*, 39. https://doi.org/10.12703/P6-39
- DeAngelis, D. L., & Mooij, W. M. (2005). Individual-based modeling of ecological and evolutionary processes. *Annual Review of Ecology, Evolution, and Systematics*, 36, 147–168. https://doi.org/10.1146/annurev.ecolsys.36.102003.152644
- DeAngelis, D. L., & Yurek, S. (2016). Spatially explicit modeling in ecology: a review. *Ecosystems*. https://doi.org/10.1007/s10021-016-0066-z
- Department of the Interior, & U.S. Geological Survey. (2016). Product Guide. *Product Guide, Version* 7, 1–27. https://doi.org/10.1080/1073161X.1994.10467258
- Derry, J. F., & Dougill, A. J. (2008). Water location, piospheres and a review of evolution in African ruminants. *African Journal of Range and Forest Science*, 25(2), 79–92. https://doi.org/10.2989/AJRFS.2008.25.2.6.485
- Deruiter, S. L., Langrock, R., Skirbutas, T., Jeremy, A., Chalambokidis, J., Friedlaender, A. S., ... College, C. (2017). A multivariate mixed hidden Markov model to analyze blue whale diving behaviour during controlled sound exposures. *Annals of Applied Statistics*. 1–26.
- Dexter, N. (2003). The influence of pasture distribution, and temperature on adult body weight of feral pigs in a semi-arid environment. *Wildlife Research*, *30*(1), 75–79. https://doi.org/10.1071/WR01026
- Dimobe, K., Goetze, D., Ouédraogo, A., Forkuor, G., Wala, K., Porembski, S., & Thiombiano, A. (2017). Spatio-temporal dynamics in land use and habitat fragmentation within a protected area dedicated to tourism in a sudanian savanna of West Africa. *Journal of Landscape Ecology(Czech Republic)*, 10(1), 75–95. https://doi.org/10.1515/jlecol-2017-0011
- Dodge, S. (2016). From observation to prediction: the trajectory of movement research in GIScience. *Advancing Geographic Information Science: The Past and Next Twenty Years*, 123–136.
- Doherty T.S., Driscoll D.A. (2018) Coupling movement and landscape ecology for animal conservation in production landscapes. *Proc R Soc B Biol Sci, 285*:20172272
- Doherty, T. S., Fist, C. N., & Driscoll, D. A. (2019). Animal movement varies with resource availability, landscape configuration and body size : a conceptual model and empirical example. *Landscape Ecology*, 34(3), 603–614. https://doi.org/10.1007/s10980-019-00795-x
- Douglas-Hamilton, I., Krink, T., Vollrath, F. (2005). Movements and corridors of African elephants in relation to protected areas. *The Science of Nature*, 158–163. https://doi.org/10.1007/s00114-004-0606-9
- Du Toit, J. T., & Cumming, D. H. M. (1999). Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation*, 8, 1643–1661.

- Duffy, K J, Dai, X., Shannon, G., Slotow, R., & Page, B. (2011). Movement patterns of African elephants (Loxodonta africana) in different habitat types. *South African Journal of Wildlife Research*, 41(1), 21–28. https://doi.org/10.3957/056.041.0107
- Duffy, Kevin J. (2009). Simulations to investigate movement effects on Population Dynamics. *Natural Resource Modeliing*, 24(March), 48–60.
- Duning, J. B. (1995). Spatially explicit population models: current forms and future uses. *Ecological Applications*, 5(1), 3–11. https://doi.org/10.2307/1942045
- Dunkin, R. C., Wilson, D., Way, N., Johnson, K., & Williams, T. M. (2013). Climate influences thermal balance and water use in African and Asian elephants: physiology can predict drivers of elephant distribution. *The Journal of Experimental Biology*, 216, 2939–2952. https://doi.org/10.1242/jeb.080218
- van de Ven, T. M. F. N., McKechnie, A. E., & Cunningham, S. J. (2019). The costs of keeping cool : behavioural trade - offs between foraging and thermoregulation are associated with significant mass losses in an arid - zone bird. *Oecologia*, 191(1), 205–215. https://doi.org/10.1007/s00442-019-04486-x
- Elmore, D., Carrol, J. M., Tanner, E. P., Hovick, T. J., Grisham, B. A., Fuhlendorf, S. D., & Windels, S. K. (2017). Implications of the thermal environment for terrestrial wildlife management. *Wildlife Society Bulletin*, 41(2), 183–193. https://doi.org/10.1002/wsb.772
- Epaphras, A. ., Gereta, E., Lejora, I. A., Ole Meing'ataki, G. ., Ng'umbi, G., Kiwango, Y., ... Mtahiko, M. G. G. (2008). Wildlife water utilization and importance of artificial waterholes during dry season at Ruaha National Park, Tanzania. *Wetlands Ecological Management*, 16, 183–188. https://doi.org/10.1007/s11273-007-9065-3
- Fauchald, P., & Tveraa, T. (2006). Hierarchical patch dynamics and animal movement pattern, *Population Ecology*, 383–395. https://doi.org/10.1007/s00442-006-0463-7
- February, E. C., & Higgins, S. I. (2016). Rapid leaf deployment strategies in a deciduous savanna. PLoS ONE, 11(6). https://doi.org/10.1371/journal.pone.0157833
- Ferreira, S. (2017). Elephant population growth in Kruger National Park, South Africa, under a landscape management approach. KOEDOE-African Protected Area Conservation and Science, 59(1). https://doi.org/10.4102/koedoe.v59i1.1427
- Folse, L. J., Packard, J. M. & Grant, W. E. (1989) AI modelling of animal movements in a heterogeneous habitat. *Ecol. Model.* 46, 57–72. (doi:10.1016/0304-3800(89) 90069-0)
- Foran, B. (1980). Change in range condition with distance from watering point and its implications for field survey. *The Rangeland Journal*, 2(1), 59. https://doi.org/10.1071/rj9800059
- Forester, J. D., Ives, A. R., Turner, M. G., Anderson, D. P., Fortin, D., Beyer, H. L., ... Boyce, M. S. (2007). State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. *Ecological Monographs*, 77(2), 285– 299. https://doi.org/10.1890/06-0534

- Fox, J. T., & Alexander, K. A. (2015). Spatiotemporal variation and the role of wildlife in seasonal water quality declines in the Chobe River, Botswana, *PLoS One*, 1–21. https://doi.org/10.1371/journal.pone.0139936
- Frank, A. S. K., Dickman, C. R., & Wardle, G. M. (2012). Habitat use and behaviour of cattle in a heterogeneous desert environment in central Australia. *Rangeland Journal*, 34(3), 319–328. https://doi.org/10.1071/RJ12032
- Franke, A., Caelli, T., Kuzyk, G., & Hudson, R. J. (2006). Prediction of wolf (Canis lupus) kill-sites using hidden Markov models. *Ecological Modelling*, 197(1–2), 237– 246. https://doi.org/10.1016/j.ecolmodel.2006.02.043
- Fraser, K. C., Davies, K. T. A., Davy, C. M., Ford, A. T., Flockhart, D. T. T., & Martins, E. G. (2018). Tracking the conservation promise of movement ecology. *Frontiers in Ecology and Evolution*, 6, 1–8. https://doi.org/10.3389/fevo.2018.00150
- Fronhofer, E. A., Hovesadt, T., & Poethke, H. (2013). From random walks to informed movement. Oikos, 857–866. https://doi.org/10.1111/j.1600-0706.2012.21021.x
- Fuller, D. O., & Prince, S. D. (1996). Rainfall and foliar determinants in tropical southern Africa: Potential impacts of global climatic change of savanna vegetation. *Climatic Change*, 33, 69–96.
- Galanti, V., Preatoni, D., Martinoli, a., Wauters, L. a., & Tosi, G. (2006). Space and habitat use of the African elephant in the Tarangire–Manyara ecosystem, Tanzania: Implications for conservation. *Mammalian Biology Zeitschrift Für Säugetierkunde*, 71(2), 99–114. https://doi.org/10.1016/j.mambio.2005.10.001
- Gallagher, A. J., Creel, S., Wilson, R. P., & Cooke, S. J. (2017). Energy landscapes and the landscape of fear. *Trends in Ecology & Evolution*, 32(2), 88–96. https://doi.org/10.1016/j.tree.2016.10.010
- Gallagher, C. A., Chudzinska, M., Larsen-Gray, A., Pollock, C. J., Sells, S. N., White, P. J. C., & Berger, U. (2021). From theory to practice in pattern-oriented modelling: identifying and using empirical patterns in predictive models. *Biological Reviews*. https://doi.org/10.1111/brv.12729
- Gandiwa, E., Tupulu, N., Zisadza-Gandiwa, P., & Muvengwi, J. (2012). Structure and composition of woody vegetation around permanent artificial and ephemeral-natural water points in northern Gonarezhou National Park, Zimbabwe. *Tropical Ecology*, 53(2), 169–175.
- Gautestad, A. O., and I. Mysterud. 2010a. The home range fractal: From random walk to memory-dependent space use. *Ecological Complexity* 7:458–470.
- Getz, W. M., & Salter, R. (2020). Simulation and analysis of animal movement paths using numerus model builder. *BioRxiv*.
- Getz, W. M., & Saltz, D. (2008). A framework for generating and analyzing movement paths on ecological landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, 105(49), 19066–19071. https://doi.org/10.1073/pnas.0801732105

- Giles, S. L., Harris, P., Rands, S. A., & Nicol, C. J. (2020). Foraging efficiency, social status and body condition in group-living horses and ponies. *PeerJ*, 1–17. https://doi.org/10.7717/peerj.10305
- Giotto, N., Picot, D., Maublanc, M., & Gerard, J. (2013). Effects of seasonal heat on the activity rhythm, habitat use, and space use of the beira antelope in southern Djibouti. *Journal of Arid Environments, 89*, 5–12.
- Goldenberg, S. Z., Douglas-hamilton, I., & Wittemyer, G. (2018). Inter-generational change in African elephant range use is associated with poaching risk, primary productivity and adult mortality. *Proceedings Royal Society B*, 285.
- Goossens, S., Wybouw, N., Van Leeuwen, T. .(2020). The physiology of movement. *Movement Ecology*, 8, https://doi.org/10.1186/s40462-020-0192-2
- Graham, M. D., Douglas-Hamilton, I., Adams, W. M., & Lee, P. C. (2009). The movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation*, 12(5), 445–455. https://doi.org/10.1111/j.1469-1795.2009.00272.x
- Grainger, M., van Aarde, R., & Whyte, I. (2005). Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa. *African Journal of Ecology*, 43(4), 369–375. https://doi.org/10.1111/j.1365-2028.2005.00592.x
- Grimm, V, & Railsback, S. (2005). Individual-based modeling and ecology. *Individual-Based Modeling and Ecology*, 1–432. https://doi.org/10.1111/j.1467-2979.2008.00286.x
- Grimm, V., Ayllón, D., & Railsback, S. F. (2016). Next-generation individual-based models integrate biodiversity and ecosystems: yes we can, and yes we must. *Ecosystems*, **20**, 229–236. https://doi.org/10.1007/s10021-016-0071-2
- Grimm, V., & Berger, U. (2016). Structural realism , emergence , and predictions in nextgeneration ecological modelling : Synthesis from a special issue. *Ecological Modelling*, 326, 177–187. https://doi.org/10.1016/j.ecolmodel.2016.01.001
- Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., & Ginot, V. (2006). A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, 198 (1-2), 115-116. https://doi.org/10.1016/j.ecolmodel.2006.04.023
- Grimm, V., Berger, U., DeAngelis, D. L., Polhill, J. G., Giske, J., & Railsback, S. F. (2010). The ODD protocol: a review and first update. *Ecological Modelling*, 221(23), 2760–2768. https://doi.org/10.1016/j.ecolmodel.2010.08.019
- Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmański, J., & Wissel, C. (1996). Pattern-oriented modelling in population ecology. *Science of the Total Environment*, 183(1–2), 151–166. https://doi.org/10.1016/0048-9697(95)04966-5
- Grimm, V., Railsback, S. F., Vincenot, C. E., Gallagher, C., Deangelis, D. L., Edmonds, B., ... Ayllón, D. (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(2).

- Grimm, V., & Railsback, S. F. (2012). Pattern-oriented modelling : a 'multi-scope ' for predictive systems ecology. *Philosophical Transactions of the Royal Society B*, 367, 298–310. https://doi.org/10.1098/rstb.2011.0180
- Gunn, D. L., & Walshe, B. M. (1941). Klino-kinesis of Paramecium. *Nature*, 148, 564–565.
- Gurarie, E. (2018). A novel method for identifying behavioural changes in animal movement data. *Ecology Letters*, 12, 395-408. https://doi.org/10.1111/j.1461-0248.2009.01293.x
- Guy, P. R. (1976). Diurnal activity patterns of elephant in the Sengwa area, Rhodesia. *East African Wildlife Journal*, 14, 285–295. https://doi.org/10.1111/j.1365-2028.1976.tb00243.x
- Hainsworth, F. R. (1974). The efficiency of sugar assimilation b y h u m m i n g b i r d s. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology, 431, 425–431.
- Hall, L. E., Chalfoun, A. D., Beever, E. A., & Loosen, A. E. (2016). Microrefuges and the occurrence of thermal specialists : implications for wildlife persistence amidst changing temperatures. *Climate Change Responses*, 1–12. https://doi.org/10.1186/s40665-016-0021-4
- Hansen, M. C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S. A., & Tyukavina, A. (2013). High-resolution global maps of 21<sup>st</sup> century forest cover change. *Science*, *134*, 2011–2014.
- Harris, G. M., Russell, G. J., van Aarde, R. I., & Pimm, S. L. (2008). Rules of habitat use by elephants Loxodonta africana in southern Africa: insights for regional management. *Oryx*, 42(01), 66–75. https://doi.org/10.1017/S0030605308000483
- He, K. S., Bradley, B. A., Cord, A. F., Rocchini, D., Tuanmu, M., Schmidtlein, S., ... Pettorelli, N. (2015). Will remote sensing shape the next generation of species distribution models ?, 4–18. https://doi.org/10.1002/rse2.7
- Hetem, R. S., Witt, B. A. De, Fick, L. G., Fuller, A., Maloney, S. K., Meyer, L. C. R., ... Kerley, G. I. H. (2011). Effects of deserti fi cation on the body temperature, activity and water turnover of Angora goats. *Journal of Arid Environments*, 75(1), 20–28. https://doi.org/10.1016/j.jaridenv.2010.08.007
- Hetem, R. S., Strauss, W. M., Fick, L. G., Maloney, S. K., Meyer, L. C. R., Shobrak, M., ... Mitchell, D. (2012). Activity re-assignment and microclimate selection of freeliving Arabian oryx : responses that could minimise the effects of climate change on homeostasis? *Zoology*, 115(6), 411–416. https://doi.org/10.1016/j.zool.2012.04.005
- Hirst, S. M. (1975). Ungulate-habitat relationships in a South African woodland/ savanna ecosystem. *Wildlife Monograms*, 44: 3?60.
- Hoare, R. E. (1999). Determinants of human elephant conflict in a land-use mosaic. *Journal of Applied Ecology*, *36(5)*; 689–700.

- Hochberg, M. E., & Menaut, J. C. (1994). The influences of tree biology and fire in the spatial structure of the West African Savannah. *Journal of Ecology*, 82(2). https://www.jstor.org/stable/2, 82(2), 217–226.
- Holdo, R. M. (2003). Woody plant damage by African elephants in relation to leaf nutrients in western Zimbabwe. *Journal of Tropical Ecology*, 19(2), 189–196. https://doi.org/10.1017/S0266467403003213
- Hooten, M B, Scharf, H. R., & Morales, J. M. (2019). Running on empty : recharge dynamics from animal movement data. *Ecology Letters*, 22, 377–389. https://doi.org/10.1111/ele.13198
- Hooten, Mevin B, & Johnson, D. S. (2017). Basis function models for animal movement. *Journal of the American Statistical Association*, *112*(518), 578–589. https://doi.org/10.1080/01621459.2016.1246250
- Horne, J. S., Garton, E. O., Krone, S. M., & Lewis, J. S. (2007). Analyzing animal movements using Brownian bridges. *Ecology*, 88(9), 2354–2363. https://doi.org/10.1890/06-0957.1
- House, J. I., Archer, S., Breshears, D. D., Scholes, R. J. (2003). Conundrums in mixed woody herbaceous plant systems. *Journal of Biogeography*, 20, 1763–1777.
- Ihwagi, F. W., Skidmore, A. K., Wang, T., Rousseau, G. B., Toxopeus, A. G., & Hamilton, I. D. (2019). Poaching lowers elephant path tortuosity : implications for conservation. *The Journal of Wildlife Management*, 83(5), 1022–1031. https://doi.org/10.1002/jwmg.21688
- Illius, A. A. W., & Connor, T. G. O. (2000). Resource heterogeneity and ungulate population dynamics. *Oikos*, 89(2), 283–294.
- Ims, R. A., & Andreassen, H. P. (2005). Density-dependent dispersal and spatial population dynamics. *Proceedings of the Royal Society B*, 272, 913-918. https://doi.org/10.1098/rspb.2004.3025
- Jachmann, H. (1989). Food selection by elephants in the "miombo" biome, in relation to leaf chemistry. *Biochemical Systematics and Ecology*, 17(1), 15–24. https://doi.org/10.1016/0305-1978(89)90037-9
- Jackson, T. P., Mosojane, S., Ferreira, S. M., & van Aarde, R. J. (2008). Solutions for elephant Loxodonta africana crop raiding in northern Botswana: moving away from symptomatic approaches. *Oryx*, 42(01), 83–91. https://doi.org/10.1017/S0030605308001117
- Jeltsch, F., Milton, S. J., & Dean, W. R. J. (1996). Tree spacing and coexistence in semiarid savannas. *Journal of Ecology*, 84(4), 583–595.
- Jenerette, G. D., & Shen, W. (2012). Experimental landscape ecology. *Landscape Ecology*, 27, 1237-1248. https://doi.org/10.1007/s10980-012-9797-1

- Johnson, a R., Wiens, J. a, Milne, B. T., & Crist, T. O. (1992). Animal movements and population-dynamics in heterogeneous landscapes. *Landscape Ecology*, 7(1), 63–75. https://doi.org/10.1007/bf02573958
- Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers what is the ecological role of a tree in a forest? *Ecology*, 78(787), 1946–1957. https://doi.org/10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2
- Jones, R. (1988). The form and consequences of random walk movement models. *Journal of Theoretical Biology*, 133, 113–131.
- Jonsen, I. D., Myers, R. A., & James, M. C. (2006). Robust hierarchical state-space models reveal diel variation in travel rates of migrating leatherback turtles. *Journal* of Animal Ecology, 75(5), 1046–1057. https://doi.org/10.1111/j.1365-2656.2006.01129.x
- Kamusoko, C., & Aniya, M. (2007). Land use/cover change and landscape fragmentation analysis in the Bindura District, Zimbabwe. *Land Degredation and Development*, *18*, 221–233.
- Kandji, S. T., Verchot, L., & Mackensen, J. (2006). Climate change and variability in the southern africa : impacts and adaptation strategies in the agricultural sector. *Climatic Variability and Change in Southern Africa*, (254 20), 36.
- Kanga, E. M., & Ogutu, J. O. (2013). Hippopotamus and livestock grazing : influences on riparian vegetation and facilitation of other herbivores in the Mara Region of Kenya. *Landscape and Ecological Engineering*, 47–58. https://doi.org/10.1007/s11355-011-0175-y
- Karasov, W.H. & Martinez del Rio, C. (2007) Physiological Ecology. Princeton University Press, Princeton and Oxford.
- Keating, K. a, Cherry, S., Keating, K. a, & Cherry, S. (2016). Modeling utilization distributions in space and time. *Ecology*, *90*(7), 1971–1980.
- Kgope, B. S., Bond, W. J., & Midgley, G. F. (2010). Growth responses of African savanna trees implicate atmospheric [CO2] as a driver of past and current changes in savanna tree cover. *Austral Ecology*, 35(4), 451–463. https://doi.org/10.1111/j.1442-9993.2009.02046.x
- Kinahan, a. a., Pimm, S. L., & van Aarde, R. J. (2007). Ambient temperature as a determinant of landscape use in the savanna elephant, Loxodonta africana. *Journal of Thermal Biology*, *32*(1), 47–58. https://doi.org/10.1016/j.jtherbio.2006.09.002
- Klappstein, N. J., & Potts, J. R. (2021). Energy selection functions : modelling the energetic drivers of animal movement and habitat use. https://doi.org/10.22541/au.160640483.30543006/v2
- Kramer-schadt, S., Revilla, E., Wiegand, T., & Grimm, V. (2007). Short communication Patterns for parameters in simulation models. *Ecological Modelling*, 4, 553–556. https://doi.org/10.1016/j.ecolmodel.2007.01.018

