UNIVERSITY OF READING

MODELLING ELEPHANT MOVEMENTS AND POPULATION DYNAMICS USING REMOTE SENSING OF FOOD AVAILABILITY

A thesis submitted for the degree of

Doctor of Philosophy

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December 2018

Preface

This thesis includes two published manuscripts (Chapters 3 and 4, respectively):

Boult, V. L., Sibly, R. M., Quaife, T., Fishlock, V., Moss, C. J. & Lee, P. C., 2018. Modelling large herbivore movement decisions: beyond food availability as a predictor of ranging patterns. *African Journal of Ecology*, 57(1), 10–19.

Boult, V. L., Quaife, T., Fishlock, V., Moss, C. J., Lee, P. C. & Sibly, R. M., 2018. Individual-based modelling of elephant population dynamics using remote sensing to estimate food availability. *Ecological Modelling*, 387, 187–195.

In this thesis, Chapter 5 has also been submitted for publication as follows:

Boult V.L., Fishlock, V., Quaife, T., Hawkins, E., Moss, C.J., Lee, P.C. & Sibly, R.M., in review. Human-driven habitat conversion is a more immediate threat to Amboseli elephants than climate change.

Declaration

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

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Victoria L. Boult

For published chapters, author contributions are detailed below.

Chapter 3 - *Modelling large herbivore movement decisions: beyond food availability as a predictor of ranging patterns*:

VLB retrieved satellite data, performed modelling and analysis, and wrote the manuscript; RMS contributed to model design; TQ provided scripts for, and technical guidance on, satellite data; PCL contributed to model and long-term study design; VF contributed to model design; CM founded the long-term study and is holder of intellectual property; all authors contributed to revisions.

Chapter 4 - *Individual-based modelling of elephant population dynamics using remote sensing to estimate food availability*:

VLB retrieved satellite data, performed modelling and analysis, and wrote the manuscript; RMS, TQ, PCL and VF contributed to model design; TQ provided scripts for, and technical guidance on, satellite data; PCL contributed to long-term study design; CM founded the long-term study and is holder of intellectual property; all authors contributed to revisions.

Chapter 5 - *Human-driven habitat conversion is a more immediate threat to Amboseli elephants than climate change*:

VLB retrieved satellite, climate and habitat data, performed modelling and simulations, and wrote the manuscript; TQ provided scripts for, and technical guidance on, satellite data; EH provided technical guidance on climate data; RMS, TQ, EH, PCL and VF contributed to scenario designs; PCL contributed to long-term study design; CM founded the long-term study and is holder of intellectual property; all authors contributed to revisions.

Abstract

Biodiversity conservation has limited resources so must identify and prioritise the most critical threats facing species and ecosystems. This is especially apparent in light of current rates of global change which alter the abundance, distribution and resilience of species and habitats. Traditional approaches to understand the impacts of change have generally related variation in environmental factors to species' dynamics, but these methods are unreliable when making predictions under novel conditions. Process-based approaches are built on fitness-maximising mechanisms that are robust to change and thus present the opportunity to both project the effects of global change and identify the most significant threats facing species.

This PhD aimed to develop process-based models to simulate the impacts of environmental change on the elephants of Amboseli in Kenya. Food availability was considered a key driver of elephant movement decisions and demographic rates throughout. Satellite-derived measures of vegetation were calibrated with ground-based measures of biomass and used to estimate the food available to elephants through time and space. Elephant tracking data was used to confirm the importance of food availability as a key driver of elephant movement decisions and to identify additional explanatory variables, including risk and reproductive state, which mediated elephant space-use. An individual-based model (IBM) was developed and calibrated to accurately predict historic elephant population dynamics emerging from temporal variation in food availability. The IBM was subsequently used to project the impacts of changes in food availability resulting from anthropogenic climate change and habitat conversion on Amboseli's elephants. Using climate projections for different greenhouse gas emissions scenarios and land use scenarios based on empirical data and stakeholder opinion, the model predicted elephant population size through the 21st century. Model results identified habitat conversion, rather than climate change, as the primary threat facing Amboseli's elephants.

Future model developments through the incorporation of behavioural mechanisms, spatially explicit landscapes and multiple stressors would provide more robust predictions of elephant population responses to environmental change. Nonetheless, the work presented here documents an early example of a process-based model developed to inform land management decisions and the conservation of Amboseli elephants.

Acknowledgements

No doubt, I could not have achieved the work presented in this thesis without the time, effort and belief of so many people.

First, thank you to Richard Sibly for your unrivalled patience and support. I cannot thank you enough for all you have taught me, for your tireless enthusiasm and for sharing so much of your time with me over the past years. We've become a great team and I hope we'll work together again. I couldn't have asked for a better supervisor, so thank you a-hundred times.

To my co-supervisors, thank you for your support and insight throughout. To Tristan Quaife, thank you for introducing me to the exciting world of remote sensing and for your enduring belief in me. Thanks to Phyllis Lee for sharing with me your unparalleled wisdom on all things elephant. To Vicki Fishlock, thank you for welcoming me so wholeheartedly into your world of elephants and Amboseli.

I'm extremely grateful to have played even the tiniest role in the story of Amboseli. This magical place exists thanks to the commitment of countless people and organisations. Special thanks to all involved throughout the lifetime of the Amboseli Elephant Research Project for creating such a rich source of data and knowledge on elephants. Thanks also to Big Life Foundation and Amboseli Ecosystem Trust for providing data and insight. I also appreciate the advice of Keith Lindsay during the early part of the project. In the hands of so many dedicated people, I'm certain Amboseli, its wildlife and people will thrive for years to come.

Thank you to my funders, NERC, for making this project possible. I would also like to thank my monitoring committee Manuela Gonzalez-Saurez and Mark Fellowes, for your valuable feedback. To my fellow PhD students at the University of Reading, I'm grateful that we tackled it as a team and wish you the best of luck. Plus, everyone else in the School of Biological Sciences, especially the 11 o'clock coffee crew.

To my two best friends, Dominic Kotlarzewski and Mum, thank you for being my top cheerleaders always. I truly and honestly couldn't have done it without your unconditional love and support.

My dear friend Heike Zitzer, I hope you know that you started me on this crazy journey. Thank you for sharing with me your knowledge and passion. I'm in this for life because of you and those special elephants, and I can't thank you enough.

And, maybe madly, I'm grateful for elephants. Whilst they may not be the most straightforward model organism, they are nothing short of inspirational, and I wouldn't have it any other way.

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Chapter 1. Introduction

In this thesis I use process-based models to show how food availability and other environmental factors drive the population dynamics of the elephants inhabiting the Amboseli ecosystem in Kenya. In this introductory chapter, I begin by identifying the value of process-based models then introduce the Amboseli ecosystem and its elephants. I conclude by outlining the aims and objectives of this thesis, and provide a guide to the structure of the thesis.

1.1 The need for predictive modelling in ecology and conservation

Global change is expected to create conditions beyond those previously recorded. Changes in global temperatures and precipitation patterns will present novel climates which may push species beyond physiological thresholds or cause shifts in species distributions, which in combination with the human-assisted spread of species creates novel species assemblages (Wood, Stillman and Hilton, 2018). In addition, the world's growing human population puts increasing pressures on species through overexploitation, pollution and habitat conversion.

The future of many species will depend on their ability to cope and adapt to new circumstances. Given the current unprecedented rate of global change, adaptation by evolution is likely to be outpaced in most cases. Rather species adaptation may involve behavioural changes and innovations (Sol *et al.*, 2005) or geographical shifts in a species range (Laidre *et al.*, 2018) or in how an individual utilises its existing range (Olden *et al.*, 2004; Tucker *et al.*, 2018).

Predictive models are required to answer questions about the likely future state of the world's ecosystems in order to assess possible risks and inform decision-making (Evans, 2012). Biodiversity conservation in the face of expected global change especially relies on predictive models to forecast how changes will impact species and their habitats (Clark *et al.*, 2001; Sutherland, 2006; Wood, Stillman and Hilton, 2018). The capacity to anticipate ecological responses to global change will improve our ability to adapt and initiate crucial conservation actions (Clark *et al.*, 2001).

A process-based approach

Traditional modelling approaches to understand how ecological dynamics respond to environmental variation are based on observed or empirical relationships between an ecological property of interest and an environmental variable (reviewed in Sutherland 2006). However, such relationships are usually only recorded under a narrow range of environmental variation and are unlikely to hold under novel future conditions, especially when considering complex non-linear responses (Stillman *et al.*, 2015).

Process-based approaches improve our mechanistic understanding of the processes underlying ecological dynamics and extend our predictive ability to novel environmental conditions (Evans *et al.*, 2013). They do so by assuming that natural selection has shaped behaviours and processes to maximise fitness (Grimm and Railsback, 2005). The mechanisms underlying these fitness-maximising behaviours are not expected to change under novel conditions and this feature allows robust predictions beyond environmental conditions in which the model was parameterised (Grimm and Railsback, 2005; Wood, Stillman and Goss-Custard, 2015).

Individual-based models

Individual-based models (IBMs) present a process-based approach which is well suited for modelling the mechanisms underlying species' responses to environmental change. Individual-based ecology considers population-level properties to emerge from individual-level behaviours and interactions between individuals and with the environment (Grimm and Railsback, 2005). IBMs refer to simulation models in which individuals are the basic entity. More specifically, IBMs represent the processes and behaviours of a system's individual components which are often too complicated to describe through traditional differential equations. Individuals are represented as autonomous and adaptive entities: autonomous because each individual pursues its own objectives through fitness-maximising behaviours and adaptive because individuals respond and adjust to the current state of the system (Railsback and Grimm, 2012). IBMs are also able to incorporate heterogeneity between individuals (Grimm and Railsback, 2005), allowing responses to drivers to vary between individuals depending on, for example, their age, sex and reproductive state. As a result of individual behaviours and interactions with others and the environment, system dynamics emerge (DeAngelis and Mooij, 2005; Grimm and Railsback, 2005; Wood, Stillman and Goss-Custard, 2015).