- Kranstauber, B., Kays, R., Lapoint, S. D., Wikelski, M., & Safi, K. (2012). A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology*, 81(4), 738–746. https://doi.org/10.1111/j.1365-2656.2012.01955.x
- Kumar, T., Swamy, T. S. L., Bijalwan, A., & Dobriyal, M. J. R. (2019). Assessment of biomass and net primary productivity of a dry tropical forest using geospatial technology. *Journal of Forestry Research*, 30(1), 157–170. https://doi.org/10.1007/s11676-018-0607-8
- Landman, M., Schoeman, D. S., Hall-martin, A. J., & Kerley, G. I. H. (2012). Understanding long-term variations in an elephant piosphere effect to manage impacts. *PLoS One*, 7(9). https://doi.org/10.1371/journal.pone.0045334
- Lange, R. (1969). The Piosphere : Sheep track and dung patterns. Journal of Range Management, 22(6), 396–400.
- Langrock, R., & Patterson, T. A. (2016). moveHMM : an R package for the statistical modelling of animal movement data using hidden Markov models. *Methods in Ecology and Evolution*, 1308–1315. https://doi.org/10.1111/2041-210X.12578
- Larson-Praplan, S., George, M. R., Buckhouse, J. C., & Laca, E. A. (2015). Spatial and temporal domains of scale of grazing cattle. *Animal Production Science*, 55, 284– 297.
- Latombe, G., Parrott, L., Basille, M., & Fortin, D. (2014). Uniting statistical and individual-based approaches for animal movement modelling. *PLoS One*, *9*(6). https://doi.org/10.1371/journal.pone.0099938
- Leggett, A., Keith, E. A., & Leggett, K. E. A. (2006). Home range and seasonal movement of elephants in the Kunene Region, northwestern Namibia. *African Zoology*, *41*(1), 17–36.
- Leos-barajas, V., Gangloff, E. J., Adam, T., Langrock, R., Beest, F. M. Van, Nabenielsen, J., & Morales, J. M. (2017). Multi-scale modeling of animal movement and general behavior data using hidden markov models with hierarchical structures. *Journal of Agricultural, Biological and Environmental Statistics*, 22(3), 232–248. https://doi.org/10.1007/s13253-017-0282-9
- Lillywhite, H. ., & Stein, B. . (1987). Surface sculpturing and water retention of elephant skin. *Journal of Zoology, London, 211*, 727–734.
- Lindsay, K., Chase, M., Landen, K., & Nowak, K. (2017). The shared nature of Africa's elephants. *Biological Conservation*, *215*, 260–267. https://doi.org/10.1016/j.biocon.2017.08.021
- Lindstedt, S. L., Miller, B. J., & Buskirk, S. W. (1986). Home range, time, and body size in mammals. *Ecology*, 67(2), 413–418.
- Loarie, S. R., Aarde, R. J. Van, & Pimm, S. L. (2009a). Fences and artificial water affect African savannah elephant movement patterns. *Biological Conservation*, 142(12), 3086–3098. https://doi.org/10.1016/j.biocon.2009.08.008

- Loarie, S. R., van Aarde, R. J., & Pimm, S. L. (2009b). Elephant seasonal vegetation preferences across dry and wet savannas. *Biological Conservation*, 142(12), 3099– 3107. https://doi.org/10.1016/j.biocon.2009.08.021
- Long, J. A. (2018). Modeling movement probabilities within heterogeneous spatial fields. *Journal of Spatial Information Sciences*, 85–116. https://doi.org/10.5311/JOSIS.2018.16.372
- Lunstrum, E. (2014). Green Militarization : Anti-poaching efforts and the spatial contours of Kruger National Park. *Annals of the Association of American Geographers ISSN:*, 104(4), 816–832. https://doi.org/10.1080/00045608.2014.912545
- Macfadyen, S., Zambatis, Nick, Van Teeffelen, A. J. A., & Hui, C. (2018). Long-term rainfall regression surfaces for the Kruger National Park, South Africa: a spatiotemporal review of patterns from 1981 to 2015. *International Journal of Cimatology*, 38, 2506–2519. https://doi.org/10.1002/joc.5394
- Maloney, S. K., Moss, Æ. G., & Cartmell, Æ. T. (2005). Alteration in diel activity patterns as a thermoregulatory strategy in black wildebeest (Connochaetes gnou). *Journey of Comparitive Physiology*, 1055–1064. https://doi.org/10.1007/s00359-005-0030-4
- Manning, A. D., Fischer, J., & Lindenmayer, D. B. (2006). Scattered trees are keystone structures – Implications for conservation Scattered trees are keystone structures – Implications for conservation. *Biological Conservation*, 132, 311–321. https://doi.org/10.1016/j.biocon.2006.04.023
- Manning, A. D., Gibbons, P., & Lindenmayer, D. B. (2009). Scattered trees: a complementary strategy for facilitating adaptive responses to climate change in modified landscapes? *Journal of Applied Ecology*, 915–919. https://doi.org/10.1111/j.1365-2664.2009.01657.x
- Martin, J., van Moorter, B., Revilla, E., Blanchard, P., Dray, S., Quenette, P. Y., ... Swenson, J. E. (2013). Reciprocal modulation of internal and external factors determines individual movements. *Journal of Animal Ecology*, 82(2), 290–300. https://doi.org/10.1111/j.1365-2656.2012.02038.x
- Mason, T. H. E., Brivio, F., Stephens, P. A., & Apollonio, M. (2017). The behavioral trade-off between thermoregulation and foraging in a heat- sensitive species. *Behavioral Ecology*, *28*, 908–918. https://doi.org/10.1093/beheco/arx057
- Massé, A., & Cote, S. D. (2013). Spatiotemporal variations in resources affect activity and movement. *Canadian Journal of Zoology*, 263, 252–263.
- Mason, T. H. E., Stephens, P. A., Apollonio, M., & Willis, S. G. (2014). Predicting potential responses to future climate in an alpine ungulate : interspecific interactions exceed climate effects. *Global Change Biology*, (20), 3872–3882. https://doi.org/10.1111/gcb.12641
- Matthysen, E. (2005). Density-dependent dispersal in birds and mammals. *Ecography*, 403–416.

- McClintock, B., M., London, J. M., Cameron, M. F., & L, B. P. (2017). Bridging the gaps in animal movement : hidden behaviors and ecological relationships revealed by integrated data streams. *Ecosphere*; 8 https://doi.org/10.1002/ecs2.1751
- McIlvain, E.H., & Shoop, M. C. (1971). Shade for improving cattle grains and rangeland use. *Journal of Range Management*, 24(3), 181–184.
- Mcintyre, N. E., & Wiens, J. A. (1999). Interactions between landscape structure and animal behavior : the roles of heterogeneously distributed resources and food deprivation on movement patterns. *Landscape Ecology*, *14*, 437–447.
- Mcloughlin, P. D. (2000). A hierarchical pattern of limiting factors helps explain variation in home range size. *Ecoscience*, 7(2), 123-130. https://doi.org/10.1080/11956860.2000.11682580
- Mcnab, B. K. (1963). Bioenergetics and the determination of home range size. *The American Naturalist*, *97*(894), 133–140.
- Mduma, S. A. R., Sinclair, A. R. E., & Hilborn, R. A. Y. (1999). Food regulates the Serengeti wildebeest : a 40-year record. *Journal of Animal Ecology, 68*, 1101–1122.
- Merkle, J. A., Monteith, K. L., Aikens, E. O., Hayes, M. M., Hersey, K. R., Middleton, A. D., ... Kauffman, M. J. (2016). Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society B: Biological Sciences*, 283(1833), 1–8. https://doi.org/10.1098/rspb.2016.0456
- Mole, M. (2015). Behavioural thermoregulation in free-ranging savanna elephants (Loxodonta africana). [Master's thesis, University of Pretoria] UPSpace Institutional Repository.
- Mole, M. A, Aarde, R. J. Van, Mitchell, D., & Fuller, A. (2016). Coping with heat: behavioural and physiological responses of savanna elephants in their natural habitat. *Conservation Physiology*, 4, 1–11. https://doi.org/10.1093/conphys/cow044
- Moorcroft, P. R. (2012). Mechanistic approaches to understanding and predicting mammalian space use: recent advances, future directions. *Journal of Mammalogy*, 93(4), 903–916. https://doi.org/10.1644/11-MAMM-S-254.1
- Morales, Juan M, Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., ... Haydon, D. T. (2010). Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2289–2301. https://doi.org/10.1098/rstb.2010.0082
- Morales, Juan Manuel, Fortin, D., Frair, J. L., & Merrill, E. H. (2005). Adaptive models for large herbivore movements in heterogeneous landscapes. *Landscape Ecology*, 20, 301–316. https://doi.org/10.1007/s10980-005-0061-9
- Morris, D. (1988). Habitat-dependent population regulation and community structure. *Evolutionary Ecology*, *2*, 253–269.

- Mosugelo, D. K., Moe, S. R., Ringrose, S., & Nellemann, C. (2002). Vegetation changes during a 36-year period in northern Chobe National Park, Botswana. *African Journal of Ecology*, 40(3), 232–240. https://doi.org/10.1046/j.1365-2028.2002.00361.x
- Mumby, H. S., Courtiol, A., Khyne, U. ., & Lummaa, V. (2013). Climatic variation and age-specific survival in Asian elephants from Myanmar. *Ecology*, 94(5), 1131–1141.
- Mutanga, O., & Rugege, D. (2007). Integrating remote sensing and spatial statistics to model herbaceous biomass distribution in a tropical savanna. *International Journal of Remote Sensing*, *27*, 3499–3514. https://doi.org/10.1080/01431160600639735
- Nagaoka, L. (2002). The effects of resource depression on foraging efficiency, diet breadth, and patch use in southern New Zealand. *Journal of Anthropological Archeaology, 21*, 419–442.
- Naidoo, R., Du, P., Weaver, G. S. L. C., Jago, M., & Wegmann, M. (2012). Factors affecting intraspecific variation in home range size of a large African herbivore, *PLoS One*, 7(5), 1523–1534. https://doi.org/10.1007/s10980-012-9807-3
- Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, 105(49), 19052–19059. https://doi.org/10.1073/pnas.0800375105
- Nathan, Ran, Getz, W., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. (2008). What is movement Ecology? *Pnas*, *105*(49), 19052–19059. https://doi.org/10.1017/CBO9781107415324.004
- Ndaimani, H., Murwira, A., Masocha, M., & Zengeya, F. M. (2017). Elephant (Loxodonta africana) GPS collar data show multiple peaks of occurrence farther from water sources. *Cogent Environmental Science*, 3(1). https://doi.org/10.1080/23311843.2017.1420364
- Neil, E., Madsen, J. K., Carrella, E., Payette, N., & Bailey, R. (2020). Agent-based modelling as a tool for elephant poaching mitigation. *Ecological Modelling*, 427(May), 109054. https://doi.org/10.1016/j.ecolmodel.2020.109054
- Ngene, S. M., Van Gils, H., Van Wieren, S. E., Rasmussen, H., Skidmore, A. K., Prins, H. H. T., ... Douglas-Hamilton, I. (2010). The ranging patterns of elephants in Marsabit protected area, Kenya: The use of satellite-linked GPS collars. *African Journal of Ecology*, 48(2), 386–400. https://doi.org/10.1111/j.1365-2028.2009.01125.x
- O'Connor, T. G., Goodman, P. S., & Clegg, B. (2007). A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. *Biological Conservation*, *136*(3), 329–345. https://doi.org/10.1016/j.biocon.2006.12.014
- Owen-Smith, N. (1993). Evaluating optimal diet models for an African browsing ruminant, the kudu : how constraining are the assumed constraints ? *Evolutionary Ecology*, 7, 499–524

- Owen-Smith, N., Kerley, G. I. H., Page, B., Slotow, R., & Van Aarde, R. J. (2006). A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. *South African Journal of Science*, *102*(9–10), 389–394. https://doi.org/10.1016/j.actbio.2010.06.025
- Owen-Smith, N. (1996). Ecological guidelines for waterpoints. South African Journal of Wildlife Research, 26(4).
- Owen-Smith, N., & Chafota, J. (2012). Selective feeding by a megaherbivore, the African elephant (Loxodonta africana). *Journal of Mammalogy*, *93*(3), 698–705. https://doi.org/10.1644/11-MAMM-A-350.1
- Owen-Smith, N., Hopcraft, G., Morrison, T., Chamaillé-Jammes, S., Hetem, R., Bennitt, E., & Van Langevelde, F. (2020). Movement ecology of large herbivores in African savannas: current knowledge and gaps. *Mammal Review*, 50(3), 252–266. https://doi.org/10.1111/mam.12193
- Pandey, C. B., & Singh, J. S. (1992). Rainfall and grazing effects on net primary productivity in a tropical savanna, India. *Ecology*, 73(6), 2007–2021.
- Patterson, T. A., Parton, A., Langrock, R., Blackwell, P. G., Thomas, L., & King, R. (2017). Statistical modelling of individual animal movement : an overview of key methods and a discussion of practical challenges. *AStA Advances in Statistical Analysis*, 101(4), 399–438. https://doi.org/10.1007/s10182-017-0302-7
- Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O., & Matthiopoulos, J. (2008). State-space models of individual animal movement. *Trends in Ecology and Evolution*, 23(2), 87–94. https://doi.org/10.1016/j.tree.2007.10.009
- Peck, S. L. (2004). Simulation as experiment : a philosophical reassessment for biological modeling. *TRENDS in Ecolog and Evolution*, 19(10). https://doi.org/10.1016/j.tree.2004.07.019
- Pekel, J.-F., Cottam, A., Gorelick, N., & Belward, A. S. (2016). High-resolution mapping of global surface water and its long-term changes. *Nature*, 1–19. https://doi.org/10.1038/nature20584
- Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., & Kausrud, K. (2011). The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. *Climate Research*, 46(1), 15–27. https://doi.org/10.3354/cr00936
- Philips, I. (2020). An agent based model to estimate lynx dispersal if re-introduced to Scotland. *Applied Spatial Analysis and Policy*, 13(1), 161–185. https://doi.org/10.1007/s12061-019-09297-4
- Pinheiro, Jose; Bates, Douglas; DebRoy, Saikat; Sarkar, D. (2011). Package ' nlme .'
- Plessis, K. L. D. U., Martin, R. O., Hockey, P. A. R., & Susan, J. (2012). The costs of keeping cool in a warming world : implications of high temperatures for foraging , thermoregulation and body condition of an arid-zone bird. *Global Change Biology*, 3063–3070. https://doi.org/10.1111/j.1365-2486.2012.02778.x

- Polansky, L., Kilian, W., & Wittemyer, G. (2015). Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state-space models. *Proceedings of the Royal Society B: Biological Sciences*, 282(1805), 20143042–20143042. https://doi.org/10.1098/rspb.2014.3042
- Polansky, Leo, Douglas-Hamilton, I., & Wittemyer, G. (2013). Using diel movement behavior to infer foraging strategies related to ecological and social factors in elephants. *Movement Ecology*, 1(1), 13. https://doi.org/10.1186/2051-3933-1-13
- Powell, R. A., & Mitchell, M. S. (2012). What is a home range ? *Journal of Mammalogy*, *93*(4), 948–958. https://doi.org/10.1644/11-MAMM-S-177.1
- Preisler, H. K., Ager, A. A., Johnson, B. K., & Kie, J. G. (2004). Modeling animal movements using stochastic differential equations. *Environmetrics*, 15(7), 643–657. https://doi.org/10.1002/env.636
- Pretorius, Y., de Boer, F. W., van der Waal, C., de Knegt, H. J., Grant, R. C., Knox, N. M., ... Prins, H. H. T. (2011). Soil nutrient status determines how elephant utilize trees and shape environments. *Journal of Animal Ecology*, 80(4), 875–883. https://doi.org/10.1111/j.1365-2656.2011.01819.x
- Purdon, A. (2015). Environmental determinants of the movement patterns of elephants in the Kruger National Park [Master's thesis, University of Pretoria] UPSpace Institutional Repository.
- Purdon, A., & van Aarde, R. J. (2017a). Water provisioning in Kruger National Park alters elephant spatial utilisation patterns. *Journal of Arid Environments*, 141(February), 45–51. https://doi.org/10.1016/j.jaridenv.2017.01.014
- Purdon, A., & van Aarde, R. J. (2017b). Water provisioning in Kruger National Park alters elephant spatial utilisation patterns. *Journal of Arid Environments*, 141(October), 45–51. https://doi.org/10.1016/j.jaridenv.2017.01.014
- Railsback, S. F. (2001). Concepts from complex adaptive systems as a framework for individual-based modelling. *Ecological Modelling*, 139(1), 47–62. https://doi.org/10.1016/S0304-3800(01)00228-9
- Ramoelo, A., Skidmore, A.K., Cho, M.A., Schlerf, M., Mathieu, R., Heitkönig, I.M.A (2012). Regional estimation of savanna grass nitrogen using the red-edge band of the spaceborne RapidEye sensor. *International Journal of Applied Earth Observations and Geoinformation*, 19, 151–162.
- Ramoelo, A., Cho, M.A. (2018). Explaining leaf nitrogen distribution in a semi-arid environment predicted on Sentinel-2 imagery using a field spectroscopy derived model. *Remote Sensing*, 10, 269.
- Redfern, JV. (2003). Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, 84(8). https://doi.org/10.1016/j.socscimed.2013.05.029