The early use of IBMs arose for both pragmatic and paradigmatic reasons (Grimm, 1999). Pragmatically, some questions simply could not be addressed using classical approaches which do not consider individuals (Botkin, Janak and Wallis, 1972; DeAngelis, Cox and Coutant, 1979). Paradigmatically, some believed that classical approaches were severely limited in their ability to understand general ecological theory (Lomnicki, 1978, 1988; Kaiser, 1979). However, the use of IBMs only really took off following a review by Huston et al. (1988) who hypothesised that IBMs could unify ecological theory. Despite an increase in the number of so-called IBMs, the true contribution of IBMs to ecology was hard to determine as the lack of a solid definition meant many models were wrongly coined "IBMs". Uchmański & Grimm (1996) attempted to address this issue and defined IBMs as models in which: 1) individual life cycles are considered, 2) the dynamics of resources sought by individuals are represented, 3) populations are defined by integer rather than real numbers, and 4) variation between individuals of the same age is considered. Following this clarification, Grimm (1999) reviewed Huston et al.'s earlier hypothesis, but concluded that whilst individual IBMs had successfully achieved their intended purpose, very few had aimed to address general ecological theory and as such, little ground had been made by IBMs. Grimm & Railsback (2005) added that the complexity of IBMs and the lack of a standardised approach to such models likely also contributed. With the added complexity of IBMs, the development, analysis and communication of models is difficult, more data are required to inform the increasing number of parameters, which in turn leads to greater uncertainty in predictions and models which are less general (Grimm and Railsback, 2005). In later work, Grimm and colleagues have attempted to address many of these issues. Grimm et al. (2006) proposed the ODD protocol as a standardised method for documenting IBMs and subsequently found the protocol provided additional benefits in standardising the formulation of IBMs and outlining the theory underlying complex models (Grimm *et al.*, 2010). Further advances in the documentation of IBMs were proposed by Schmolke et al. (2010) and Grimm et al. (2014). Theoretical advances of IBMs have also been made (Grimm and Railsback, 2005), whilst significant guidance for practically approaching IBMs (Railsback and Grimm, 2012) has been aided by the development of tools including NetLogo (Wilensky, 1999) and RNetLogo (Thiele, Kurth and Grimm, 2012).

Thanks therefore to significant advancements in the field of individual-based modelling, increasingly realistic IBMs are possible. In addition, the predictive ability of IBMs under novel conditions (Stillman *et al.*, 2015) and when incorporating the cumulative impacts of multiple stressors (Nabe-Nielsen *et al.*, 2018) has established IBMs as a key decision support tool to inform evidence-based environmental decision-making (Schmolke *et al.*, 2010; Wood, Stillman and Goss-Custard, 2015).

Incorporating energy budgets

Conservation biology is often concerned with the dynamics of populations, since population dynamics can determine the resilience of a population to stochastic or directional changes in the environment (Grimm and Railsback, 2005). IBMs aiming to capture population dynamics should include energy budgets if the population is to realistically respond to variation in food availability (Sibly *et al.*, 2013). Energy budget models allow growth and reproduction when food is sufficient, and starvation and death during periods of food shortage. The conservation of energy means that energy utilised by one process cannot be used simultaneously by another. Energy is therefore divided between the energy expending processes of life, but how it is divided is the cause of some debate. The widely used dynamic energy budget (DEB) model uses the ‘kappa rule’ which assumes that a constant fraction of energy is allocated to maintenance and growth with the rest going to growth in juveniles and reproduction in adults (Kooijman, 2000). An alternative approach is described in Sibly et al. (2013) in which energy is allocated to processes by order of priority. The idea is that if an individual cannot cover the costs of maintenance it will die. Hence, energy is first allocated to maintenance and then to reproduction or growth (depending on life stage) if sufficient energy remains. Sibly et al.’s model has successfully been used to model the population dynamics of earthworms (Johnston *et al.*, 2014) and mackerel (Boyd *et al.*, 2018).

The potential of remote sensing in IBMs

A key criteria of IBMs is the representation of resources to which individuals respond (Uchmański and Grimm, 1996). Satellite remote sensing (referred to hereafter as remote sensing or RS) presents the opportunity to estimate key environmental drivers consistently through space and time with little effort by the user (Kerr and Ostrovsky, 2003). The global coverage and long timespan of RS data provides information on environmental drivers at scales which would be impossible using traditional ground-based approaches. When using energy budgets to model population dynamics, information on the spatiotemporal dynamics of food availability may be derived using RS. The use of RS in ecology has grown dramatically over the past few decades thanks to improved computing power, technical expertise and freely available data (Kerr and Ostrovsky, 2003; Turner *et al.*, 2003; Pettorelli *et al.*, 2014), but the use of RS in the analysis of IBMs or to represent key drivers in IBMs remains limited.

In the following chapters, an individual-based approach is adopted to predict the impact of global change on one of the world's most charismatic and vulnerable mega-herbivores, the African elephant (*Loxodonta africana*). RS data are employed to estimate the food available to elephants inhabiting the Amboseli ecosystem over a 17-year period, a task which would be logistically unfeasible using traditional methods. Models are used to identify factors influencing elephant movement decisions and population dynamics in order to contribute to the conservation of the species.

1.2 The African elephant

General elephant biology

Elephants are the only extant members of the Mammalian order Proboscidea (Meyer *et al.*, 2017) and comprise three species: the African savannah or bush elephant (*Loxodonta africana*), the African forest elephant (*Loxodonta cyclotis*) and the Asian elephant (*Elephas maximus*). This thesis focuses only on African savannah elephants, hereafter referred to as either African elephants or elephants.