- Redfern, J. V., Grant, C. C., Gaylard, a., & Getz, W. M. (2005). Surface water availability and the management of herbivore distributions in an African savanna ecosystem. *Journal of Arid Environments*, 63(2), 406–424. https://doi.org/10.1016/j.jaridenv.2005.03.016
- Redhead, J. W., Dreier, S., Bourke, A. F. G., Heard, M. S., Redhead, J. W., Dreier, S., ... Carvell, C. (2019). Effects of habitat composition and landscape structure on worker foraging distances of five bumble bee species. *Ecological Applications*, 26(3), 726– 739.
- Robson, A. S., Trimble, M. J., Purdon, A., Young-overton, K. D., Pimm, S. L., & van aarde, R. J. (2017). Savanna elephant numbers are only a quarter of their expected values. *PLoS One*, *12(4)*, 1–14.
- Roese, J. H., Risenhover, K. L., & Folse, J. L. (1991). Habitat heterogeneity and foraging efficiency : an individual-based model. *Ecological Modelling*, *57*, 133–143.
- Roever, C. L., van Aarde, R. J. Van, & Chase, M. J. (2013a). Incorporating mortality into habitat selection to identify secure and risky habitats for savannah elephants. *Biological Conservation*, 164, 98–106. https://doi.org/10.1016/j.biocon.2013.04.006
- Roever, C. L., van Aarde, R. J., & Leggett, K. (2012). Functional responses in the habitat selection of a generalist mega-herbivore, the African savannah elephant. *Ecography*, 35(11), 972–982. https://doi.org/10.1111/j.1600-0587.2012.07359.x
- Roever, C. L., van Aarde, R. J., & Leggett, K. (2013b). Functional connectivity within conservation networks: Delineating corridors for African elephants. *Biological Conservation*, 157, 128–135. https://doi.org/10.1016/j.biocon.2012.06.025
- Roug, A., Muse, E.A., Clifford, D.L...(2020). Seasonal movements and habitat use of African buffalo in Ruaha National Park, Tanzania. *BMC Ecol* 20, 6. https://doi.org/10.1186/s12898-020-0274-4
- Roshier, D., Doerr, V., & Doerr, E. (2008). Animal movement in dynamic landscapes : interaction between behavioural strategies and resource distributions. *Behavioral Ecology*, *156*, 465–477. https://doi.org/10.1007/s00442-008-0987-0
- Rowe, M. F., Bakken, G. S., Ratliff, J. J., & Langman, V. a. (2013). Heat storage in Asian elephants during submaximal exercise: Behavioral regulation of thermoregulatory constraints on activity in endothermic gigantotherms. *The Journal* of Experimental Biology, 216, 1774–1785. https://doi.org/10.1242/jeb.076521
- Rozen-Rechels, D., Valls-Fox, H., Mabika, C. T., & Chamaillé-Jammes, S. (2020). Temperature as a constraint on the timing and duration of African elephant foraging trips. *Journal of Mammalogy*, 101(6), 1670-1679
- Ryan, S. J., Cross, P. C., Winnie, J., Hay, C., Bowers, J., & Getz, W. M. (2012). The utility of normalized difference vegetation index for predicting African buffalo forage quality. *Journal of Wildlife Management*, 76(7), 1499–1508. https://doi.org/10.1002/jwmg.407

- Sai, S., & Bourgoin, G. (2009). What shapes intra specific variation in home range size ? A case study of female roe deer What shapes intra-specific variation in home range size ? A case study of female roe deer, *Oikos*, *118*, 1299-1306. https://doi.org/10.1111/j.1600-0706.2009.17346.x
- Samanta, S., Pal, D. K., & Lohar, D. (2012). Interpolation of climate variables and temperature modeling. *Theoretical and Applied Climatology*. https://doi.org/10.1007/s00704-011-0455-3
- Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., ... Zambatis, N. (2005). Determinants of woody cover in African savannas. *Nature*, 438(7069), 846–849. https://doi.org/10.1038/nature04070
- Scheiter, S., & Higgins, S. I. (2009). Impacts of climate change on the vegetation of Africa: An adaptive dynamic vegetation modelling approach. *Global Change Biology*, 15(9), 2224–2246. https://doi.org/10.1111/j.1365-2486.2008.01838.x
- Schick, R. S., Loarie, S. R., Colchero, F., Best, B. D., Boustany, A., Conde, D. a., ... Clark, J. S. (2008). Understanding movement data and movement processes: Current and emerging directions. *Ecology Letters*, 11(12), 1338–1350. https://doi.org/10.1111/j.1461-0248.2008.01249.x
- Schmitt, M. H., Shuttleworth, A., Shrader, A. M., & Ward, D. (2020). The role of volatile plant secondary metabolites as pre-ingestive cues and potential toxins dictating diet selection by African elephants. *Oikos*, 129(1), 24–34. https://doi.org/10.1111/oik.06665
- Schultz, C. B., & Crone, E. E. (2016). Edge-Mediated Dispersal Behavior in a Prairie Butterfly, *Ecology*, 82(7), 1879–1892.
- Schütz, K. E., Rogers, A. R., Poulouin, Y. A., Cox, N. R., & Tucker, C. B. (2010). The amount of shade influences the behavior and physiology of dairy cattle. *Journal of Dairy Science*, 93(1), 125–133. https://doi.org/10.3168/jds.2009-2416
- Seidel, D. P., & Boyce, M. S. (2015). Patch-use dynamics by a large herbivore. *Movement Ecology*, 3(1), 3–7. https://doi.org/10.1186/s40462-015-0035-8
- Seigle-ferrand, J., Atmeh, K., Gaillard, J., & Ronget, V. (2021). A systematic review of within-population variation in the size of home range across ungulates : What Do We Know After 50 Years of Telemetry Studies ?, *Frontiers in Ecology and Evolution*, 1–20. https://doi.org/10.3389/fevo.2020.555429
- Semeniuk, C. A. D., Musiani, M., Hebblewhite, M., Grindal, S., & Marceau, D. J. (2012). Incorporating behavioral – ecological strategies in pattern-oriented modeling of caribou habitat use in a highly industrialized landscape. *Ecological Modelling*, 243, 18–32. https://doi.org/10.1016/j.ecolmodel.2012.06.004
- Semeniuk, C. A. D., Musiani, M., & Marceau, D. J. (2011). Integrating spatial behavioral ecology in agent-based models for species conservation. *Biodiversity*, (1), 3–26. https://doi.org/10.5772/23055

- Shannon, G., Matthews, W. S., Page, B. R., Parker, G. E., & Smith, R. J. (2009). The affects of artificial water availability on large herbivore ranging patterns in savanna habitats : a new approach based on modelling elephant path distributions, *Diversity* and Distributions, 776–783. https://doi.org/10.1111/j.1472-4642.2009.00581.x
- Shannon, G., Page, B. R., Mackey, R. L., Duffy, K. J., & Slotow, R. O. B. (2008). Activity budgets and sexual segregation in African elephants (Loxodonta Africana), *Journal of Mammology*, 89(2), 467–476.
- Shannon, G., Page, B., Slotow, R., & Duffy, K. (2006). African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *African Zoology*, 41(1), 37–44. https://doi.org/10.3377/1562-7020(2006)41[37:AEHRAH]2.0.CO;2
- Shaw, A. K. (2020). Causes and consequences of individual variation in animal movement. *Movement Ecology*, 1–12. 10.1186/s40462-020-0197-x
- Shrader, A. M., Bell, C., Bertolli, L., & Ward, D. (2012a). Forest or the trees: At what scale do elephants make foraging decisions? *Acta Oecologica*, *42*, 3–10. https://doi.org/10.1016/j.actao.2011.09.009
- Shrader, A. M., Kerley, G. I. H., Brown, J. S., & Kotler, B. P. (2012b). Patch use in freeranging goats : does a large mammalian herbivore forage like other central place foragers ?, *Ethology*, 967–974. https://doi.org/10.1111/j.1439-0310.2012.02090.x
- Shrader, A. M., Pimm, S. L., & Aarde, R. J. Van. (2010). Elephant survival, rainfall and the confounding effects of water provision and fences. *Biodiversity Conservation*, 9(18), 2235-2245. https://doi.org/10.1007/s10531-010-9836-7
- Shrader, A. M., Owen-Smith, N., Ogutu, A.O. (2006). How a mega-grazer copes with the dry season: food and nutrient intake rates by white rhinoceros in the wild. *Funct. Ecol.* 20: 376–384.
- Sianga, K., and Fynn, R. (2017). The vegetation and wildlife habitats of the Savuti-Mababe-Linyanti ecosystem, northern Botswana. *Koedoe* 59(2). doi: 10.4102/koedoe.v59i2.1406
- Sibly, R.M. & Calow, P. (1986) Physiological Ecology of Animals.Blackwell Scientific Publications, Oxford.
- Sibly, R. M., Grimm, V., Martin, B. T., Johnston, A. S. A., Kulakowska, K., Topping, C. J., ... Deangelis, D. L. (2013). Representing the acquisition and use of energy by individuals in agent-based models of animal populations. *Methods in Ecology and Evolution*, 4(2), 151–161. https://doi.org/10.1111/2041-210x.12002
- Smit, I. P. (2013). Systems approach towards surface water distribution in Kruger. *Pachyderm*, (53), 91–98.
- Smit, I. P J, & Grant, C. C. (2009). Managing surface-water in a large semi-arid savanna park: Effects on grazer distribution patterns. *Journal for Nature Conservation*, 17(2), 61–71. https://doi.org/10.1016/j.jnc.2009.01.001

- Smit, I. P.J., Grant, C. C., & Devereux, B. J. (2007). Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*, 136(1), 85–99. https://doi.org/10.1016/j.biocon.2006.11.009
- Solomon, S., Plattner, G.-K., Knutti, R., & Friedlingstein, P. (2009). Irreversible climate change due to carbon dioxide emissions. *Proceedings of the National Academy of Sciences of the United States of America*, 106(6), 1704–1709. https://doi.org/10.1073/pnas.0812721106
- Somparn, P., Gibb M.J., V. C. (2006). Wallowing behavior of swamp buffalo (Bubalus bubalis) heifers under continuous stocking during the summer in northeastern Thailand. *Buffalo Journal*, 1, 11-14.
- Stillman, R. A., Railsback, S. F., Giske, J., Berger, U., & Grimm, V. (2015). Making predictions in a changing world: The benefits of individual-based ecology. *BioScience*, 65(2), 140–150. https://doi.org/10.1093/biosci/biu192
- Stokke, S., & Du Toit, J. T. (2002). Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *African Journal of Ecology*, 40(4), 360–371. https://doi.org/10.1046/j.1365-2028.2002.00395.x
- Strydom, S., & Savage, M. J. (2016). A spatio-temporal analysis of fires in South Africa. South African Journal of Science, 112(11), 1–8. https://doi.org/10.17159/sajs.2016/20150489
- Sun, Z., Lorscheid, I., Millington, J. D., Lauf, S., Magliocca, N. R., Groeneveld, J., ... Buchmann, C. M. (2016). Environmental Modelling & Software Simple or complicated agent-based models ? A complicated issue. *Environmental Modelling* and Software, 86(3), 56–67. https://doi.org/10.1016/j.envsoft.2016.09.006
- Sutherland, A., & Sutherland, K. (2021). Use of artificial waterholes by animals in the southern region of the Kruger National Park, South Africa. *BioOne*, 48(2).
- Synes, N. W., Brown, C., Watts, K., White, S. M., Gilbert, M. A., & Travis, J. M. J. (2016). Emerging opportunities for landscape ecological modelling. *Current Landscape Ecology Reports*, 146–167. https://doi.org/10.1007/s40823-016-0016-7
- Tang, W., & Bennett, D. (2010). Agent based modeling of animal movement: a review. *Geography Compass*, 7, 1–30. https://doi.org/10.1111/j.1749-8198.2010.00337.x
- Technitis, G., Othman, W., Safi, K., & Weibel, R. (2015). From A to B, randomly: a point-to-point random trajectory generator for animal movement. *International Journal of Geographical Information Science*. https://doi.org/10.1080/13658816.2014.999682
- Tempe, A. S. ., Chase, M. J., Roger, T. ., & Leggett, K. E. . (2017). Taking the elephant out of the room and into the corridor: can urban corridors work? *Oryx*, 51(2), 347– 353. https://doi.org/10.1017/S0030605315001246

- Thaker, M., Gupte, P. R., Prins, H. H. T., & Slotow, R. (2019). Fine-scale tracking of ambient temperature and movement reveals shuttling behavior of elephants to water, *Frontiers in Ecology and Evolution*, 1–12. https://doi.org/10.3389/fevo.2019.00004
- Thomas, B., Holland, J. D., & Minot, E. O. (2008). Elephant (Loxodonta africana) home ranges in Sabi Sand Reserve and Kruger National Park: A five-year satellite tracking study. *PLoS ONE*, *3*(12). https://doi.org/10.1371/journal.pone.0003902
- Thomas, B., Holland, J. D., & Minot, E. O. (2011). Seasonal home ranges of elephants ( Loxodonta africana) and their movements between Sabi Sand Reserve and Kruger National Park. *African Journal of Ecology*, 50, 131–139.
- Thrash, I. (2000). Determinants of the extent of indigenous large herbivore impact on herbaceous vegetation at watering points in the north-eastern lowveld, South Africa. *Journal of Arid Environments*, (44), 61–72. https://doi.org/10.1006/jare.1999.0452
- Thrash, I., & Dfrry, J. F. (1999). The nature and modelling of piospheres: A review. *Koedoe*, 42(2), 73–94. https://doi.org/10.4102/koedoe.v42i2.234
- Thums, M., Fernández-gracia, J., Sequeira, A. M. M., & Eguíluz, V. M. (2018). How big data fast tracked human mobility research and the lessons for animal movement ecology. *Frontiers in Marine Science*, 5(February), 1–12. https://doi.org/10.3389/fmars.2018.00021
- Traill L.W. (2004). Seasonal utilization of habitat by large grazing herbivores in semiarid Zimbabwe. *South African Journal of Wildlife Research* 34: 13–24.
- Troup, G., Doran, B., Au, J., King, L. E., Douglas-Hamilton, I., & Heinsohn, R. (2020). Movement tortuosity and speed reveal the trade-offs of crop raiding for African elephants. *Animal Behaviour*, 168, 97–108. https://doi.org/10.1016/j.anbehav.2020.08.009
- Tsalyuk, M., Kilian, W., Reineking, B., & Getz, W. M. (2019). Temporal variation in resource selection of African elephants follows long-term variability in resource availability. *Ecological Monographs*, 89(2), 1–19. https://doi.org/10.1002/ecm.1348
- Tufto, J., Andersen, R., & Linnell, J. (1996). Habitat use and ecological correlates of home range size in a small cervid : the roe habitat use and ecological correlates of home range size in a small cervid : the roe deer, *Journal of Animal Ecology*, 65(6), 715–724.
- Tulloch, D. G., & Litchfield, R. T. (1981). Wallows for buffalo. Australian Wildlife Research 8(3), 555 - 565.
- Turner, M. G., Wu, Y., Romme, W., & Wallace, L. (1993). A landscape simulation model of winter foraging by large ungulates. *Ecological Modelling*, 69(1993), 163– 184.
- Valeix, M., Fritz, H., Matsika, R., Matsvimbo, F., & Madzikanda, H. (2008). The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores. *African Journal of Ecology*, 46(3), 402–410. https://doi.org/10.1111/j.1365-2028.2007.00874.x

- Valls-fox, H., Garine-wichatitsky, M. De, Herve, F., & Chamaille, S. (2018). Resource depletion versus landscape complementation : habitat selection by a multiple central place forager, *Landscape Ecology*, 127–140. https://doi.org/10.1007/s10980-017-0588-6
- van Beest, F. M. Van, Mcloughlin, P. D., Vander, E., & Ryan, W. (2014). Density dependent habitat selection and partitioning between two sympatric ungulates. *Behavioral Ecology*, 175, 1155–1165. https://doi.org/10.1007/s00442-014-2978-7
- van de Ven, T. M. F. N., McKechnie, A. E., & Cunningham, S. J. (2019). The costs of keeping cool : behavioural trade - offs between foraging and thermoregulation are associated with significant mass losses in an arid - zone bird. *Oecologia*, 191(1), 205–215. https://doi.org/10.1007/s00442-019-04486-x
- Van Moorter, B., Bunnefeld, N., Panzacchi, M., Rolandsen, C. M., Solberg, E. J., & Sæther, B. E. (2013). Understanding scales of movement: Animals ride waves and ripples of environmental change. *Journal of Animal Ecology*, 82(4), 770–780. https://doi.org/10.1111/1365-2656.12045
- Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M. S., & Gaillard, J. M. (2009). Memory keeps you at home: A mechanistic model for home range emergence. *Oikos*, 118(5), 641–652. https://doi.org/10.1111/j.1600-0706.2008.17003.x
- Vanak, A. T., Thaker, M., & Slotow, R. (2010). Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? *Biological Conservation*, 143(11), 2631–2637. https://doi.org/10.1016/j.biocon.2010.07.005
- Vanschoenwinkel, B., Waterkeyn, A., Nhiwatiwa, T., Pinceel, T., Spooren, E., Geerts, A., ... Brendonck, L. (2011). Passive external transport of freshwater invertebrates by elephant and other mud-wallowing mammals in an African savannah habitat. *Freshwater Biology*, 56(8), 1606–1619. https://doi.org/10.1111/j.1365-2427.2011.02600.x
- Veldhuis, M. ., Kihwele, E. ., Cromsigt, J. P. G. ., Ogutu, J. ., Hopcraft, J. G. C., Owen-Smith, N., & Olff, H. (2019). Large herbivore assemblages in a changing climate : incorporating water dependence and thermoregulation. *Ecology Letters*, 22, 1536– 1546. https://doi.org/10.1111/ele.13350
- Venter, F. ., & Bristow, J. . (1986). An account of the geomorphology and drainage of the Kruger National Park. *Koedoe*, 29, 117–124.
- Verlinden, A., & Masogo, R. (1997). Satellite remote sensing of habitat suitability for ungulates and ostrich in the Kalahari of Botswana, *Journal of Arid Environments*, 563–574.
- Viljoen, P.J. (1989). Spatial distribution and movements of elephants (Loxodonta africana) in the northern Namib Desert region of the Kaokoveld, South West Africa/Namibia. *Journal of Zoology*, 219, 1–19.

- Vincenot, C. E., Mazzoleni, S., Moriya, K., Cartenì, F., & Giannino, F. (2015). How spatial resource distribution and memory impact foraging success: A hybrid model and mechanistic index. *Ecological Complexity*, 22, 139–151. https://doi.org/10.1016/j.ecocom.2015.03.004
- Vuilleumier, S., & Metzger, R. (2006). Animal dispersal modelling: handling landscape features and related animal choices. *Ecological Modelling*, 190(1–2), 159–170. https://doi.org/10.1016/j.ecolmodel.2005.04.017
- Walker, B. H., H, E. R., Owen-Smith, R. N., & Scholes, R. J. (1987). To cull or not to cull : lessons from a Southern African drought. *Journal of Applied Ecology*, 24(2), 381–401.
- Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V., Blake, S., Strindberg, S., ... Douglas-Hamilton, I. (2021). Human footprint and protected areas shape elephant range across Africa. *Current Biology*, 1–9. https://doi.org/10.1016/j.cub.2021.03.042
- Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V., & Douglas-Hamilton, I. (2013). Characterizing properties and drivers of long distance movements by elephants (Loxodonta africana) in the Gourma, Mali. *Biological Conservation*, 157, 60–68. https://doi.org/10.1016/j.biocon.2012.07.019
- Wallisdevries, M. F. (1996). Effects of resource distribution patterns on ungulate foraging behaviour : a modelling approach. *Forest Ecology and Management*, 127(96), 167–177.
- Watkins, A., Noble, J., Foster, R. J., Harmsen, B. J., & Doncaster, C. P. (2015). A spatially explicit agent-based model of the interactions between jaguar populations and their habitats. *Ecological Modelling*, 306, 268–277. https://doi.org/10.1016/j.ecolmodel.2014.10.038
- Wato, Y. A., Prins, H. H. T., Heitkönig, I. M. A., Wahungu, G. M., Ngene, S. M., Njumbi, S., & van Langevelde, F. (2018). Movement patterns of African Elephants (Loxodonta africana) in a Semi-arid Savanna suggest that they have information on the location of dispersed water sources. *Frontiers in Ecology and Evolution*, 6, 1–8. https://doi.org/10.3389/fevo.2018.00167
- Weeber, J., Hempson, G. P. & February, E. C. (2020) Large herbivore conservation in a changing world: surface water provision and adaptability allow wildebeest to persist after collapse of long-range movements. *Glob. Change Biol.* 26(5), 2841–2853.
- Western, D., & Lindsay, W. K. (1984). Seasonal herd dynamics of a savanna elephant population. *African Journal of Ecology*, *22*, 229–244. https://doi.org/10.1111/j.1365-2028.1984.tb00699.x
- White, R. G., Proceedings, L., Held, S., & White, R. G. (1983). Foraging patterns and their multiplier effects on productivity of northern ungulates. *40*(3), 377–384.