African elephants once had a near continental distribution, but are now confined to only scattered fragments of their former range across sub-Saharan Africa (Chase *et al.*, 2016). As generalist herbivores, feeding on a mixture of plant materials from grass and leaves, to bark, roots and fruit (Owen-Smith and Chafota, 2012), elephants can exist in a range of habitats including dense forests, savannahs and arid deserts. Throughout their range elephants are considered to play a vital role in the maintenance of ecosystems, earning them designation as a keystone species (Western, 1989): feeding on woody vegetation prevents bush encroachment, maintaining savannah grasslands (Laws, Parker and Johnstone, 1975); elephants act as important seed dispersers (Campos-Arceiz and Blake, 2011); elephants dig to access groundwater in dry seasons, providing a vital water source for other species as well as their own (Ramey *et al.*, 2013). Seasonal ranging patterns naturally maintain the grassland-woodland matrix of African habitats and in doing so are crucial for the maintenance of biodiversity and ecosystem function.

Elephants live in complex fission-fusion societies in which groups merge and divide through time (Couzin, 2006). The central unit, known as a family group, is made up of related females and their immature offspring (Moss and Poole, 1983), and is headed by a matriarch. Matriarchs are usually the eldest female because older elephants act as important repositories of social and ecological information (McComb *et al.*, 2001, 2011). Males leave their natal family group as they near sexual maturity and spend most of their time associating with other males or alone, only interacting with female groups for mating purposes (Moss and Poole, 1983; Chiyo, Archie, *et al.*, 2011).

Elephants are long-lived and slow breeding. Individual elephants can live for over 70 years (Lee *et al.*, 2012) and females have one of the longest reproductive life spans of any animal, potentially producing calves for over 40 years (Moss and Lee, 2011). Females become sexually mature at around age 10, gestation lasts for 22 months and lactation can extend for several years (Lee *et al.*, 2016). Males mature later at around 20 years of age but are unlikely to successfully sire offspring until their mid-30s (Hollister-Smith *et al.*, 2007).

Their ecological importance and slow life histories make elephants of particular concern to conservation practitioners: being slow to adapt and recover from environmental or anthropogenic disturbances, elephants are particularly vulnerable to change, whilst the loss of elephants from an ecosystem can have cascading impacts on biodiversity and ecosystem function.

The current status of Africa's elephants

The African elephant simultaneously represents a species of conservation concern and a problem for coexisting humans (Hoare, 2000; Evans and Adams, 2018). Poaching has been responsible for the drastic reduction of Africa's elephant population from an estimated one million in 1970 (Douglas-Hamilton, 1987) to roughly 400,000 in 2016 (Chase *et al.*, 2016). The recent spike in poaching following the one-time legal sale of ivory in 2008 (UNEP *et al.*, 2013) continues to threaten the persistence of elephant populations worldwide (Wittemyer *et al.*, 2014; Bennett, 2015), but many working in conservation now believe elephants face greater challenges.

In 2009, Africa's human population hit one billion, having doubled since 1982, and is expected to double again by 2050 (UNDESA 2017). The associated conversion of natural habitats to human dominated landscapes has squeezed wildlife into smaller and more isolated pockets of land, reducing the availability of resources and the ability of individuals to disperse and migrate. Habitat fragmentation has also increased the interface between wildlife and people (Hoare, 1999). Here, undesirable elephant behaviours compromise human lives and livelihoods, reducing the tolerance of people who may in turn retaliate through injuring or killing elephants (Dickman, 2010; Browne-Nunez, Jacobson and Vaske, 2013).

Whilst absolute space available to wildlife is reduced, the quality of remaining habitats is altered by changing climates. Rising global temperatures and shifting rainfall regimes are expected to alter the distribution and composition of plant communities, with implications rising through the trophic web (Walther, 2010). At the same time landscapes may be degraded through overgrazing by large herbivore populations confined to habitat fragments or through overexploitation by Africa's growing human population. As a result, not only will the absolute space available to elephants continue to decline in coming decades, but the quality of remnant habitats may become insufficient to support sustainable elephant populations in the long-term without heavy (and expensive) management interventions.

Thus, whilst poaching and human-elephant interactions (HEI) can alter elephant demographics and cohort survival (Jones *et al.*, 2018), greater threats may lie in the loss of sufficient space for elephants. Changes in habitats and vegetation owing to climate change and land use strategies will have large scale implications for the persistence of elephant populations, which may act to counter or exacerbate the effects of poaching and HEI.

The Amboseli elephants

The Amboseli ecosystem is an ancient lake basin (bounding coordinates: -2.02N, -3.28S, 38.03E, 36.67W) covering an area of approximately 8000km^2 straddling the southern border of Kenya and the northern border of Tanzania (Figure 1.1). The ecosystem comprises the central Amboseli National Park (ANP; 392km^2) and surrounding landscape, stretching from the Chyulu Hills in the east to the granitic outcrops and volcanic cones in the west, and from Kilimanjaro in the south to the broken basement hills in the north (Croze and Lindsay, 2011). The habitat is made up of mostly grass dominated savannah dotted with Acacia trees and thickets. Plant biomass is generally low due to low average annual rainfall (340mm). Indeed, water is a key limiting factor in the ecosystem. Rain falls in two wet seasons: the short wet season spans November and December, whilst the long rains begin in March and end in May (Altmann *et al.*, 2002). Wet seasons are interspersed by a short, hot dry season in January and February, and a longer, cooler dry season from June until October. An 'Amboseli year' runs October to September to align rainfall regimes and is the standard annual cycle used throughout this thesis. There is considerable inter-annual variation in rainfall but no clear pattern. Standing water in Amboseli is limited to the central system of swamps, with the exception of rivers and Lake Amboseli which hold water for a few short weeks following heavy rains. The swamps are fed by poorly understood groundwater flows from rain falling on the forested catchments of the Chyulu Hills and Kilimanjaro (Croze and Lindsay, 2011). They support a diverse assemblage of bird species and large populations of herbivores, along with the local Maasai people and their livestock (Western, 1975).

Alongside the distinct Maasai culture and looming presence of Kilimanjaro, Amboseli is best known for its population of ca. 1700 elephants (Lee *et al.*, 2013). Since its inception in 1972 the Amboseli

Elephant Research Project (AERP) has monitored the elephants of Amboseli as individuals, meticulously recording identities, births and deaths. Now in its 46th year, the AERP represents the longest-running study of wild elephants anywhere in the world and has hugely expanded our understanding of elephants as highly intelligent, social and thoughtful animals. In this time, the AERP has monitored over 3300 individuals from more than 60 family groups.

When the AERP started, Kenya was home to some 130,000 elephants (Braude, 1992). In 2016, Kenya's elephant population had fallen to around 26,000 (Chase *et al.*, 2016). Like elsewhere in Africa, this loss has been largely attributed to poaching for ivory (Douglas-Hamilton, 1987). However, Amboseli's elephants have been largely spared the poaching onslaught probably because of the constant presence of researchers in ANP and the surrounding Maasai communities who do not tolerate poaching (Croze, Moss and Lindsay, 2011; Kioko *et al.*, 2015). In fact, during this time, the Amboseli population has actually increased from approximately 600 individuals in 1972 to around 1700 today, and as a result boasts an un-skewed population structure with individuals ranging from new born to over 70 years of age, and adult males in their mid-50s (AERP long-term data).

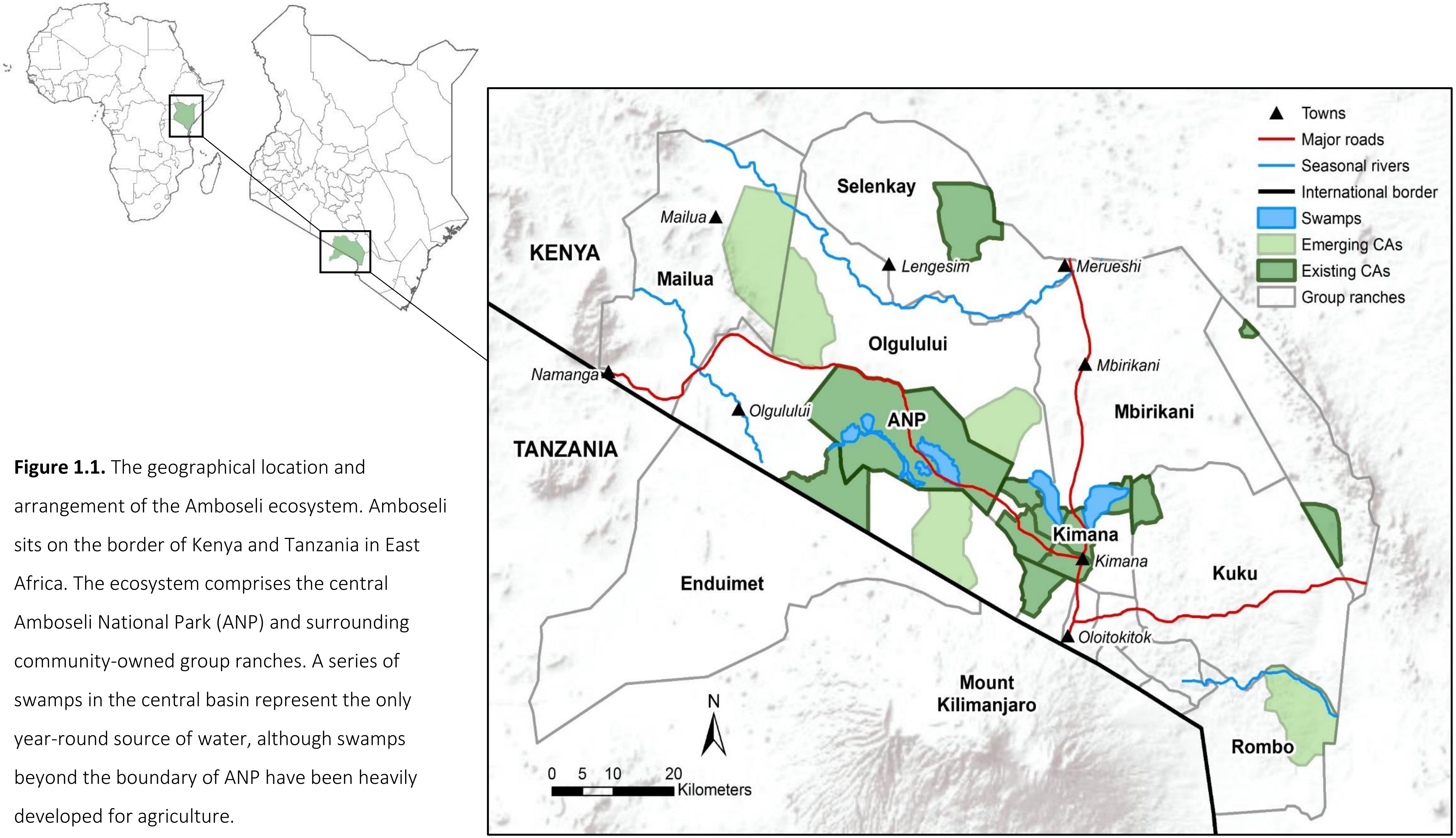

Figure 1.1. The geographical location and arrangement of the Amboseli ecosystem. Amboseli sits on the border of Kenya and Tanzania in East Africa. The ecosystem comprises the central Amboseli National Park (ANP) and surrounding community-owned group ranches. A series of swamps in the central basin represent the only year-round source of water, although swamps beyond the boundary of ANP have been heavily developed for agriculture.