- Whitecross, M. A., Witkowski, E. T. F., & Archibald, S. (2017). Savanna tree-grass interactions: A phenological investigation of green-up in relation to water availability over three seasons. *South African Journal of Botany*, 108, 29–40. https://doi.org/10.1016/j.sajb.2016.09.003
- Wiegand, T., Jeltsch, F., Hanski, I., & Grimm, V. (2020). Using pattern-oriented modeling for revealing hidden information : A key for reconciling ecological theory and application. *Oikos, 100,* 209-222. https://doi.org/10.1034/j.1600-0706.2003.12027.x
- Wiens, A. J. A. (1989). Spatial Scaling in Ecology. Functional Ecology, 3(4), 385–397.
- Wiggins, N. L., McArthur, C., Davies, N. W., & McLean, S. (2006). Spatial scale of the patchiness of plant poisons: A critical influence on foraging efficiency. *Ecology*, 87(9), 2236–2243. https://doi.org/10.1890/0012-9658(2006)87[2236:SSOTPO]2.0.CO;2
- Wijeyakulasuriya, D. A., Eisenhauer, E., Shaby, B., & Hanks, E. (2020). Machine learning for modeling animal movement, 1–30. https://doi.org/10.1371/journal.pone.0235750
- Wittemyer, G., Douglas-Hamilton, I., & Getz, W. M. (2005). The socioecology of elephants: Analysis of the processes creating multitiered social structures. *Animal Behaviour*, 69(6), 1357–1371. https://doi.org/10.1016/j.anbehav.2004.08.018
- Wittemyer, G., Getz, W. M., Vollrath, F., & Douglas-Hamilton, I. (2007). Social dominance, seasonal movements, and spatial segregation in African elephants: A contribution to conservation behavior. *Behavioral Ecology and Sociobiology*, *61*(12), 1919–1931. https://doi.org/10.1007/s00265-007-0432-0
- Wittemyer, George, Polansky, L., Douglas-hamilton, I., & Getz, W. M. (2008). Disentangling the effects of forage, social rank, and risk on movement autocorrelation of elephants using Fourier and wavelet analysis, *Proceedings of the National Academy of Sciences of the United States of America*, 105(49), 1–6.
- Wood, K. A., Stillman, R. A., & Hilton, G. M. (2018). Conservation in a changing world needs predictive models. *Animal Conservation*, 21(2), 87–88. https://doi.org/10.1111/acv.12371
- Wright, J. P., & Jones, C. G. (2006). The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. *BioScience*, 56(3), 203. https://doi.org/10.1641/0006-3568(2006)056[0203:TCOOAE]2.0.CO;2
- Yoganand K., Owen-Smith N. (2014) Restricted habitat use by an African savanna herbivore through the seasonal cycle: key resources concept expanded. *Ecography*, 37: 969–982.
- Young, K. D., Ferreira, S. M., & Van Aarde, R. J. (2009). Elephant spatial use in wet and dry savannas of southern Africa. *Journal of Zoology*, 278(3), 189–205. https://doi.org/10.1111/j.1469-7998.2009.00568.x

- Young, K. D., & van Aarde, R. J. (2010). Density as an explanatory variable of movements and calf survival in savanna elephants across southern Africa. *Journal of Animal Ecology*, 79(3), 662–673. https://doi.org/10.1111/j.1365-2656.2010.01667.x
- Zhang, Y., Feng, X., Fu, B., Chen, Y., & Wang, X. (2021). Satellite-observed global terrestrial vegetation production in response to water availability, *Remote Sensing*, 1–20.

## Appendix

# A. Supplementary material for Chapter 3

# A.1 ODD Protocol

### A.1.1 Model description

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al. 2006, 2010, 2019; Railsback and Grimm 2019). The model was implemented in MatLab version 2017a.

## A.1.1.1 Purpose and patterns

The model's purpose is to simulate the fine-scale space use and movement patterns of the African savanna elephant *(Loxodonta africana)*, with the ultimate goal of utilizing the model as a predictive tool to explore how different scenarios of environmental change affect elephant movement. We used elephant movement paths for the years 2012-2014 to identify test patterns that would be used for model validation. To consider our model realistic enough for its purpose, we used patterns associated with home range size, diel displacement distance, net displacement distance, and maximum distance traveled from a permanent water source between parks and between seasons. We determined whether differences existed in these movement characteristics, using a total of 200 empirical trajectories from four cows in CNP and nine cows in KNP and implementing Linear Mixed Models (LMMs).

Each simulated trajectory was paired with one empirical trajectory, such that the first location of a given simulated trajectory was the first location of its paired empirical

186

trajectory. We used Linear Mixed models (LMMs) to determine whether there were significant differences between the movement characteristics calculated from the simulated and empirical trajectories. A second LMM was used with structure similar to the first, with the addition of a third binary fixed effect, "Sim". "Sim" was set as "1" for a data point that was calculated from a simulated trajectory and "2" for a data point calculated from an empirical trajectory. Additionally, a third random effect was added and nested within "Year", so that paired trajectories were only compared to each other, as opposed to other trajectories within the same year.

We made quantitative and qualitative comparisons to the empirical data to validate model outputs. For quantitative comparisons, we standardized our data and used LMMs to express all parameter estimates in terms of effect sizes. Effect sizes were determined for "Sims", "Sims\*Park", "Sims\*Season", and "Sims\*Park\*Season", for each movement characteristic. Smaller effect sizes indicated that the model was relatively successful at reproducing the movement characteristics. For qualitative comparisons, we assessed whether our model was able to reproduce the nine movement patterns present in the empirical data using LMMs.

# A.1.1.2 Entities, state variables and scales

The model includes the following entities: the agents, which represent an elephant family unit and one of the simplest levels of social hierarchy in elephant populations (Wittemyer,Douglas-Hamilton, & Getz, 2005), the landscape cells, and the overall environment. The entities are characterized by the state variables and attributes in Table A.1 (possible units and values are also listed). The agent is mobile and can respond to environmental stressors by changing its behavior and subsequent movement across the landscape. Behaviors are determined utilizing a hierarchical decision process, whereby the agent responds to stressors before employing foraging behavior. The agent is characterized by the following state variables and attributes: 1) its state, which represents the differences in sensitivity to environmental temperatures between family groups with calves and those without calves, 2) its position on the landscape (x, and y coordinates), at any given time step, 3) the time since it last visited a water source, 4) the behavior that it is employing, and 5) the environmental temperature that it is experiencing at a given time (perceived environmental temperature). Landscape cells are characterized by the following attributes: 1) the Enhanced Vegetation Index (EVI) within the cell, 2) the percent tree cover within the cell, and 3) a binary value indicating whether a water source is within the cell. These values were static and did not change for the duration of the simulation, except for the greenness value, which decreased when the agent foraged within a cell, and may have increased stochastically at a given time step due to vegetation changes. The Enhanced Vegetation Index (EVI) is a measure of vegetation "greenness" values ranging from 0-1, where values closer to one indicate greener vegetation. Several studies have concluded that EVI and Normalized Digital Vegetation Index (NDVI) may be a good proxy for productivity, vegetation biomass, and forage quality within the landscape (Pettorelli et al., 2011; Ryan et al., 2012). Each cell contained a value between 0 and 1 representing the vegetation greenness within the cell. Percent tree cover, defined as canopy closure for vegetation taller than five meters, was used as a measure of shade availability. Each cell contained a value ranging from 0 to 100 representing the percent tree cover underlying the cell.

The overall environment is characterized by the following state variables: 1) environmental temperature, and 2) the percent of the landscape that increases in greenness. Environmental temperature was retrieved from the nearest weather station to the study area and was updated every time step as a global variable.

The spatial resolution and extent are 30 m by 30 m, and the extent for each area modeled differs and is approximately 360 km by 120 km for Kruger National Park, and 160 km by 128 km for Chobe National Park. The model "landscapes" are composed of several rasters representing two protected areas in southern Africa: Kruger National Park in South Africa and Chobe National Park in Botswana (including parts of Kasane Forest Reserve, Kasane Forest Extension, Chobe Forest Reserve, and Maikaelelo Forest Reserve). These rasters include one representing vegetation quality, water source presence, and tree cover percentage. The temporal resolution and extent are hourly time steps, and 336 timesteps, respectively. Simulations were run for both the wet season and hot, dry season of both Kruger National Park and Chobe National Park.

*Rationale*: A fine resolution was chosen to capture as closely as possible the finest spatial scale that elephants might make movement decisions at hourly time steps. Simulations were run for 336 time steps, representing two weeks in real-time. This duration was chosen to strike a balance between avoiding simulations that were impractically long and running simulations long enough to be able to determine meaningful averages of movement characteristics.

### A.1.1.3 Process overview and scheduling

Each time step, the following actions are scheduled in the given order. They are implemented by corresponding submodels which are described in detail in the ODD section 1.1.7 below. Here we only list the names of the actions and a very brief description of their purposes; the information in parentheses shows which entity is running which action and, if applicable, under which condition it is run. Each time step, entities ran their actions in the order below:

## Agent initialization (agent)

An agent is initialized on a given cell in the landscape according to the empirical trajectory it is paired with. The initial location of the agent in each simulation is thus the first location of its paired empirical trajectory. Agents are then assigned one of two states, affecting both their sensitivity to high environmental temperatures and subsequent probability of thermoregulating, and their speed when foraging.

The following processes occur in order at the beginning of every time step. A flow diagram of the simplified model process is depicted in the manuscript. Assumptions made concerning model parameterization are described in Table A.2 of the Appendix.

# Update landscape greenness (environment)

The greenness level of any cell may change throughout the simulation period by a small amount, reflecting the vegetation changes that occur throughout the wet and dry seasons. By the end of the two-week simulation, a percentage of the model landscape has increased in greenness consistent with the increase in greenness that occurs in the realworld within the specific landscape during the specific month in which the simulation occurs.

# *Update environmental temperature (environment)*

The environmental temperature, which is a global variable, is updated every time step.

## Updating perceived by environmental temperature (agent)

Elephants have been observed utilizing behavioral thermoregulation, in the form of shade use and wetting (among other behaviors), when environmental temperatures are high. These behavioral adjustments serve to dissipate heat from the animal's body and reduce ambient heat load, potentially reducing thermal discomfort. The *perceived* environmental temperature, which reflects the temperature the agent may experience as a result of a behavioral adjustment due to high environmental temperatures, is updated every time step. If the agent employs behavioral thermoregulation, the environmental temperature perceived by the agent is then decreased. This process serves to mimic the benefits of thermoregulatory behaviors, which is longer lasting for wetting behavior due in part to enhanced evaporative cooling.

# Updating the time elapsed since the agent visited a water source (agent)

The amount of time elapsed since the agent visited a water source is updated every time step. If the agent visited a water source at time t, the time elapsed resets to 0. If the agent did not visit a water source at time t, the time elapsed increases by 1.

### Deciding whether to thermoregulate (agent)

The agent first decides whether it must employ thermoregulation. This decision is influenced by the current perceived temperature, the agent's "state", and the temperature threshold above which behavioral thermoregulation is likely to occur. If the probability of thermoregulation is greater than a randomly generated number, the agent will select either "wetting" or "shade use".

## Deciding whether to drink water (agent)

If the agent does not have to employ thermoregulation, it will decide whether it has to employ drinking. This decision is determined by the time since the agent last visited a water source (including instances of wetting), and the perceived environmental temperature. If the probability of drinking is greater than a randomly generated number, the agent will select drinking and will move to the closest water source or the cell within the search radius that is closest to the nearest water source.

## Deciding to forage (agent)

If the agent does not decide to employ thermoregulatory behavior or drinking, it will forage. If the agent is moving towards water but decides to forage, there is a greater likelihood that the agent will select cells with higher EVI values that are also closer to the nearest water source. When the elephant is foraging in a particular cell, the EVI value of that cell is decreased.

### A.1.1.4 Design concepts

**Basic principles:** The following basic concepts are taken into account in the model's design:

- Animal movement and space use patterns reflect the underlying behaviors.
- Elephants are large-bodied herbivores known to spend the majority of the day engaging in foraging behavior, with foraging activity ceasing if the individual needs to responds to stressors.
- We utilize concepts from optimal foraging theory to model foraging behavior.

**Emergence:** Movement characteristics including home range size, displacement distances, and maximum distances traveled from permanent water sources emerge from the agent's interactions with the environment, behaviors, and subsequent space use.

Adaptation: The agents are mobile entities that can adapt to changes in their internal state (i.e., how long the agent has gone without visiting a water source and how the agent perceives the environmental temperature) and environment. Behaviors are probabilistic, such that the agent's selection of a behavior is strongly dependent on the intensity of the stressors it is facing, namely overheating effects of temperature and the need to drink water. Each cell selection criterion associated with each behavior is assumed to indirectly convey fitness.

**Objectives:** Agent movement decisions are aimed at maintaining a high level of intake of energy from foraging while satisfying the needs of thermoregulation and obtaining water. When agents are performing area-restricted search movement and must decide where to forage, they begin by ranking the surrounding landscape cells by their

'greenness/distance to the agent' score. Cells with higher scores have a higher probability of being selected. Additionally, agents rank landscape cells by their 'percent shade/distance to the agent' score when employing shade use, and cells with higher scores have a higher probability of being selected.

**Learning:** The agents do not change their behavior over time as a result of their experiences.

**Prediction:** The agent does not predict future conditions.

**Sensing:** The agents can sense the environmental temperature as well as the time elapsed since they visited a water source; both of these state variables influence the agents' behaviors at any given time step. The agents can also sense the location of water sources in the landscape and can make directed movements towards them. At a local scale (within the searching radius), the agent can also sense the greenness and tree cover percentage within the cells within the landscape, influencing their decisions concerning where to forage and seek shade.

**Interactions:** Only one agent is modeled on the landscape during a simulation; therefore, there are no interactions among agents.

**Stochasticity:** The agents' decisions to select a behavior and their selection of cells when moving are heavily influenced by their internal states and attributes of the landscape cells. To mimic the stochasticity inherent in animal behavior and movement patterns, random number generators were used to ultimately determine the behavior that the agent employed and the cell that the agent moved to within a time step. **Collectives**: There are no collectives within the model. Although an agent represents a family group of elephants, it is technically a single agent in the model.

**Observation:** The x and y positions of the agent at every time step for the duration of two weeks (336 time steps) are collected and transformed into real-world coordinates. From the positions, a trajectory is formed, and movement characteristics can be determined. In addition to the agents' positions, the behavior employed at every time step is collected (vector "Behavior"), as well as the number of hours that elapsed before the agent returned to a water source (vector "Trip duration").

## A.1.1.5 Initialization

At the beginning of every simulation, one agent is initialized onto the landscape at an x and y position corresponding the first location of its paired empirical trajectory. The agent is assigned a random state, and its initial behavior is set as foraging. To obtain an estimate of the time since the agent has visited a water source, we divide the distance between the agent and the closest water source by the speed an agent is assumed to travel when moving towards water. For simplicity, the initial perceived environmental temperature is the same as the environmental temperature at time t=0 of a simulation run. The initialization of the model agent is always the same in every simulation.

## A.1.1.6 Input data

### Environmental temperature

We obtained two-week hourly temperature recordings from the closest weather station to the center of each study area that contained the most complete records for each month and year. Hourly temperatures for the wet season and dry season months were downloaded from the National Oceanic and Atmospheric Administration's (NOAA) National Center for Environmental Information (NCEI) Integrated Surface Dataset, and the information was converted into a vector of temperature values. For CNP and surrounding protected areas, we used temperature values from the weather station located in Kasane (Station ID 68029099999). For KNP, all temperature values except for those from August 2014 were obtained from the weather station located in Phalaborwa (Station ID: 68191099999). Temperature values for August 2014 were obtained from the weather station in Punda Maria (Station ID: 68196099999). At the beginning of every time step, the element of the vector corresponding to the time step *t* was fed into the model, representing the environmental temperature.

# Enhanced vegetation index (EVI)

A raster corresponding to initial EVI conditions in the landscape at the time of each empirical trajectory was created from Landsat 8 Operation Land Imager (OLI) images ( U.S. Geological Survey, 2016) by merging tiles with similar acquisition dates in order to cover the entirety of the model landscapes. Ideally, we would have utilized one raster corresponding to initial EVI conditions at the beginning of each simulated trajectory; however, cloud cover made this impossible to achieve for the wet season months in both parks. Consequently, we selected one raster with minimal cloud cover to represent initial EVI conditions for all wet season simulations in each respective park. Obtaining cloud cover-free rasters representing initial EVI conditions for the dry season was more feasible, and we utilized a separate raster representing initial EVI conditions for most months in the dry season for both parks.

To determine the percentage of the landscape that increases in greenness during a 16-day period for each month in the wet and dry seasons, we utilized a time-series of 16-day

Moderate Resolution Imaging Spectroradiometer (MODIS 13Q1 product) EVI datasets for the years 2012-2014. The MODIS 13Q1 product achieves cloud-free coverage by selecting the higher quality, cloud-free pixels in the 16-day time period. The calculated percentage of the landscape that increases in greenness during a 16-day period was then used to determine the number of cells within the model landscape that would have to have an increase in EVI every time step to reflect the percentage.

Detailed information regarding the Landsat and MODIS data used, as well as the calculated percentages of the landscape increasing in greenness during a 16-day period per month, is given in Table A.3 of the Appendix.

### Presence of water

For the dry season raster, a shapefile of points representing permanent water across the study areas was used to determine the cells that contained a water source. Permanent water was defined as water sources containing water year-round. We supplemented the layer with permanent water source data from the Global Surface Water dataset (Pekel, Cottam, Gorelick, & Belward, 2016). Specifically, we downloaded the "Water Seasonality (2014-2015)" dataset. Permanent sources not included in the original shapefile were added using the "Editor" toolbox in ArcGIS 10.5. We used high-resolution imagery from Google Earth to locate permanent bodies of water smaller than 30 meters. The "Historical imagery" toolbar was used to determine whether these smaller sources of water contained water year-round for multiple years. We were able to confirm the permanency of the majority of these sources through the internet. For example, some water sources near lodges are pumped year-round in order to attract game for the viewing enjoyment of tourists, and this is generally stated on the lodges' respective websites. For
the wet season raster, we supplemented the dry season raster with a shapefile of points representing seasonally available water. We used the "Historical imagery" toolbar from Google Earth to locate water sources that were present for at least two consecutive years during the wet season but not present during the dry season.

#### Percent tree cover

Percent tree cover (values 0 to 100) within each cell was obtained from (Hansen et al., 2013) Global Forest Change's tree cover dataset. Tree cover is defined as canopy closure for vegetation taller than five meters and is generally determined during the wet season.

# A.1.1.1.7 Submodels

## Update landscape greenness

The greenness level of any cell may change throughout the simulation period by a small amount, reflecting the vegetation changes that occur throughout the wet and dry seasons. To determine the percentage of the landscape that increases in greenness during an approximately two-week period for each month in the wet and dry seasons, time-series of 16-day EVI datasets for the years 2012-2014 were acquired for each of the model landscapes. This percentage was then used to determine the number of cells within the model landscape that would have to have an increase in EVI every time step to reflect the empirical percentage. Generally, the number of cells increasing in greenness during the dry season is less than the number of cells increasing in greenness during the landscape increases in greenness during a 16-day period. To reflect this, 32,000 cells within the model landscape increase in greenness by a value of .001 every time step. By the end of the two-week simulation, approximately 90% of the model landscape has increased in greenness. In incorporating this process, spatiotemporal changes in the landscape's vegetation are more realistically represented within the model.