Specific challenges facing the Amboseli elephants

Alongside avoiding the worst of the poaching crisis, the previous success of Amboseli's elephants has relied on their continued access to the ecosystem beyond the boundaries of the national park. Indeed, ANP alone makes up just 5% of the total ecosystem, meaning the surrounding group ranches (an artefact of the British colonial system, representative of the collective ownership key for pastoralism to work in semi-arid environments) provide important dispersal areas and movement corridors for wildlife (Western and Lindsay, 1984; Kioko, Okello and Muruthi, 2006; Croze and Moss, 2011). The future of Amboseli's elephants, wildlife and people depends hugely upon the ongoing accessibility of the greater ecosystem, but growing human populations and land use changes threaten to reduce access.

The human population of Amboseli is growing both internally and via immigration from elsewhere in Kenya (Campbell *et al.*, 2000). With more people come more livestock and the increased conversion of land for the development of infrastructure, settlements and farming. Growing numbers of people and livestock in the ecosystem increases competition for resources, including water and forage, which can create contact points around key resources between humans and wildlife and act as a platform for negative interactions (Thouless, 1994; Smith and Kasiki, 2000).

With growing competition for space across Kenya, the government has encouraged people to settle on increasingly marginalised land, resulting in the subdivision and sometimes fencing of small plots (Western, Groom and Worden, 2009). Such small plots are rarely appropriate for livestock production in semi-arid systems where rainfall is patchy, and so people have largely turned to crop production (Kangwana and Browne-Nunez, 2011).

There has been an expansion of intensive, irrigated agriculture around the swamps beyond the boundaries of ANP (Kioko & Okello 2010; Schüßler et al. 2018). Not only has this removed important habitats for wildlife, it has also restricted access to a crucial water source for wildlife, people and livestock and is rapidly degrading nearby soils and polluting waterways (Githaiga *et al.*, 2003). At the same time, rain-fed agriculture has expanded down the northern foothills of Kilimanjaro, encroaching on wildlife habitats from a second direction (Kioko and Okello, 2010; Schüßler, Lee and Stadtmann, 2018). Both means of crop production present a platform for further HEI, where crop consumption by elephants threatens peoples' lives and livelihoods, and low tolerance by people results in the retaliatory spearing of elephants (Browne-Nunez, Jacobson and Vaske, 2013).

In addition to land use change, social challenges threaten Amboseli's elephants. Across Kenya in 2015, it was estimated that 36% of people lived below the international poverty line of US$1.90 per day (World Bank Group, 2018) and unemployment is high, especially for young rural people.

Dissatisfaction with government policy and practise often motivates the political spearing of wildlife, including elephants (Lindsay, 1987).

The challenges in Amboseli are not unique and come down to two omissions: 1) a lack of land use planning has allowed human populations to encroach into natural habitats and 2) there have been no large-scale plans to secure the benefits of wildlife for local communities. Urgent land management policy is required to prevent further conversion of natural habitats into human-dominated landscapes, protecting dispersal areas and securing movement corridors throughout the ecosystem. In combination, efforts must be made to promote the benefits of wildlife for local people through realisation of the ecosystem services provided by natural ecosystems and through the direct benefits of employment in, and income from, the wildlife-tourism industry. The Amboseli Ecosystem Trust and Kenya Wildlife Service are working to coordinate the efforts of NGOs operating in the ecosystem and to establish data-driven protocols to prevent land conversion and mitigate negative human-wildlife interactions (more details in 6.2). The research presented here hopes to support evidence-based discussions.

1.3 Aims and Objectives

Given the range of threats facing Africa's elephants and the limited resources available for biodiversity conservation and land management, there is an urgent need to develop tools which can identify priority areas for threat mitigation. This PhD aims to develop models that simulate the impacts of environmental change scenarios on elephant populations to identify the drivers posing the greatest threats. The primary scientific objectives to address this aim are:

- Synthesise current knowledge on the environmental drivers of elephant distribution and demographic rates,
- Estimate the spatiotemporal variation in key environmental drivers by translating satellite remote sensing into food availability measurements,
- Test the influence of spatial variation in food availability on the movement decisions of elephants and identify any additional explanatory variables,
- Accurately replicate historic elephant population dynamics using temporal variation in food availability to drive an energetic model,
- Project the effects of environmental change (habitat loss and climate change) scenarios on the food availability and elephant population dynamics in Amboseli,
- Identify primary threats facing Amboseli's elephants to inform land management decisions.

1.4 Outline of the thesis

The models presented in this PhD are based on the fundamental principle that animal population dynamics and behaviours are governed largely by the availability of food (Sinclair, 1975; Morales *et al.*, 2010). Long-term monitoring of elephants has found that vital demographic rates, including conception and parturition (Rasmussen, Wittemyer and Douglas-Hamilton, 2006; Wittemyer, Ganswindt and Hodges, 2007; Wittemyer, Rasmussen and Douglas-Hamilton, 2007), coincide with peaks in food availability, whilst limitations in food availability increase mortality rates (Wato *et al.*, 2016). Spatiotemporal dynamics in food availability also drive elephant ranging behaviours, with movements targeted towards the highest quality and quantity of vegetation (Loarie, Van Aarde and Pimm, 2009; Bohrer *et al.*, 2014). Food availability is expected to change under future environmental scenarios and will therefore be a crucial component driving the response of elephant populations to global change. Throughout this thesis, food availability is considered a key environmental driver of elephant demographic rates and movement behaviours.