# Update perceived environmental temperature

The environmental temperature, which is a global variable, is updated every time step. Elephants have been observed utilizing behavioral thermoregulation, in the form of shade use and wetting (among other behaviors), when environmental temperatures are high. These behavioral adjustments serve to dissipate heat from the animal's body and reduce ambient heat load, potentially reducing thermal discomfort.

The *perceived* environmental temperature, which reflects the temperature the agent may experience as a result of a behavioral adjustment due to high environmental temperatures, is updated every time step. If the agent employed behavioral thermoregulation, the environmental temperature perceived by the agent is decreased. If the agent employed wetting during time step *t*, the agent will perceive an environmental temperature of *current\_temperature-10* during t+1. The agent will then perceive temperatures of 6, 4 and 2 degrees lower than the current temperature during time steps t+2, t+3, and t+4, respectively, even if no thermoregulatory behaviors are employed during these time steps. Contrarily, if the agent employed shade use during time step *t*, the agent will perceive a temperature of *current\_temperature-3* during t+1. This process serves to mimic the benefits of thermoregulatory behaviors, which is longer lasting for wetting behavior due in part to enhanced evaporative cooling.

The agent first decides whether it must employ thermoregulation. This decision is determined by the following equation for probability of employing thermoregulation:

$$P_{thermoregulation} = \frac{1}{1 + e^{state(Temp_{current} - Temp_{threshold})}}$$

Eqn. A1: Equation used to determine the probability of thermoregulation, where "*Temp threshold*" is the ambient temperature above which thermoregulatory behavior is most likely to occur (set at 30 degrees Celsius), and "*Temp current*" is either the ambient temperature (which changes every time step, "current\_temperature"), or a temperature lower than the ambient temperature due to the agent employing thermoregulatory behavior during a previous time step. "State" represents the sensitivity of the agent to high environmental temperatures and is set randomly to either -0.1 or -0.2. The "state" of -0.2 represents the coefficient of the logistic regression equation that was used to estimate the probability of employing thermoregulation for African elephants in Botswana (Mole, 2015). Agents represented by a "state" of -0.1 are more sensitive to high temperatures and have a higher probability of employing thermoregulatory behavior at lower temperatures compared to agents represented by a "state" or -0.2. Thus, these agents may represent family groups with small calves that are more susceptible to the stresses of high temperatures.

If the probability of thermoregulation is greater than a randomly generated number, the agent will select either "wetting" or "shade use". We make the assumption that an elephant would most likely select "wetting" as a thermoregulatory behavior if there is

water nearby and the individual does not have to travel far distances to reach it. A "search radius" is formed which delineates the area that an elephant can search for a water source, and may vary in size from 900 m or 1.8 km. There is a lower probability of forming a larger search radius, as it is unlikely that elephants will travel large distances to reach a water source if they are experiencing thermal stress. If there is a water source within the search radius, the agent will move to the closest water source, and the foraging trip duration is reset to 1.

If there is no water within the search radius, the search radius is set to 900 meters (30 cells) and the agent will seek shade. Because elephants will prefer to seek shade where they can also forage, the tree cover values of the cells within this radius are weighted by their EVI values (tree cover values are multiplied by 0.7, and the corresponding EVI values are multiplied by 0.3. The two resulting values are then summed). As such, cells with the highest tree cover values and EVI values will have the highest weighted values. The weighted value of each cell is then divided by its distance to the agent's position for a preference score, such that cells with higher weighted values that are closer to the agent's position will have higher scores. The top 10% of cells with high resultant values are identified. Because animal movement is generally characterized by a high degree of directional persistence, cells in the current direction of the agent are more likely to be selected. The angle formed between the current direction the agent was heading, and every potential destination cell is calculated, known as the turning angle. Then, we generate 10 000 random numbers representing turning angles, in which the resulting distribution is positively skewed towards smaller numbers. A random number (turning angle) is selected from this distribution, and a cell (from the top 10% of cells identified

above) characterized by the selected turning angle is then identified. The agent then moves to this cell. Thus, cells with higher weighted scores, closer to the agent and in the same general direction that an agent was moving have a higher probability of being selected. The EVI of the cell that the agent moves to is decreased by a value of .04 to represent instances of browsing.

If there is no tree cover within the radius, the agent increases its search radius to 45 cells (1.35 km) and the aforementioned process is executed again. If the agent has performed a thermoregulatory behavior (which includes 'drinking' as the agents are at a water source), for three consecutive time steps, the probability of thermoregulation is automatically lower than the randomly generated number. This is to prevent the agents from thermoregulating for unrealistic periods of time.

# Update time elapsed since the agent visited a water source

The amount of time elapsed since the agent visited a water source is updated every time step. If the agent visited a water source at time t, the time elapsed resets to 0. If the agent did not visit a water source at time t, the time elapsed increases by 1.

## Decide whether to drink water

If the agent does not have to employ thermoregulation, it will decide whether it has to employ drinking. This decision is determined by the time since the agent last visited a water source (including instances of wetting), and the ambient temperature. The following equations illustrate this:

$$T_{water} = \sum_{t=t_{water}}^{t_{current}} I(Temp_{current})$$

where

$$I(Temp_{current}) = \begin{cases} 1 & if \ Temp_{current} \leq Temp_{threshold} \\ Temp_{current} & / \ Temp_{threshold} & if \ Temp_{current} > Temp_{threshold} \end{cases}$$

Eqn. A2: Equation used to determine the weighted cumulative time since the agent last visited a water source,

where  $t_{current}$  is the current time step and  $t_{water}$  is the time that has elapsed since the agent last visited a water source. The weighted cumulative time,  $T_{water}$ , can then be used to calculate the probability of employing drinking:

$$P_{drinking}(t_{water}) = \frac{1}{1 + e^{-.1(T_{water} - \beta_1)}}$$

Eqn. A.1: Equation used to determine the probability of drinking

where  $\beta_i$  is the parameter representing when the temperature at which the probability of switching to seeking water rises to  $\frac{1}{2}$ . While trip duration frequency varies, elephants generally drink water once a day. However, setting the  $\beta_i$  parameter to 24 led to a large number of very short trips, likely due to the agent also returning to water sources for thermoregulatory purposes. Preliminary model results led us to set this parameter to 50 hours, in order to achieve a likely frequency distribution of trip durations.

If the probability of drinking is greater than a randomly generated number, the agent will select drinking. If there is a water source within a 1.8 km radius (60 cells), the agent will move to the water source, and the foraging trip duration is then reset to 1. If there is no

water within a 1.8 km radius, the agent will move to the cell within the search radius closest to the nearest water source.

The agent's decision to drink influences the cell selection strategies associated with foraging behavior, as described below.

## Decide where to forage

If the agent does not decide to employ the higher priority behaviors of thermoregulatory behavior or drinking, it will forage. For the agent's foraging strategy and cell selection process, we mirror the cognitive mechanisms potentially utilized by large herbivores when foraging as in (Bailey et al., 1996). The agent keeps track of the EVI values for areas (search radii) visited within the last three time steps and uses a running average of these values to decide where to forage. The agent first compares the average EVI value of the current search radius to the running average. If the average EVI value of the current search radius is greater than or equal to the running average, there is a high probability that the agent will turn more often and move shorter distances when selecting a cell, in order to stay in the profitable location. To reflect this area-restricted searching mode within the model, the agent identifies all of the cells within the current search radius with an EVI value greater than or equal to the running average as acceptable cells. The EVIs of the acceptable cells are divided by their distances to the agent's position, and cells with the highest resultant values are identified. Finally, the angle formed between the current direction in which the agent was heading, and every cell with the highest resultant values as determined above, is calculated. Then, we generate 10 000 random numbers representing turning angles, in which the resulting distribution is skewed to generate

larger numbers, representing more tortuous movement. A random number (turning angle) is selected from this distribution, and a cell (one of the cells with the highest resultant value) is identified. The agent then moves to this cell.

If the average EVI value of the current search radius is less than the running average, there is a high probability that the agent will move straighter and to farther distances when selecting a cell, in order to move away from the location with less desirable EVI values. To reflect this within the model, the agent identifies all of the cells within the current search radius with an EVI value greater than or equal to the running average as acceptable cells. If there are acceptable cells within the search radius, the cells farthest from the agent are identified. Then, the angle formed between the current direction the agent was heading, and the farthest cells as determined above, is calculated. We then generate 10 000 random numbers representing turning angles, in which the resulting distribution is skewed to generate very small numbers, representing straighter movements. A random number (turning angle) is selected from this distribution, and a cell (one of the acceptable cells furthest from the agent) is identified. The agent then moves to this cell.

When the agent is foraging, the EVI value of the cell that the agent moved to is decreased by a value ranging from 0.6 to .04. If the agent moved to a cell close to its previous position, the EVI decreases by .6, as the agent had more time to remove forage biomass within the time step. If the agent moved to a farther position, the EVI decreases by .04, as the agent had less time to remove forage biomass within the time step. If the agent is heading towards water to drink (as decided at a previous time step), and

decides to forage at the current timestep, the agent's movement is oriented towards water.

First, the distance between the nearest water source and all of the cells in the search radius is calculated. The agent identifies the top twenty percent of search radius cells that are closest to the closest water source as acceptable cells. The EVIs of the acceptable cells are divided by their distances to the closest water source, and cells with the highest resultant values are identified. We then generate 10 000 random numbers representing these values, in which the resulting distribution is skewed to generate larger numbers. A random number is selected from this distribution, and one of the acceptable cells cells

#### A.2 Sensitivity analysis

To asses the extent to which the model was sensitive to changes in certain parameters, we performed linear mixed models (LMMs) in which we compared the original model outputs with the outputs obtained when a given parameter was changed (see Table A.4 for the parameter changes made), in order to determine effect sizes. Effect sizes shed light on the magnitude of the model's sensitivity to a given parameter change; larger effect sizes indicate greater sensitivity to a parameter change. We assessed the model's sensitivity at four levels for each parameter change, and for each movement characteristic: 1) "Sims", which indicated overall sensitivity of the model outputs to the change, 2) "Season\*Sims", which indicated sensitivity of the seasonal patterns produced by the model to the change, 3) "Park\*Sims", which indicated sensitivity of patterns associated with each park to change, and 4) "Season\*Park\*Sims", which indicated sensitivity of patterns associated with the park and season interactions to the change. Absolute values of effect sizes less than 0.2 were considered small, larger than 0.2 but smaller than 0.5 were considered moderate, and larger than .5 were considered large.

Effect sizes associated with each movement characteristic are shown in tables A.5-A.8. For brevity, we will focus on the parameter changes that were associated with effect sizes greater than 0.1 for all movement characteristics at the level of "Sims".

Home range size was sensitive to a 10% increase in the coefficient in the logistic regression equation utilized in drinking behavior with an effect size of -0.117. A 10% increase in this parameter increased the probability of drinking for any given time since the agent last visited a water source. Subsequently, agents may not have been able to traverse as much of the landscape before having to return to a water source, thereby reducing their home range sizes compared to original model outputs. Home range size was also sensitive to a 10% increase and decrease in the parameter ultimately determining the turning angles when an agent is foraging in a favorable environment, with effect sizes of -0.326 and 0.153, respectively. A 10% increase in the parameter ultimately determining the turning angles when an agent is foraging in an ufavorable environment had an effect size of -0.181. A 10% increase in these parameters increased the chances of the agent selecting a cell that, when moving to it, would represent a movement with a larger turning angle. Foraging movements with larger turning angles resulted in smaller areas traversed compared to foraging movements with smaller turning angles. Thus, home range sizes were reduced compared to original model outputs. For the opposite reason, a 10% decrease in this parameter resulted in foraging movements with smaller turning angles, which ultimately led to an increase in home range sizes due to a possible increase in the area traversed throughout a simulation. Home range size was also sensitive to a 10% decrease in the temperature threshold for employing behavioral thermoregulation, with an effect size of -0.222. In lowering the temperature threshold,

agents likely remained closer to water sources due to having to employ behavioral thermoregulation at lower temperatures, thereby decreasing the total area traversed thourhgout a simulation compared to original model outputs.

For daily displacement distance, the largest effect sizes at the level of "Sims" were associated with a 10% increase in the parameter ultimately determining the turning angles when an agent is foraging in a favorable environment, with an effect size of -0.133. A 10% increase in the parameter determining the turning angles when an agent is foraging in a favorable environment increased the chances of the agent moving with greater tortuosity when foraging and with smaller step lengths, resulting in a decreased daily displacement distance compared to original model outputs. Daily displacement distance was also sensitive to a 10% decrease in the temperature threshold for employing behavioral thermoregulation, with an effect size of -0.358. With a lower temperature threshold, it is likely that agents were not traveling far from water before returning to employ behavioral thermoregulation, thereby decreasing the total distance traveled throughout the simulation.

For net displacement distance, the largest effect sizes were associated with a 10% increase in the coefficient in the logistic regression equation utilized in drinking behavior, with an effect size of -0.145, a 10% decrease in the parameter ( $\beta_1$ ) in the logistic regression equation utilized in drinking behavior, with an effect size of -0.124, and a 10% increase and decrease in the parameter determining the turning angles when an agent is foraging in a favorable environment, with an effect size of -0.359 and 0.251, respectively. A 10% increase in the parameter ( $\beta_1$ ) in the logistic regression equation utilized in the parameter ( $\beta_1$ ) in the logistic regression equation utilized in the parameter ( $\beta_1$ ) in the logistic regression equation utilized in drinking behavior, with an effect size of -0.359 and 0.251, respectively. A 10% increase in the parameter ( $\beta_1$ ) in the logistic regression equation utilized in drinking behavior, and a 10% decrease in the parameter ( $\beta_1$ ) in the logistic regression equation

regression equation utilized in drinking behavior increased the probability of employing drinking behavior for any given time since the agent last visited a water source, and this in turn decreased net displacement distances compared to original model outputs. It's possible that by increasing the probability of drinking, the agents did not travel as far from water before they returned to a water source. This may have resulted in smaller net displacement distances if the agents returned to the same water source repeatedly. A 10% increase in the parameter determining the turning angles when an agent in foraging in a favorable environment increased the chances of the agent moving with greater tortuosity when foraging, thereby resulting in a decreased net displacement compared to original model outputs. A 10% decrease in the same parameter may result in foraging movements that are straighter, increasing the net displacement compared to the original model outputs. Net daily displacement was also sensitive to a 10% increase in the temperature threshold for employing behavioral thermoregulation, with an effect size of 0.117. By increasing the temperature threshold, agents employed behavioral thermoregulation at higher temperatures, and this likely resulted in the agent being able to move away from water sources rather than repeatedly returning to the same water source for wetting. An equally plausible reason for the larger net daily displacements compared to original model outputs is that agents were likely not utilizing shade as often and were able to travel longer distances to forage.

For maximum distance traveled from a permanent water source, the largest effect sizes were associated with a 10% increase in the parameter ultimately determining the turning angles when an agent is foraging in a favorable environment with an effect size of - 0.128. If an agent moved with greater tortuosity before returning to a water source, it is

likely that the agent remained closer to a water source than if its movements were straighter, thus decreasing the maximum distance traveled from a permanent water source.

Table A.2 introduces the assumptions made during model development and the relevant literature supporting these assumptions. Table A.3 lists the MOD13Q1 products used to determine the percentage of the landscape increasing in greenness during a simulation period, and the percentage. Tables A.4 describes the parameters and parameter changes involved in the sensitivity analysis, and Tables A.5 through A.8 show the results of the sensitivity analysis for each parameter change and for each of the movement characteristics.

Entity	Variable name	Description	Possible values
Agent	State	Sensitivity to environmental temperature	-0.1 or -0.2
	Position (x and y)	The agent's position on the landscape	
	T_water	Amount of time elapsed since the agent last visited a water source	1 – undefined hours
	Behavior	The behavior the agent is employing	Foraging, drinking, wetting, shade use
	Perceived_temp	Temperature the agent experiences (due to thermoregulatory behaviors)	Current temperature or lower
Cells	Greenness	Indicates the EVI that	0 – 1
	Tree cover	Indicates the percentage of tree cover that underlies the cell	0 – 100 %
	Water	Indicates whether a water source underlies the cell	0 (absent) or 1 (present)
Environment	Current_temp	Current environmental temperature	5 – 44 Celsius
	Vegetation change	Number of cells that increase in greenness every time step	5500 – 180000 cells

**Table A.1**: Variables used within the model, their descriptions, associated entities and possible values

Assumptions	Parameter	Parameter value	Supporting references
Model concept		orrunge	L
The agent will forage unless it must respond to stressors such as increasing temperatures and the need to drink water			Elephants spent average of approximately half their day feeding (Shannon et al.,, 2008) Elephants spent average of 85% of their time feeding, and little time spent walking, drinking, wetting, and resting
			<ul> <li>(Mole et al., 2016)</li> <li>Elephants fed for approximately 12 to 14 hours per day (Guy, 1976)</li> <li>Elephants spent approximately 75%-90% of the study period feeding (Wyatt &amp; Eltringham, 1974)</li> </ul>
Thermoregulatory behavior		•	
The maximum distance that the agent can travel during one time- step while employing 'shade use' is set	Shade-use radius	30 cells corresponding to a speed of .9 km/h	High temperatures influence the relationship between locomotion and heat storage in elephants (Rowe et al.,, 2013)
Some agents may be more susceptible to increases in temperatures than others, reflecting family groups with younger calves	Coefficient in the logistic regression equation used to determine the probability of thermoregulation	2 or1	Compared to adult elephants, calves may be more susceptible to heat stress (Mumby et al., 2013)
The probability of an agent employing thermoregulation	Coefficient in the logistic regression equation used to	2 or1	With increased environmental temperatures over 20 degrees Celsius,

increases as environmental temperature increases	determine the probability of thermoregulation		the probability of an elephant returning to a water source increased (Purdon, 2015) As environmental temperature increased, the probability of an elephant employing wetting and shade use increased (Mole et al., 2016)
The agent moves to the closest cell characterized as having higher percent tree cover and vegetation greenness		Cells within the radius having the top 10% of values are weighed by their distance to the agent's position as follows: Weight_value = Treecover_EVI_v alue/distance_to_th e_agent	"Relative to availability, female elephants select areas withhigh tree cover" (Roever et al.,, 2013)
The agent experiences lower environmental temperatures after employing thermoregulation	Degrees by which perceived environmental temperature is lowered after wetting or shade use	After wetting, the environmental temperature perceived is 10 degrees lower than the actual environmental temperature, and increases every subsequent time step that the agent	Elephants experienced a median difference of temperature of 3.5 and 8.5 degrees Celsius after shade use and wetting, respectively (Mole, 2015)

		does not thermoregulate, until the perceived temperature is the actual temperature After shade use, the environmental temperature perceived is 3 degrees lower than the actual environmental temperature	
Unless a water source is "close", the agent is more likely to access shade for thermoregulation	Probability of moving to a water source when needing to thermoregulate	<ul> <li>75% probability that the agent will only move to a water source if it is within 30 cells (900 m)</li> <li>25% probability that the agent will move to a water source if it is within 60 cells (1.8 km)</li> </ul>	Elephants use water sources for behavioral thermoregulation as well as to replenish water reserves and movement is thus anchored to water sources when water is scarce (Thaker, Gupte, Prins, & Slotow, 2019)
Thermoregulatory benefits of wetting behavior last for hours after the behavior is employed	Number of hours that agent experiences reduced environmental temperatures after employing wetting behavior	Directly after employing wetting behavior, the agent experiences temperatures of 10 degrees Celsius lower than actual	African elephant skin is "sculptured" and retains water and mud, which when places on the skin, dries after an average of about 23 hours (Lillywhite & Stein, 1987)