An individual-based approach was adopted throughout as heterogeneity in the responses of known individuals to key drivers can help to identify additional factors influencing animal demographics and behaviours. Under this approach, models were developed relating variation in food availability to the movement patterns and population dynamics of Amboseli's elephants.

The first task was to estimate the food available to elephants through time and space. Since elephants can live for over 70 years and range over hundreds of kilometres, quantifying food available to elephants using traditional methods was unfeasible. Instead, satellite remote sensing (RS) presented the opportunity to monitor vegetation dynamics over appropriate spatiotemporal scales. In **Chapter 2**, satellite-derived measures of greenness (NDVI) were calibrated against ground-based live plant biomass. Greenness measures from the Terra-MODIS (Moderate Resolution Imaging Spectroradiometer) satellite were related to biannual measures of biomass across the major habitat types of ANP. Most ground-based measures of vegetation were unsuitable for the calibration due to mismatches between the scale of the satellite and ground-based measures or due to interference of non-food vegetation. However, a relationship between NDVI and biomass was established and used in subsequent chapters to estimate food available to Amboseli elephants. In **Chapter 3**, satellite data were used to estimate the relative food available in seasonal home ranges of five GPS-collared elephants and their families. The movements of these individuals were monitored over the course of a year and compared to modelled elephant locations based on maximising resource availability (food and water). The model predictions represented the locations of two elephants well, highlighting the importance of seasonal migration for maximising resource availability. The movements of other individuals were less well predicted by the model. Using detailed knowledge about these individuals and their ecosystem, additional factors moderating elephant movement choices were identified, including reproductive events and perceived risks. In **Chapter 4**, an IBM relating food availability to elephant demographic rates was developed. Food availability was translated to demographic rates through an energy budget: elephants ingested energy from food available in the environment then allocated it to maintenance, growth and reproduction. When food was abundant, elephants allocated energy maximally to all processes, but when food was limited elephant reproductive capacity was reduced, individuals starved and eventually died. Elephants were represented as individuals in the model and responded independently to food availability depending on their age, sex, reproductive and physiological state. In this way, birth and death rates, and ultimately population size, emerged because of variation in food availability. The model was calibrated using approximate Bayesian computation to fit the historic population dynamics of four Amboseli elephant families and validated using an additional six family groups. In **Chapter 5**, the IBM was applied to identify the impacts of global change scenarios, including climate change and habitat loss, on Amboseli's elephants. The historic relationship between NDVI and climate variables was established and used to project the food available to elephants under different greenhouse gas emissions scenarios. Habitat loss scenarios were developed based on stakeholder opinions and empirical records of human population growth and HEI. The effects of climate change and habitat loss scenarios on the Amboseli elephant population was simulated throughout the 21st century. Results revealed that habitat loss presents the most significant threat to the persistence of the Amboseli elephants and highlighted the importance of management plans to secure elephant access beyond the boundaries of conservation areas. In **Chapter 6**, the implications of these results for the Amboseli elephants and their ecosystem are discussed alongside the benefits of a process-based approach for informing conservation actions and landscape planning. The general mechanisms underlying models presented in Chapters 3 and 4 and the use of freely available RS (Chapter 2) and climate (Chapter 5) data allow these models to be easily adapted to understand the implications of global change for other elephant or herbivore populations. Finally, the value of developing an interactive toolkit incorporating these models and data is presented.

Chapter 2. Using satellite remote sensing to estimate food available to the Amboseli elephants

2.0 Abstract

The abundance and distribution of food is a key driver of animal population dynamics, behaviours and distribution. With an understanding of spatiotemporal variation of food, we should therefore be able to make predictions about animal demographic rates and movement behaviours. However, quantifying food availability at the spatial and temporal scales at which an animal lives can be challenging for traditional ground-based measures, as is often the case when animals live for many years and range over huge expanses. Remote sensing presents the opportunity to estimate biophysical parameters, such as food availability, in a way which remains consistent through space and time. To properly understand how remote sensing data relates to ground-based metrics and thus animal population dynamics, calibration is required. Here we present a method for calibrating MODIS-NDVI to provide estimates of herb-layer biomass, the predominant food for the Amboseli elephants. Estimation of herb-layer biomass was limited by interference of canopy layers and mismatches in the scales of the data; it nevertheless sufficed for the purpose of estimating relative food available to elephants through space and time. The process demonstrates key challenges in calibrating remote sensing data and suggests future options for minimising their effects, but alongside subsequent chapters, also highlights the benefits of remote sensing for improving understanding of animal energetics, movement behaviours and population dynamics under global change. The calibration of satellite NDVI presented in this chapter facilitates its use to estimate food availability in the subsequent chapters of this thesis.