		environmental temperature The temperature then gradually increases to the current environmental temperature at time <i>t</i>	Evaporative water loss is increased in sculptured surfaces compared to unsculptured surfaces (Lillywhite & Stein, 1987)
Drinking behavior			
The maximum distance that the agent can travel during one time- step while employing 'drinking' is set	Drinking radius	60 cells (1.8 km) corresponding to a speed of 1.8 km/h	Maximum speeds when traveling to water are approximately 3 km/h (Chamaillé-Jammes, Mtare, Makuwe, & Fritz, 2013)
The probability of an agent employing drinking behavior increases as the time since the agent last visited a water source increases	Coefficient in the logistic regression equation used to determine the probability of drinking	-0.1	Elephants generally return to water sources every 12 to 36 hours (Purdon & van Aarde, 2017)
The agent moves to the closest cell containing a water source within the radius, or to cell within the radius that is closest to the closest water source			Elephants have relatively good spatial memory and travel to the closest water source 90% of the time. Their movements towards water are also highly directional (Polansky, Kilian, & Wittemyer, 2015) Elephants traveled to a water source other than the closest water source about 39% of the time, however, the

			distance traveled to the further water source was usually only a few kilometers more than if the elephants traveled to the closest water source ((Chamaillé-Jammes et al., 2013)
Foraging behavior			-
The maximum distance that the agent can travel during one time- step while employing 'foraging' varies according to the agent's "state"	Foraging radius	State 1: 30 cells (900 m) corresponding to a speed of .9 km/h, and representing greater sensitivity to high temperature State 2: 60 cells (1.8 km) corresponding to a speed of 1.8 km/h, and representing lower sensitivity to high temperature	Maximum speeds traveled by female elephants was approximately 0.7 km/h (Duffy, Dai, Shannon, Slotow, & Page, 2011) Mean speed traveled by elephants was .36 km/h (Graham, Adams, & Lee, 2009) Foraging movement 'mode' described as a maximum movement of approximately 750 m/30 min, with a peak at approximately 250 m/30 min (Supplementary information, Polansky et al 2015) Family groups with calves had a lower likelihood of walking, compared to family groups with no calves (Mole et al., 2016)
If the EVI of the search radius is greater than or equal to the three previously visited cells, the agent's movement will be characterized by higher turning angles and shorter		The agent identifies all of the cells within the current search radius with on EVI value	Herbivore foraging decisions are influenced by "[the] nutritional value [of the food resources] and their distribution in the habitat (distance,
step lengths (e.g., the agent's movement will be more tortuous)		greater than or equal to the running	(Roguet, Dumont, & Prache, 1998)

	average as	The Normalized Difference
	acceptable cells.	Vegetation Index (similar to the
	The EVI of the	Enhanced Vegetation Index) is a
	acceptable cells are	useful proxy for dietary quality
	divided by their	(Rvan et al. 2012)
	distance to the	Flenhants avoid less green vegetation
	agent's position	and favor greener than average
	and cells with the	landscapes
	highest resultant	(Loarie van Aarde & Pimm 2009)
	voluos oro	(Loane, van Aarde, & Thinn, 2007)
	identified Finally	When foreging movement can be
	the angle formed	characterized as an 'area restricted
	h at the angle formed	characterized as all area-restricted
	direction the corrent	search, with higher turning angles
	direction the agent	and short moves (Bennamou, 1992)
	was neading, and	in lavorable nabitals, elephanis turn
	every cell with the	
	highest resultant	(Duffy, Dai, Shannon, Slotow, &
	values as	Page, 2011)
	determined above,	
	1s calculated. Then,	
	we generate 10 000	
	random numbers	
	representing turning	
	angles, in which the	
	resulting	
	distribution is	
	skewed to generate	
	larger numbers,	
	representing more	
	tortuous movement.	
	A random number	
	(turning angle) is	
	selected from this	

	distribution, and a cell (one of the cells with the highest resultant value) is identified. The agent then moves to this cell.	
If the EVI of the search radius is less than the three previously visited cells, the agent's movement will be characterized by smaller turning angles and longer step lengths (e.g., the agent's movement will be more directed)	The agent identifies all of the cells within the current search radius with an EVI value greater than or equal to the running average as acceptable cells. If there are acceptable cells within the search radius, the cells furthest from the agent are identified. Then, angle formed between the current direction the agent was heading, and the farthest cells as determined above, is calculated. We then generate 10 000 random numbers	In unfavorable habitats, elephant movement can be characterized as having small turning angles and being straighter (Duffy, Dai, Shannon, Slotow, & Page, 2011)

angles, in which the	
resulting	
distribution is	
skewed to generate	
very small	
numbers,	
representing	
straighter	
movements. A	
random number	
(turning angle) is	
selected from this	
distribution, and a	
cell (one of the	
acceptable cells	
farthest from the	
agent) is identified.	
The agent then	
moves to this cell.	

**Table A.2** : Model assumptions and relevent parameters used in the ABM, along with supporting references.

Park	Month	Year	Product used	Dates of product used	% of landscape
					increasing in EVI
CNP	January	2013	MOD13Q1	2012-353 and 2013-1	69
CNP	January	2014	MOD13Q1	2014-1 and 2014-17	42
CNP	February	2013	MOD13Q1	2013-17 and 2013-49	32
CNP	February	2014	MOD13Q1	2014-33 and 2014-49	14
CNP	March	2013	MOD13Q1	2013-65 and 2013-49	12
CNP	March	2014	MOD13Q1	2014-65 and 2014-81	9
CNP	November	2013	MOD13Q1	2013-305 and 2013- 321	73
CNP	November	2014	MOD13Q1	2014-305 and 2014- 321	75
CNP	December	2013	MOD13Q1	2014-305 and 2014- 321***	93
CNP	December	2014	MOD13Q1	2014-353 and 2014- 321	93
KNP	January	2013	MOD13Q1	2012-353 and 2013-11	94
KNP	January	2014	MOD13Q1	2014-1 and 2013-353	91
KNP	February	2013	MOD13Q1	2013-49 and 2013-17	85
KNP	February	2014	MOD13Q1	2013-49 and 2013- 17***	85
KNP	March	2013	MOD13Q1	2013-65 and 2013-49	10
KNP	March	2014	MOD13Q1	2014-65 and 2014 49	42
KNP	November	2013	MOD13Q1	2013-321 and 2013- 305	91
KNP	November	2014	MOD13Q1		
KNP	December	2013	MOD13Q1	2013-337 and 2013- 231	61
KNP	December	2014	MOD13Q1		
CNP	August	2013	MOD13Q1	2013-225 and 2013- 209	51
CNP	August	2014	MOD13Q1	2014-225 and 2014- 209	15
CNP	September	2013	MOD13Q1	2013-257 and 2013- 241	65

CNP	September	2014	MOD13Q1	2014-257 and 2014- 241	64
CNP	October	2013	MOD13Q1	2013-289 and 2013- 273	55
CNP	October	2014	MOD13Q1	2013-289 and 2013- 273***	55
KNP	August	2013	MOD13Q1	2013-225 and 2013- 209	36
KNP	August	2014	MOD13Q1	2014-225 and 2013- 209	24
KNP	September	2013	MOD13Q1	2013-257 and 2013- 241	31
KNP	September	2014	MOD13Q1	2014-257 and 2013- 241	64
KNP	October	2013	MOD13Q1	2013-289 and 2013- 273	56
KNP	October	2014	MOD13Q1	2014-289 and 2014- 273	45

\*\*\* Products for the specific month were unable to be obtained, so we utilized the products from the same month of the previous year.

----- We did not simulate movement during the months of November and December of 2014 in KNP because of drought.

**Table A.3:** Year month, and dates of products used, along with the calculated percent of landscape increasing in EVI for each park. Cells highlighted in blue correspond to wet season months and cells highlighted in orange correspond to hot, drys season months. We utilized MOD13Q1 products to determine the percentage of the landscape that increased in EVI during an approximately two-week period in both parks. Moderate Resolution Imaging Spectroradiometer (MODIS) MOD13Q1 data are generated every 16 days at a spatial resolution of 250 meters. Two vegetation layers are provided; we use the EVI layer. The temporal resolution of the data is close to the duration of the simulations (two-weeks). An algorithm selects the "best" (no or little cloud coverage, low view angle, and highest EVI value) pixel from data collected over the 16 days. We select two products representing two 16-day periods in one month (or two products as temporally close to one another as possible to represent a month) and subtract the pixel values of the earlier products from the pixel values of the later product.

Reference	Parameter value/ range	Change in parameter
parameter		value
Probability of	75% probability that the agent will	65% probability that the
moving to a water	only move to a water source if it is	agent will move to a
source when	within 30 cells (900 m) and 25%	water source if it is
needing to	probability that the agent will move to	within 30 cells and 35%
thermoregulate	a water source if it is within 60 cells	
	(1.8 km)	85% probability that the
		agent will move to a
		water source if is not
		within 30 cells and 15%
The maximum	30 cells (900 m)	10% increase (33 cells)
distance the agent		10% decrease (27 cells)
can travel during		
one time-step		
while employing		
'shade use'		100/ 1 ((( 11 )
The maximum	60 cells (1.8 km)	10% increase (66 cells)
distance the agent		10% decrease (54 cells)
can travel during		
one time-step		
vnile employing		
Coefficient in the	0.1 in the equation:	100/imanaga (0.00)
Logistic regression	-0.1 in the equation:	10% increase (-0.09)
equation utilized	$D_{1}$	10% decrease (-0.11)
in drinking	$\Gamma$ drinking $(l_{water}) = \frac{1}{1 + e^{1(T_{water} - \beta_1)}}$	
hehavior which	I+e	
determines how		
sharn the		
switching		
behavior (to		
drinking) is as a		
function of $T_{water}$		
Parameter $(\beta_1)$ in	50 is $\beta_1$ in the equation:	10% increase (55)
the logistic	1	10% decrease (45)
regression	$P_{drinking}(t) = \frac{1}{1}$	
equation utilized	$1 + e^{1(T_{water} - \beta_1)}$	
in drinking		
behavior, which		
determines when		
the probability of		
switching to		
seeking water		
rises to $\frac{1}{2}$		

Parameter	5 is x in the equation:	10% increase ( $x = 3$ ;
determining	-	generates vector in
values in a vector	<i>x</i> =5	which 30% of values
from which a	X=round((1+(180-	are greater than or equal
turning angle is	$1)^{*}$ power(rand(1,10000),x)))	to 60 degrees )
selected when the	num=randsample(1:10,(numel(find(X=	
agent is foraging	=1)),true)	10% decrease ( $x = 9$ ;
in a favorable	X(X==1)=num	generates vector where
environment (the	ran cells=round(randsample(X,1),2)	10% of values are
EVI of the search		greater than or equal to
radius is greater	(This generates a vector (X) where	60 degrees)
than or equal to	20% of values are greater than or equal	6 )
the three <sup>1</sup>	to 60 degrees)	
previously visited		
cells). Smaller		
values of this		
parameter		
produce a vector		
with larger		
turning angles.		
Parameter	15 is x in the equation:	10% increase ( $x = 6$ ;
determining	1	generates vector where
values in a vector	x=15	17% of values are
from which a	X=round((1+(180-	greater than or equal to
turning angle is	1)*power(rand(1,10000),x)))	60 degrees)
selected when the	num=randsample(1:10,(numel(find(X=	
agent is foraging	=1)),true)	10% decrease ( $x = 70$ ;
in a non-favorable	X(X==1)=num	generates vector where
environment (the	ran cells=round(randsample(X,1),2)	1% of values are greater
EVI of the search		than or equal to $60$
radius is less than	(This generates a vector (X) where 7%	degrees)
the three	of values are greater than or equal to	
previously visited	60 degrees)	
cells). Larger		
values produce		
smaller turning		
angles.		
Temperature	30 Celcius	10% increase (33
threshold for		Celcius)
employing		
behavioral		10% decrease (27
thermoregulation		Celcius)

**Table A.4:** Reference parameters and corresponding parameter values or ranges, along with the parameter changes used for the sensitivity analysis

Reference	Reference	Parameter	Model	Effect
parameter	parameter	change		size
	value/ range	100/		0.050
The maximum	30 cells	10% increase	Sims	0.053
distance the agent			Season*Sims	-0.134
can travel during			Park*Sims	0.059
while omploying			Season*Park*Sims	0.345
'shade use'		10% decrease	Sims	-0.021
shade use			Season*Sims	-0.055
			Park*Sims	.112
			Season*Park*Sims	-0.117
The maximum	60 cells	10% increase	Sims	-0.008
distance the agent			Season*Sims	-0.015
can travel during			Park*Sims	0.055
one time-step			Season*Park*Sims	-0.151
while employing		10% decrease	Sims	078
'drinking'			Season*Sims	01
			Park*Sims	018
			Season*Park*Sims	246
Coefficient in the	-0.1	10% increase	Sims	-0.117
logistic regression equation utilized			Season*Sims	-0.002
			Park*Sims	0.152
in drinking			Season*Park*Sims	0.0059
behavior		10% decrease	Sims	039
			Season*Sims	-0.066
			Park*Sims	.0059
			Season*Park*Sims	406
Parameter $(\beta_1)$ in	50	10% increase	Sims	0.022
the logistic			Season*Sims	-0.002
regression			Park*Sims	0.182
equation utilized			Season*Park*Sims	-0.129
in drinking		10% decrease	Sims	-0.066
behav1or			Season*Sims	-0.074
			Park*Sims	-0.122
			Season*Park*Sims	-0.233
Probability of	75% probability	65% probability	Sims	-0.076
moving to a water	of forming 30	that the agent	Season*Sims	-0.014
source when	cells radius,	will move to a	Park*Sims	0.035
needing to	25% probability	water source if	Season*Park*Sims	-0.187
thermoregulate	of forming 60 cells radius	it is within 30 cells and 35% that the agent will move to a water source if		

		it is within 60		
		cells		
		85% probability	Sims	-0.01
		that the agent	Season*Sims	-0.188
		will move to a	Park*Sims	0.177
		water source if	Season*Park*Sims	-0.222
		1s not within 30		
		cells and 15%		
		that the agent		
		will move to a		
		water source if		
		it is within 60		
	5		<u> </u>	226
Parameter	5	10% increase	Sims	326
determining			Season*Sims	206
values in a vector			Park*Sims	.054
from which a		100/ 1	Season*Park*Sims	.099
turning angle is		10% decrease	Sims	.153
selected when the			Season*Sims	.0123
in a favorable			Park*Sims	.469
environment			Season*Park*Sims	.084
Parameter	15	10% increase	Sims	-0.181
determini values			Season*Sims	-0.069
in a vector from			Park*Sims	0.167
which a turning			Season*Park*Sims	-0.029
angle is selected		10% decrease	Sims	-0.078
when the agent is			Season*Sims	.134
foraging in a			Park*Sims	.118
unfavorable environment			Season*Park*Sims	-0.168
Temperature	30	10% increase	Sims	-0.023
threshold for			Season*Sims	-0.055
employing			Park*Sims	0.012
behavioral			Season*Park*Sims	0.042
thermoregulation		10% decrease	Sims	-0.222
			Season*Sims	-0.062
			Park*Sims	0.307
			Season*Park*Sims	0.014

 Table A.5: Sensitivity analysis for home range size

Reference	Reference	Parameter	Model	Effect
parameter	parameter	change		size
	value/ range	100/1	~:	0.044
The maximum	30 cells	10% increase	Sims	0.041
distance the agent			Season*Sims	112
can travel during			Park*Sims	027
while employing			Season*Park*Sims	092
'shade use'		10% decrease	Sims	0003
shade use			Season*Sims	055
			Park*Sims	-0.091
			Season*Park*Sims	-0.017
The maximum	60 cells	10% increase	Sims	-0.005
distance the agent			Season*Sims	0.057
can travel during			Park*Sims	-0.076
one time-step			Season*Park*Sims	018
while employing		10% decrease	Sims	-0.091
urmking			Season*Sims	.094
			Park*Sims	-0.182
			Season*Park*Sims	0.0005
Coefficient in the logistic regression	-0.1	10% increase	Sims	-0.048
			Season*Sims	0.012
equation utilized			Park*Sims	0.0004
in drinking			Season*Park*Sims	0.049
benavior		10% decrease	Sims	.031
			Season*Sims	-0.091
			Park*Sims	-0.047
			Season*Park*Sims	-0.285
Parameter $(\beta_1)$ in	50	10% increase	Sims	-0.004
the logistic			Season*Sims	0.045
regression			Park*Sims	-0.038
equation utilized			Season*Park*Sims	0.022
in drinking		10% decrease	Sims	-0.002
Denavior			Season*Sims	0.02
			Park*Sims	-0.245
			Season*Park*Sims	-0.351
Probability of	75% probability	65% probability	Sims	-0.002
moving to a water	of forming 30	that the agent	Season*Sims	-0.006
source when	cell radius,	will move to a	Park*Sims	-0.065
needing to thermoregulate	25% probability of forming 60 cell radius	water source if it is within 30 cells and 35% that the agent will move	Season*Park*Sims	-0.331

		to a water source if it is within 60 cells 85% probability that the agent will move to a water source if is not within 30 cells and 15% that the agent will move to a water source if it is within 60 cells	Sims Season*Sims Park*Sims Season*Park*Sims	-0.076 -0.034 0.077 -0.269
Parameter	5	10% increase	Sims	-0.133
determining			Season*Sims	-0.217
values in a vector			Park*Sims	-0.092
from which a			Season*Park*Sims	0.118
turning angle is		10% decrease	Sims	0.017
selected when the			Season*Sims	0.037
in a favorable			Park*Sims	0.169
environment			Season*Park*Sims	0.357
Parameter	15	10% increase	Sims	-0.086
determining			Season*Sims	-0.032
values in a vector			Park*Sims	0.051
from which a			Season*Park*Sims	-0.120
turning angle is		10% decrease	Sims	-0.074
selected when the			Season*Sims	0.115
in a unfavorable			Park*Sims	0.031
environment			Season*Park*Sims	-0.319
Temperature	30	10% increase	Sims	-0.099
threshold for			Season*Sims	-0.022
employing			Park*Sims	-0.155
behavioral			Season*Park*Sims	.222
thermoregulation		10% decrease	Sims	-0.358
			Season*Sims	-0.195
			Park*Sims	0.44
			Season*Park*Sims	0.352

Table A.6: Sensitivity analysis for daily displacement distance

Reference	Reference	Parameter	Model	Effect
parameter	parameter	change		size
	value/ range			
The maximum	30 cells	10% increase	Sims	0.057
distance the agent			Season*Sims	-0.099
can travel during			Park*Sims	-0.058
one time-step			Season*Park*Sims	-0.245
'shade use'		10% decrease	Sims	0004
shade use			Season*Sims	-0.085
			Park*Sims	-0.057
			Season*Park*Sims	0.0005
The maximum	60 cells	10% increase	Sims	0.004
distance the agent			Season*Sims	0.018
can travel during			Park*Sims	-0.162
one time-step			Season*Park*Sims	-0.119
while employing		10% decrease	Sims	-0.076
di inking			Season*Sims	0.140
			Park*Sims	0.209
			Season*Park*Sims	0.055
Coefficient in the logistic regression equation utilized in drinking	-0.1	10% increase	Sims	-0.145
			Season*Sims	0.073
			Park*Sims	-0.005
			Season*Park*Sims	0.045
behavior		10% decrease	Sims	0.057
			Season*Sims	0.015
			Park*Sims	0.202
			Season*Park*Sims	-0.531
Parameter $(\beta_1)$ in	50	10% increase	Sims	0.069
the logistic			Season*Sims	0.034
regression			Park*Sims	0.063
equation utilized			Season*Park*Sims	0.086
he havior		10% decrease	Sims	-0.124
UCHAVIOI			Season*Sims	0.028
			Park*Sims	-0.251
			Season*Park*Sims	-0.290
Probability of	75% probability	65% probability	Sims	-0.065
moving to a water	of forming	that the agent	Season*Sims	0.003
source when	radius of 30	will move to a	Park*Sims	-0.043
needing to thermoregulate	cells, 25% probability of forming radius of 60 cells	water source if it is within 30 cells and 35% that the agent will move to a water source	Season*Park*Sims	-0.240

		if it is within 60 cells		
		85% probability that the agent	Sims	-0.030
			Season*Sims	-0.099
		will move to a	Park*Sims	0.207
		water source if is not within 30	Season*Park*Sims	-0.369
		cells and 15%		
		that the agent		
		will move to a		
		is within 60 cells		
Parameter	5	10% increase	Sims	-0.359
determining			Season*Sims	-0.127
values in a vector			Park*Sims	-0.221
from which a			Season*Park*Sims	0.119
turning angle is		10% decrease	Sims	0.251
selected when the			Season*Sims	0.0004
agent is foraging			Park*Sims	0.226
in a favorable environment			Season*Park*Sims	-0.023
Parameter	15	10% increase	Sims	-0.233
determining			Season*Sims	0.008
values in a vector			Park*Sims	0.225
from which a			Season*Park*Sims	-0.053
turning angle is		10% decrease	Sims	-0.044
selected when the			Season*Sims	-0.017
agent is foraging			Park*Sims	0.033
environment			Season*Park*Sims	-0.129
Temperature	30	10% increase	Sims	0.117
threshold for			Season*Sims	-0.025
employing			Park*Sims	-0.262
benavioral thormorequistion			Season*Park*Sims	0.045
mermoregulation		10% decrease	Sims	-0.022
			Season*Sims	-0.014
			Park*Sims	0.033
			Season*Park*Sims	0.295

 Table A.7: Sensitivity analysis for net displacement distance

Reference	Reference	Parameter	Model	Effect
parameter	parameter	change		size
	value/ range		~ 1	
The maximum	30 cells	10% increase	Sims	-0.007
distance the agent			Season*Sims	0.046
can travel during			Park*Sims	0.115
while employing			Season*Park*Sims	0.212
'shade use'		10% decrease	Sims	0.001
shade use			Season*Sims	0.045
			Park*Sims	0.112
			Season*Park*Sims	-0.041
The maximum	60 cells	10% increase	Sims	-0.009
distance the agent			Season*Sims	-0.031
can travel during			Park*Sims	0.049
one time-step			Season*Park*Sims	-0.037
while employing		10% decrease	Sims	-0.060
drinking			Season*Sims	-0.051
			Park*Sims	-0.087
			Season*Park*Sims	0.038
Coefficient in the	-0.1	10% increase	Sims	-0.054
logistic regression			Season*Sims	-0.098
equation utilized			Park*Sims	-0.052
in drinking			Season*Park*Sims	0.166
behavior		10% decrease	Sims	0.022
			Season*Sims	-0.094
			Park*Sims	-0.053
			Season*Park*Sims	-0.109
Parameter $(\beta_1)$ in	50	10% increase	Sims	-0.015
the logistic			Season*Sims	-0.056
regression			Park*Sims	-0.046
equation utilized			Season*Park*Sims	-0.019
in drinking		10% decrease	Sims	-0.014
Dellavioi			Season*Sims	.002
			Park*Sims	-0.118
			Season*Park*Sims	-0.084
Probability of	75% probability	65% probability	Sims	-0.058
moving to a water	of forming 30	that the agent	Season*Sims	.004
source when	cell radius, 25%	will move to a water source if it is within 30 cells	Park*Sims	-0.114
needing to thermoregulate	probability of forming 60 cell		Season*Park*Sims	-0.124
	radius	and 35% that the agent will move		

		to a water source if it is within 60 cells 85% probability that the agent will move to a water source if is not within 30 cells and 15% that the agent will move to a water source if it	Sims Season*Sims Park*Sims Season*Park*Sims	-0.099 .047 .118 -0.347
		is within 60 cells		
Parameter	5	10% increase	Sims	-0.128
determining			Season*Sims	-0.164
values in a vector			Park*Sims	-0.057
from which a		100/1	Season*Park*Sims	0.085
turning angle is		10% decrease	Sims	.095
selected when the			Season*Sims	.044
in a favorable			Park*Sims	.110
environment			Season*Park*Sims	.041
Parameter	15	10% increase	Sims	-0.075
determining			Season*Sims	-0.096
values in a vector			Park*Sims	-0.060
from which a			Season*Park*Sims	-0.155
turning angle is		10% decrease	Sims	-0.027
selected when the			Season*Sims	0082
agent is foraging			Park*Sims	-0.005
in a unfavorable environment			Season*Park*Sims	0.199
Temperature	30	10% increase	Sims	-0.054
threshold for			Season*Sims	-0.143
employing			Park*Sims	-0.052
behavioral			Season*Park*Sims	0.301
thermoregulation		10% decrease	Sims	-0.052
			Season*Sims	-0.082
			Park*Sims	-0.066
			Season*Park*Sims	0.299

**Table A.8**: Sensitivity analysis for maximum distance traveled from a permanent water source

#### **B.** Supplementary material for chapter 4

## **B.1 ODD Protocol**

### B.1.1 Model description

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al. 2006, 2010, 2019; Railsback and Grimm 2019). The model was implemented in MatLab version 2017a.

### *B.1.1.1 Purpose and patterns*

The model's purpose is to simulate the fine-scale space use and movement patterns of a generic large water-dependent grazer, with the ultimate goal of utilizing the model to explore whether and how spatial differences in critical resources influence spatial differences in movement and foraging efficiency.

## *B.1.1.2 Entities, state variables and scales*

The model includes the following entities: the agents, which represents a large, waterdependent grazer, the landscape cells, and the overall environment. The entities are characterized by the state variables and attributes in Table B.2 (possible units and values are also listed).

The agent is mobile and can respond to environmental stressors by changing its behavior and subsequent movement across the landscape. Behaviors are determined utilizing a hierarchical decision process, whereby the agent responds to stressors before employing foraging behavior. The agent is characterized by the following state variables and attributes: 1) its position on the landscape (x, and y coordinates), at any given time step, 2) the time since it last visited a water source, 3) the behavior that it is employing, and 4) the environmental temperature that it is experiencing at a given time (perceived environmental temperature).

Landscape cells are characterized by the following attributes: 1) forage level within the cell, 2)) a binary value indicating whether tree cover is within the cell., and 3) a binary value indicating whether a water source is within the cell. These values were static and did not change for the duration of the simulation, except for the forage level value, which decreases to represent decreases in forage during the dry season, and when the agent foraged within a cell.

The overall environment was characterized by the following state variable: environmental temperature. We used environmental temperature data retrieved from weather stations in CNP and KNP during the hot, dry season as representative temperatures. Temperature was updated every time step as a global variable. The spatial resolution and extent are 30 m by 30 m, and 120 km by 120 km, respectively. The temporal resolution and extent are hourly time steps, and 336 timesteps, respectively.

*Rationale*: A fine resolution was chosen to capture as closely as possible the finest spatial scale that large grazers might make movement decisions at hourly time steps. Simulations were run for 336 time steps, representing two weeks in real-time. This duration was chosen to strike a balance between avoiding simulations that were impractically long and running simulations long enough to be able to determine meaningful averages of movement characteristics.
#### B.1.1.3 Process overview and scheduling

Each time step, the following actions are scheduled in the given order. They are implemented by corresponding submodels which are described in detail in the ODD section 1.1.7 below. Here we only list the names of the actions and a very brief description of their purposes; the information in parentheses shows which entity is running which action and, if applicable, under which condition it is run. Each time step, entities ran their actions in the order below:

### Agent initialization (agent)

An agent is initialized on a random cell within the landscape that is within 1 km of a water source. The following processes occur in order at the beginning of every time step. A flow diagram of the simplified model process is depicted in Figure B.2.

## *Update landscape forage levels (environment)*

The forage level of cells decreased by 90, reflecting the vegetation changes that occur in the dry season.

## Update environmental temperature (environment)

The environmental temperature, which is a global variable, is updated every time step.

#### *Updating perceived by environmental temperature (agent)*

Water-dependent grazers have been observed utilizing behavioral thermoregulation, in the form of shade use and wetting (among other behaviors), when environmental temperatures are high. These behavioral adjustments serve to dissipate heat from the animal's body and reduce ambient heat load, potentially reducing thermal discomfort. The *perceived* environmental temperature, which reflects the temperature the agent may experience as a result of a behavioral adjustment due to high environmental temperatures, is updated every time step. If the agent employs behavioral thermoregulation, the environmental temperature perceived by the agent is then decreased. This process serves to mimic the benefits of thermoregulatory behaviors, which is longer lasting for wetting behavior due in part to enhanced evaporative cooling.

## Updating the time elapsed since the agent visited a water source (agent)

The amount of time elapsed since the agent visited a water source is updated every time step. If the agent visited a water source at time t, the time elapsed resets to 0. If the agent did not visit a water source at time t, the time elapsed increases by 1.

### Deciding whether to thermoregulate (agent)

The agent first decides whether it must employ thermoregulation. This decision is influenced by the current perceived temperature, and the temperature threshold above which behavioral thermoregulation is likely to occur. If the probability of thermoregulation is greater than a randomly generated number, the agent will select either "wetting" or "shade use".

# Deciding whether to drink water (agent)

If the agent does not have to employ thermoregulation, it will decide whether it has to employ drinking. This decision is determined by the time since the agent last visited a water source (including instances of wetting), and the perceived environmental temperature. If the probability of drinking is greater than a randomly generated number, the agent will select drinking and will move to the closest water source or the cell within the search radius that is closest to the nearest water source.

## Deciding to forage (agent)

If the agent does not decide to employ thermoregulatory behavior or drinking, it will forage. There is a higher probability of selecting cells that maximize 'forage level/distance to the agent'. When the agent is foraging in a particular cell, the forage value of that cell is decreased.

#### B.1.1.4 Design concepts

**Basic principles:** In designing the model, we took the following basic concepts into account: Animal movement and space use patterns reflect an individual's underlying behaviors. Many large-bodied herbivores are known to spend the majority of the day engaging in foraging behavior, with foraging activity ceasing if the individual needs to respond to stressors, including the need to thermoregulate and the need to drink water. We modeled behavior and subsequent movement hierarchically, with the need to respond to stressors taking priority over foraging.

**Emergence**: Foraging efficiency and home range size emerged from the agent's interactions with the environment, behaviors, and subsequent space use.

Adaptation: The agents were mobile entities that adapted their behaviors to changes in their internal state (i.e. how long the agent has gone without visiting a water source and how the agent perceives the environmental temperature) and environment. Behaviors were probabilistic, such that the agent's selection of a behavior was dependent on the intensity of the stressors it was facing, namely temperature and the need to drink water.

Each cell selection criterion associated with each behavior was assumed to be based on attempts to increase fitness.

**Learning:** The agents did not change their behavior over time as a result of their experiences.

Prediction: The agent did not predict future conditions.

**Sensing:** At a local scale (within the searching radius), the agent sensed the forage level underlying the cells within the landscape, influencing their decisions concerning where to forage. The agents also sensed the environmental temperature as well as the time elapsed since they visited a water source; both state variables influenced the agents' behaviors at any given time step. An herbivore agent estimated the distance between itself and each cell within the landscape. Agent herbivores were also able to make direct movements towards water sources, even if the water sources were beyond their searching radius.

**Interactions:** As only one agent was modeled on the landscape during a simulation, there were no interactions among agents.

**Stochasticity:** The agent's decisions to select a behavior and its selection of cells when moving were influenced by their internal states and attributes of the landscape cells. To mimic the stochasticity inherent in animal behavior and movement patterns, random number generators were used to determine the behavior that the agent employed and the cell that the agent moved to within a time step.

**Collectives**: There were no higher collectives within the model

**Observation:** The amount of forage consumed, the distance traveled throughout a simulation, the x and y positions of the agent at every time step for the duration of two weeks (336 time steps), and the behaviors employed (along with the duration of time they are employed), were observed.

## B.1.1.5 Initialization

At the beginning of every simulation, one agent was initialized onto the landscape at a random location within 1 km of a water source. Its initial behavior was set as foraging, and we assumed that it had been exactly one time step since the agent last visited a water source. The initialization of the model agent was always the same.

At the beginning of a simulation, the initial amount of green vegetation biomass of each cell was set to a value between 0 to 100 g dry weight/sq meter. When scaled up to the resolution of the model landscape, these values corresponded to a range between 0 to 90000 g/ 900 sq meter. These values were close to the values of green standing biomass produced by Owen-Smith's (2002) generic grass growth model during the dry season, as well as values of standing grass biomass determined during the dry season in a Nigerian savanna (Ohiagu C.E. & Wood, 1979), the Serengeti (McNaughton, 1985), and South African savannas (Grunow, Groeneveld, & Du Toit, 1980).

## B.1.1.6 Input data

#### Environmental temperature

Hourly temperatures for the hot season months in KNP and CNP were downloaded from the National Oceanic and Atmospheric Administration's (NOAA) National Center for Environmental Information (NCEI), and the information was converted into a vector of temperature values. At the beginning of every time step, the element of the vector corresponding to the time step *t* was fed into the model, representing the environmental temperature.

#### *Forage level*

Forage level values ranged from 0 to 90000 g for each cell.

## Presence of water

Each cell contains a value of 0, representing the absence of a water source within the cell, or 1, representing the presence of a water source. High (.015 water sources/sq km) and low (.001 water sources/sq km) water source density values are consistent with densities in actual savannas (see Chamaille-James et al 2007 for water source densities n Hwange National park, for example).

## Tree cover

Overall abundances of tree cover for each landscape were set to either 5% or 25%, reflecting realistic percentages of tree cover present in savanna landscapes (see Roever et al., 2012 for mean percent tree cover of parks within Africa).

## B.1.1..7 Submodels

## Updating perceived environmental temperature

The *perceived* environmental temperature reflected the temperature the agent experienced as a result of a behavioral adjustment due to high environmental temperatures and was updated every time step. If the agent employed behavioral thermoregulation, the environmental temperature perceived by the agent was decreased. If the agent employed wetting during time step *t*, the agent perceived an environmental temperature of *current temperature-6* during t+1. The agent then perceived temperatures of 4, 2 and 1

degrees lower than the current temperature during time steps t+2, t+3, and t+4, respectively, even if no further thermoregulatory behaviors were employed during these time steps. While there were not have been, to our knowledge, studies exploring the duration of time that the benefits of evaporative cooling last after a wetting event, we made the realistic assumption that these benefits lasted for at least four hours after the wetting event.

On the contrary, if the agent employed shade use during time step t, the agent perceived a temperature of *current\_temperature-3* during t+1. In other words, the benefit of shade use only last for one time step. This process served to mimic the benefits of thermoregulatory behaviors, which is longer lasting for wetting behavior due in part to enhanced evaporative cooling.

## Updating the forage level of the cell

Every time step, the forage level of every cell in the landscape decreased by 90 g. This value was set arbitrarily.

# Updating time elapsed since the agent visited a water source

The amount of time elapsed since the agent visited a water source was updated every time step. If the agent visited a water source at time *t*, the time elapsed was reset to 0. If the agent did not visit a water source at time *t*, the time elapsed increased by 1.

## Deciding whether to thermoregulate

The agent first decided whether it had to employ thermoregulation. This decision was determined by the following equation:

where *P*<sub>thermoregulation</sub> was the probability in a time step of choosing thermoregulation behavior, where *"Temp threshold"* was the ambient temperature above which thermoregulatory behavior was most likely to occur (set at 30 degrees Celsius), *"Temp current"* was either the ambient temperature (which changes every time step), or a temperature lower than the ambient temperature due to the agent employing thermoregulatory behavior during a previous time step. The temperature threshold of 30 was selected because several mammals have been documented employing behavioral thermoregulation at temperatures at or above 30 degrees, including the pig, buffalo, and savanna elephant (Blackshaw 1994, Gu et al., 2016, Mole et al 2016).

If the probability of thermoregulation, *P*thermoregulation, was greater than a randomly generated number, the agent selected either "wetting" or "shade use". We assumed that the agent would most likely select "wetting" as a thermoregulatory behavior if there was water nearby and the individual did not have to travel a large distance to reach it. As such, we also assumed that there was a lower probability of searching for water within a larger search radius, as it was unlikely that agents would travel large distances to reach a water source if they were experiencing thermal stress. To reflect this, we set different probabilities of forming either a small or large search radius, which delineated the area that the agent searched for a water source. We set the probability of searching for water within a larger search radius, which was 60 cells (approximately 2 km), to be .25, and the probability of forming a small search radius, which was 30 cells (approximately 1 km), to be .75. The radii were selected based on maximum distances that large herbivores can easily travel in one time step. For example, African buffalo in Botswana's Okavango Delta travel average distances of approximately 500 (17 cells) to 750 meters (25 cells)

per hour (Bennitt et al 2014). Similarly, Owen-Smith et al (2014) found that buffalos travel an average of 1.66 km (65 cells) per hour in Kruger National Park. If there was a water source within the search radius, the agent moved to the closest water source, and the foraging trip duration was reset to 1. If there was no water within established search radius, the agent employed shade seeking and identified all cells with tree cover in a 30-cell radius. The top 10% of closest cells containing tree cover were identified. Because animal movement was generally characterized by a high degree of directional persistence, tree cover cells in the current direction of the agent were more likely to be selected. The angle formed between the current direction the agent was heading, and every potential destination cell from the selected cells was calculated, is known as the turning angle. To determine the shade cell towards which the agent moved, we generated 10 000 random numbers representing turning angles, in which the resulting distribution was positively skewed towards smaller numbers. A random number (turning angle) was selected from this distribution, and a cell characterized by the selected turning angle was then identified. The agent then moved to this cell. Thus, cells which are closer to the agent and in the same general direction that an agent was moving have a higher probability of being selected.

If there was no tree cover within the radius, the agent increased its search radius to 120 cells. If there was a water source within the new search radius, the agent moved to the closest water source, and the foraging trip duration was reset to 1. If there was no water within the new search radius but shade was available, the agent employed shade use and identified all cells with tree cover in the 120-cell radius as described above. If there was

no tree cover or water within the 120-cell radius, the agent heads to the cell closest a water source.

#### Deciding whether to drink water

If the agent did not have to employ thermoregulation, it decided whether it had to employ drinking. This decision was determined by the time since the agent last visited a water source (including instances of wetting), and the ambient temperature. The following equations illustrate this:

$$T_{water} = \sum_{t=t_{water}}^{t_{current}} I(Temp_{current})$$

where

$$I(Temp_{current}) = \begin{cases} 1 & if \ Temp_{current} \le Temp_{threshold} \\ Temp_{current} \ / \ Temp_{threshold} & if \ Temp_{current} > Temp_{threshold} \end{cases}$$

and where  $t_{current}$  was the agent's current time step,  $t_{water}$  was the time that had elapsed since the agent last visited a water source. The weighted cumulative time,  $T_{water}$ , was then used to calculate the probability of employing drinking:

$$P_{drinking}(t_{water}) = \frac{1}{1 + e^{-.1(T_{water} - \beta_1)}}$$

where  $\beta_i$  is the parameter representing when the probability of switching to seeking water rises to  $\frac{1}{2}$ . While trip duration frequency varies in the wild, we made the realistic assumption that the water-dependent agents generally must drink water once a day and so we set the  $\beta_i$  parameter to 50. If the probability of drinking was greater than a randomly generated number, the agent selected drinking. If there was a water source within a 60cell radius (approximately 2 kilometers), the agent moved to the water source, and the foraging trip duration was reset to 1. If there was no water within a 60-cell radius, the agent moved to the cell in the radius closest to the nearest water source.

### *Deciding to forage*

If the agent did not decide to employ thermoregulatory behavior or drinking, it foraged. The agent was assumed to know the forage level of the cells within its searching radius. Agents selected for areas containing the highest forage level but considered the traveling costs associated with reaching those areas. Agents were more likely to forage in a cell that maximized "forage biomass/distance traveled to reach the cell". Thus, a closer cell with an intermediate forage level may be selected over a farther area with a higher level.

For many herbivores, the intake rate of food generally takes the form of a Holling type 2 response (Holling, 1959, Lindsay, 1994) where intake rate increases with food availability before reaching an asymptote. To reflect this process within our model, we determined the hourly intake rate for grazer agents during any given time step via the equation below:

$$\frac{mF}{1+mhF}$$

where "m" is the fraction of the resources in the cell that the agent could remove in one hour, and "F" is food availability within the cell. 1/h is the maximum rate that food could be processed, i.e., the maximum rate of digestion. When there was a great abundance of food available for the agent, the rate of ingestion is 1/h. We did not take into account ungrazeable vegetation biomass, as the value for each cell in the forage layer was representative of green vegetation biomass, which was grazeable.

We chose to model a relatively large, generic grazing herbivore as the grazing agent. Taking note of reported wet bulk digestive capacity of kudu, we assumed that the digestive capacity, or "1/h" was 2 kg/day, or 83 g/hour (Owen-smith, 1993). We also assumed that "m" was .05.

## Quantifying foraging efficiency

We defined foraging efficiency as the ratio: 'E/D', where 'E' was the energy intake for each time step summed over the entire simulation, and 'D' was the total distance traveled throughout the entire simulation. Several simulation models have determined foraging success in a similar way; for example, Boyer and Walsh (2010) computed foraging efficiency as a measure of foraging success in an agent-based model, with the goal of exploring the advantages of using memory when foraging in spatiotemporally dynamic landscapes (Boyer and Walsh 2010). Energy intake was only counted for foraging behavior, and not shade use or wetting behavior. While herbivores can feed while in the shade, generally, the employment of thermoregulatory behaviors has negative effects on resource acquisition (Mason et al., 2017).



**Figure B.1**: Histograms of biomass for clumped and dispersed forage layers used in the model, at the beginning of a simulation, and at the end of a simulation. X-axis represents forage biomass values (x  $10^{4}$ ).



Figure B.2: Simplified flow chart of the model decision tree for every time step.

Forage	Water	Mean	SD	Sum
distribution	abundance			
Dispersed	High	4.0380e+04	1.0543e+04	6.3609e+11
		4.0349e+04	1.0377e+04	6.4558e+11
		4.0446e+04	1.0505e+04	6.4714e+11
Clumped	High	4.0270e+04	1.2893e+04	6.4432e+11
		4.0286e+04	1.2755e+04	6.4457e+11
		4.0472e+04	1.2454e+04	6.4756e+11
Dispersed	Low	4.2728e+04	8.7559e+03	6.8364e+11
		4.2028e+04	8.6383e+03	6.7244e+11
		4.2656e+04	8.8673e+03	6.8249e+11
Clumped	Low	4.2601e+04	1.1739e+04	6.8162e+11
		4.2660e+04	1.1532e+03	6.8255e+11
		4.2788e+04	1.1211e+04	6.8461e+11

**Table B.1**: Descriptive statistics for each forage layer used in the model.

Entity	Variable name	Description	Possible values
Agent	Position (x and y)	The agent's position on the landscape	
	T_water	Amount of time elapsed since the agent last visited a water source	1 – undefined hours
	Behavior	The behavior the agent is employing	Foraging, drinking, wetting, shade use
	Perceived_temp	Temperature the agent experiences (due to thermoregulatory behaviors)	Current temperature or lower
Cells	Forage level/biomass	Indicates the forage level that underlies the cell	0 – 90000 g
	Tree cover	Indicates whether tree cover underlies the cell	0 (absent) or 1 (present)
	water	Indicates whether a water source underlies the cell	0 (absent) or 1 (present)
Environment	Current_temp	Current environmental temperature	5 – 44 Celsius

**Table B.2**: Variables used within the model, their descriptions, associated entities and possible values.

<b>Behavior</b>	Cell selection strategy	Supporting references
Shade use	Move to closer cells having tree cover in the general direction of movement	Tree cover provides shade for grazers including blue wildebeest (Ben- Shahar & Fairall, 1982), white rhinoceros (Pienaar, 1994), and buffalo (Turner, Jolles, & Owen- Smith, 2005).
Wetting	Move to the closest cell containing water	Herbivores can remember the location of water points, and have good spatial memory (Provenza, 1995; Bailey et al., 2008)
Drinking	Move to the closest cell containing water, or to the cell within the search radius closest to the nearest water source	Herbivores can remember the location of water points, and have good spatial memory (Provenza, 1995; Bailey et al., 2008)
Foraging	Move to cells that maximize the following, in the general direction of movement:	When foraging, animals should "maximize their net rate of energy gain" (Wilson, Quintana, & Hobson, 2012).
	(Forage level/biomass)/distance to the agent	In general, maximizing net energy gain maximizes fitness (Mcnamara & Houston, 1997). Cost of travel to a patch plays an important role in foraging decisions (Bailey, Dumont, & WallisDeVries, 1998)

**Table B.3:** Agent behaviors and their corresponding cell selection strategies and supporting references.

Reference	Parameter value or parameter range	Change in
parameter		parameter value
Coefficient in the logistic regression equation utilized in drinking behavior which determines how sharp the switching behavior (to drinking) is as a function of $T_{water}$	-0.1 in the equation: $P_{drinking}(t_{water}) = \frac{1}{1 + e^{1(T_{water} - \beta_1)}}$	10% increase (-0.09) 10% decrease (-0.11)
Parameter $(\beta_1)$ in the logistic regression equation utilized in drinking behavior, which determines when the probability of switching to seeking water rises to $\frac{1}{2}$	50 is $\beta_1$ in the equation: $P_{drinking}(t_{water}) = \frac{1}{1 + e^{1(T_{water} - \beta_1)}}$	10% increase (55) 10% decrease (45)
Parameter determining the values in a vector from which a given turning angle is selected when the agent is foraging	$10 \text{ is } x \text{ in the equation:}$ $x=10$ $X=round((1+(180-1)*power(rand(1,10000),x)))$ $num=randsample(1:10,(numel(find(X==1)),true)$ $X(X==1)=num$ $ran_cells=round(randsample(X,1),2)$ (This generates a vector (X) where 10% of values are greater than or equal to 60	10% increase ( $x = 5$ ; generates vector where ~20% of values are greater than or equal to 60 degrees ) 10% decrease ( $x = 55$ ; generates vector where ~1% of values are greater than or
	degrees)	equal to 60 degrees)

**Table B.4:** Reference parameters and corresponding parameter values or ranges, along with the parameter changes used for the sensitivity analysis.

	Water abundance (low to high)	Tree cover distribution (dispersed to clumped)	Forage distribution (dispersed to clumped)	<b>Tree cover</b> <b>abundance</b> (low to high)
Foraging efficiency	6.2	4.2	2.9	4.2
Forage consumed	1.8	0.006	0.004	0.005
Distance traveled	4.1	5.4	3.1	4.8
Home range size	122.4	3.2	13.5	23.8
<b>Trip duration</b>	7.8	10	2	12.1
Time spent foraging	1.2	0.008	0.005	0.004
Time spent in shade	1.8	4.9	1.6	2.8
Time spent wetting/drinking	8.9	11.6	2.1	11.3

**Table B.5:** Percent changes associated with a 10% increase in the coefficient in the logistic regression equation utilized in drinking behavior which determines how sharp the switching behavior (to drinking) is as a function of  $T_{water}$ . Numbers in red represent the factor with the greatest impact on the respective response variable.

	Water abundance (low to high)	<b>Tree cover</b> <b>distribution</b> (dispersed to clumped)	Forage distribution (dispersed to clumped)	Tree cover abundance (low to high)
Foraging efficiency	5.4	2.9	3	5.1
Forage consumed	1.8	1.1	0.006	0.004
Distance traveled	3.4	4.3	3.5	5.3
Home range size	105.5	9.4	18.6	16.5
Trip duration	10.4	11.1	4.2	9.9
Time spent foraging	1.9	0.01	0.00000008	0.005
Time spent in shade	3.1	4.7	0.003	3.4
Time spent wetting/drinking	11.5	13.2	4.7	12.2

**Table B.6:** Percent changes associated with a 10% decrease in the coefficient in the logistic regression equation utilized in drinking behavior which determines how sharp the switching behavior (to drinking) is as a function of  $T_{water}$ . Numbers in red represent the factor with the greatest impact on the respective response variable.

	Water abundance (low to high)	Tree cover distribution (dispersed to clumped)	Forage distribution (dispersed to clumped)	<b>Tree cover</b> <b>abundance</b> (low to high)
Foraging efficiency	3.7	3	3.4	5
Forage consumed	1.4	0.009	0.006	0.001
Distance traveled	2.2	4.4	3.8	5
Home range size	118.7	8.2	14.1	16.6
Trip duration	7	8.8	3.1	13.7
Time spent foraging	1.3	0.0009	1	0.002
Time spent in shade	1.8	4.8	0.003	1.5
Time spent wetting/drinking	7.9	10.2	3.4	12.6

**Table B.7**: Percent changes associated with a 10% increase in the parameter determining the values in a vector from which a given turning angle is selected when the agent is foraging. Numbers in red represent the factor with the greatest impact on the respective response variable.

	Water abundance (low to high)	<b>Tree cover</b> <b>distribution</b> (dispersed to clumped)	Forage distribution (dispersed to clumped)	<b>Tree cover</b> <b>abundance</b> (low to high)
Foraging efficiency	9.8	2.7	2.2	4.3
Forage consumed	2.7	0.008	1.5	0.008
Distance traveled	6.5	4	3.5	5
Home range size	109	9.1	20	30
Trip duration	8.5	13.5	5.6	13.7
Time spent foraging	2.7	1	0.002	1
Time spent in shade	1.7	4.5	0.006	4.1
Time spent wetting/drinking	9.9	14.7	4.6	13.5

**Table B.8**: Percent changes associated with a 10% decrease in the parameter determining the values in a vector from which a given turning angle is selected when the agent is foraging. Numbers in red represent the factor with the greatest impact on the respective response variable.

	Water abundance (low to high)	Tree cover distribution (dispersed to clumped)	Forage distribution (dispersed to clumped)	<b>Tree cover</b> <b>abundance</b> (low to high)
Foraging efficiency	5.2	3.9	2.7	5
Forage consumed	2	0.003	1.3	1.8
Distance traveled	3.1	4.1	3.9	6.7
Home range size	92	13.4	19.2	7.7
Trip duration	10	14.3	6.1	9.9
Time spent foraging	2.2	0.005	0.004	2.4
Time spent in shade	3	0.002	0.007	9.1
Time spent wetting/drinking	10.3	15.6	4.9	10

**Table B.8**: Percent changes associated with a 10% increase in the parameter in the logistic regression equation utilized in drinking behavior, which determines when the probability of switching to seeking water rises to ½. Numbers in red represent the factor with the greatest impact on the respective response variable.

#### **Works Cited**

- Bailey, D. W., Dumont, B., & WallisDeVries, M. F. (1998). Utilization of heterogeneous grasslands by domestic herbivores: Theory to management. *Animal Research*, 47(5– 6), 321–333. https://doi.org/10.1051/animres:19980501
- Bailey, D. W., Gross, J. E., Laca, E. a., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., & Sims, P. L. (1996). Mechanisms That Result in Large Herbivore Grazing Distribution Patterns. *Journal of Range Management*, 49(5), 386. https://doi.org/10.2307/4002919
- Ben-Shahar, R., & Fairall, N. (1982). Comparison of diurnal activity patterns of blue wildebeest and red hartebeest. *South African Journal of Wildlife Research*, 17(2).
- Benhamou, S. (1992). Efficiency of Area-concentrated Searching Behaviour in a Continuous Patchy Environment. *Journal of Theoretical Biology*, 159, 67–81.
- Chamaillé-Jammes, S., Mtare, G., Makuwe, E., & Fritz, H. (2013). African Elephants Adjust Speed in Response to Surface-Water Constraint on Foraging during the Dry-Season. *PLoS ONE*, 8(3). https://doi.org/10.1371/journal.pone.0059164
- Department of the Interior, & U.S. Geological Survey. (2016). Product Guide. *Product Guide, Version* 7.(October), 1–27. https://doi.org/10.1080/1073161X.1994.10467258
- Duffy, K. J., Dai, X., Shannon, G., Slotow, R., & Page, B. (2011). Movement patterns of African elephants (Loxodonta africana) in different habitat types. *South African Journal of Wildlife Research*, 41(1), 21–28. https://doi.org/10.3957/056.041.0107
- Graham, M. D., Adams, W. M., & Lee, P. C. (2009). The movement of African elephants in a human-dominated land-use mosaic, *12*, 445–455. https://doi.org/10.1111/j.1469-1795.2009.00272.x
- Grunow, J. ., Groeneveld, H. ., & Du Toit, S. H. . (1980). Above-Ground Dry Matter Dynamics of the Grass Layer of a South African Tree Savanna. *Journal of Ecology*, 68(3), 877–889.
- Guy, P. R. (1976). Diurnal activity patterns of elephant in the Sengwa area, Rhodesia. *East African Wildlife Journal*, 14, 285–295. https://doi.org/10.1111/j.1365-2028.1976.tb00243.x
- Hansen, M. C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S. A., & Tyukavina, A. (2013). High-Resolution Global Maps of, *134*(November), 2011–2014.
- Lillywhite, H. ., & Stein, B. . (1987). Surface sculpturing and water retention of elephant skin. *Journal of Zoology, London, 211*, 727–734.
- Loarie, S. R., van Aarde, R. J., & Pimm, S. L. (2009). Elephant seasonal vegetation preferences across dry and wet savannas. *Biological Conservation*, 142(12), 3099– 3107. https://doi.org/10.1016/j.biocon.2009.08.021

- Mason, T. H. E., Brivio, F., Stephens, P. A., & Apollonio, M. (2017). The behavioral trade-off between thermoregulation and foraging in a heat- sensitive species, 28, 908–918. https://doi.org/10.1093/beheco/arx057
- Mcnamara, J. M., & Houston, A. I. (1997). Currencies for foraging based on energetic gain. *American Naturalist*, 150(5), 603–617. https://doi.org/10.1086/286084
- Mole, M. (2015). Behavioural thermoregulation in free-ranging savanna elephants (Loxodonta africana).
- Mole, M. a, Aarde, R. J. Van, Mitchell, D., & Fuller, A. (2016). Coping with heat: behavioural and physiological responses of savanna elephants in their natural habitat, *4*, 1–11. https://doi.org/10.1093/conphys/cow044
- Mumby, H. S., Courtiol, A., Khyne, U. ., & Lummaa, V. (2013). Climatic variation and age-specific survival in Asian elephants from Myanmar. *Ecology*, 94(5), 1131–1141.
- Ohiagu C.E., & Wood. (1979). Grass Production and Decomposition in Southern Guinea Savanna, Nigeria. *Oecologia*, 165, 155–165.
- Owen-smith, N. (1993). Evaluating optimal diet models for an African browsing ruminant , the kudu : how constraining are the assumed constraints ?, (1984), 499–524.
- Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., & Kausrud, K. (2011). The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. *Climate Research*, 46(1), 15–27. https://doi.org/10.3354/cr00936
- Pienaar, D. J. (1994). Habitat preference of the white rhino in the Kruger National Park. Proceeding of Symposium on "Rhinos as Gam Ranch Animals." Retrieved from http://www.rhinoresourcecenter.com/pdf\_files/127/1275004167.pdf
- Polansky, L., Kilian, W., & Wittemyer, G. (2015). Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state-space models. *Proceedings of the Royal Society B: Biological Sciences*, 282(1805), 20143042–20143042. https://doi.org/10.1098/rspb.2014.3042
- Provenza, F. D. (1995). Tracking variable environments: There is more than one kind of memory. *Journal of Chemical Ecology*, 21(7), 911–923. https://doi.org/10.1007/BF02033798
- Purdon, A. (2015). Environmental determinants of the movement patterns of elephants in the Kruger National Park, (July).
- Purdon, A., & van Aarde, R. J. (2017). Water provisioning in Kruger National Park alters elephant spatial utilisation patterns. *Journal of Arid Environments*, 141(October), 45–51. https://doi.org/10.1016/j.jaridenv.2017.01.014
- Roever, C. L., van Aarde, R. J., & Leggett, K. (2013). Functional connectivity within conservation networks: Delineating corridors for African elephants. *Biological Conservation*, 157, 128–135. https://doi.org/10.1016/j.biocon.2012.06.025

- Roguet, C., Dumont, B., & Prache, S. (1998). Selection and use of feeding sites and feeding stations by herbivores: A review. *Annales de Zootechnie*, 47(4), 225–244. https://doi.org/10.1051/animres:19980401
- Rowe, M. F., Bakken, G. S., Ratliff, J. J., & Langman, V. a. (2013). Heat storage in Asian elephants during submaximal exercise: Behavioral regulation of thermoregulatory constraints on activity in endothermic gigantotherms. *The Journal* of Experimental Biology, 216, 1774–1785. https://doi.org/10.1242/jeb.076521
- Ryan, S. J., Cross, P. C., Winnie, J., Hay, C., Bowers, J., & Getz, W. M. (2012). The utility of normalized difference vegetation index for predicting African buffalo forage quality. *Journal of Wildlife Management*, 76(7), 1499–1508. https://doi.org/10.1002/jwmg.407
- Shannon, G., Page, B. R., Mackey, R. L., Duffy, K. J., & Slotow, R. O. B. (2008). Activity Budgets and Sexual Segregation in African Elephants (Loxodonta Africana), 89(2), 467–476.
- Thaker, M., Gupte, P. R., Prins, H. H. T., & Slotow, R. (2019). Fine-Scale Tracking of Ambient Temperature and Movement Reveals Shuttling Behavior of Elephants to Water, 7(January), 1–12. https://doi.org/10.3389/fevo.2019.00004
- Turner, W. C., Jolles, A. E., & Owen-Smith, N. (2005). Alternating sexual segregation during the mating season by male African buffalo (Syncerus caffer). *Journal of Zoology*, 267(3), 291–299. https://doi.org/10.1017/S095283690500748X
- Wilson, R. P., Quintana, F., & Hobson, V. J. (2012). Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proceedings of the Royal Society B: Biological Sciences*, 279(1730), 975–980. https://doi.org/10.1098/rspb.2011.1544
- Wittemyer, G., Douglas-Hamilton, I., & Getz, W. M. (2005). The socioecology of elephants: Analysis of the processes creating multitiered social structures. *Animal Behaviour*, 69(6), 1357–1371. https://doi.org/10.1016/j.anbehav.2004.08.018
- Wyatt, J. ., & Eltringham, S. . (1974). The daily activity of the elephant in the Rwenzori National. *East African Wildlife Journal*, *12*, 273–289.