2.1 Introduction

The abundance and distribution of food is an important bottom-up driver of animal ranging behaviour and population dynamics (Lack, 1955; Birnie-Gauvin *et al.*, 2017). At a global scale, animals are unable to exist where food availability is insufficient or food types are inappropriate. Locally, animals generally move to maximise the food available to them in order to achieve maximum fitness (Wilmshurst *et al.*, 1999; Fryxell, Wilmshurst and Sinclair, 2004; Bartlam-Brooks *et al.*, 2013). Whilst food type preferences and feeding behaviours are often well documented for a species, it can be difficult to quantify food availability at the spatial and temporal scales at which an individual lives, particularly for long-lived and wide-ranging species.

One species for which this challenge is evident is the African elephant (*Loxodonta africana*). Demographic rates and movement behaviours of elephants are to a large extent governed by the availability of food and water (Viljoen, 1989; Trimble, Ferreira and Van Aarde, 2009). Feeding behaviours in elephants, including preferences and ingestion rates, are well understood (Buss, 1961;

Guy, 1976; Barnes, 1982; Stokke and du Toit, 2000; Shannon, Page, Duffy, *et al.*, 2006b). Elephants are considered generalist herbivores, for which almost all standing plant biomass can be considered food. Estimating the food available to elephants would therefore require quantification of all plant biomass over the spatial and temporal scales at which an elephant lives. Considering a single elephant may range over hundreds of kilometres and live for 70 years (Moss, Croze and Lee, 2011a), this presents an unfeasible task for traditional ecological methods (Kerr and Ostrovsky, 2003; Pfeifer *et al.*, 2012), where the challenge lies in collecting such huge volumes of data whilst maintaining spatiotemporal consistency.

Satellite remote sensing (RS) provides a relatively 'hands-free-low-effort' approach to collecting standardised, repeated measures of the Earth's surface, in a way which is consistent over time and space (Le Roux *et al.*, 1997; Kerr and Ostrovsky, 2003; Nilsen, Herfindal and Linnell, 2005; Willems, Barton and Hill, 2009). The use of RS in ecology and biodiversity conservation has grown dramatically in the past two decades (Kerr and Ostrovsky, 2003; Turner *et al.*, 2003; Pettorelli *et al.*, 2014), thanks in part to improved computing power, increased accessibility of freely-available RS data, and rising technical expertise.

Using RS, biodiversity has been monitored both directly – identifying individuals or groups of individuals – and indirectly – using indices and proxies. Direct monitoring of individual animals and plants (reviewed in Hollings et al., 2018) generally requires high resolution, hyperspectral sensors which are often prohibitively expensive, hence their use remains limited. However direct RS has been achieved for, for example, whales (Fretwell, Staniland and Forcada, 2014), polar bears (LaRue *et al.*, 2015), zebras and wildebeest (Yang *et al.*, 2014), and nesting bird colonies (Barber-Meyer, Kooyman and Ponganis, 2007), and the detection of the species-specific electromagnetic signals of plants allows identification plant individuals (Pu, 2009; He *et al.*, 2011). Indirect monitoring of biodiversity relies on the assumption that plant and animal species are generally associated with certain biophysical characteristics of the Earth's surface which can be detected by RS (Turner *et al.*, 2003). Variables such as temperature and elevation can be combined with land cover classifications, which estimate the variety, type, and extent of different land cover classes, to inform species distribution models and predict the occurrence of species and species assemblages (He *et al.*, 2015).

RS is also widely used to detect aspects of global change, such as changes to the length of the growing season (Myneni *et al.*, 1997), sea level rise (Nerem, Leuliette and Cazenave, 2006) and the northern shift of the treeline (Zhou *et al.*, 2001), and to monitor threats to biodiversity, including deforestation (Achard *et al.*, 2002), expanding mining operations (Kusimi, 2008) and fires (Li and Cihlar, 2000).

Notably, the Normalised Difference Vegetation Index (NDVI) has proven useful to a wide variety of ecological applications (reviewed in Pettorelli et al., 2011, 2005). NDVI measures the normalised ratio of the near-infrared and red reflectance bands:

$$NDVI = \frac{(NIR - red)}{(NIR + red)}, \qquad \textbf{eqn 1}$$

where NIR is near-infrared radiation and red is red radiation reflected from the Earth's surface. The ratio concept underlying NDVI helps to reduce sources of multiplicative noise, such as illumination differences, cloud shadows, atmospheric attenuation and some topographical variations. Healthy green vegetation absorbs strongly in the red band, but is highly reflective in the NIR band, hence green vegetation generates positive NDVI values, whilst bare soil, cloud, snow and water give low or negative NDVI values (Jensen, 2007). NDVI correlates closely with ground-based measures of many biophysical parameters including biomass, net primary productivity and leaf area index, and has been demonstrated to predict the space use and population dynamics of a wide variety of animals (reviewed in Pettorelli et al., 2014, 2011, 2005), though may be influenced by the canopy background and saturates at high biomass conditions.

For elephants in particular, NDVI has been shown to relate to aspects of space use, including presence-absence (Hien *et al.*, 2007; de Boer *et al.*, 2013), densities (Chamaillé-Jammes and Valeix, 2007; Young, Ferreira and van Aarde, 2009; Duffy and Pettorelli, 2012) and habitat selection (Young, Ferreira and van Aarde, 2009; Marshal *et al.*, 2011; Matawa, Murwira and Schmidt, 2012; Wall *et al.*, 2013; Bohrer *et al.*, 2014), and at a range of scales from local forage site selection (Young, Ferreira and Van Aarde, 2009; Marshal *et al.*, 2011) to continental distribution (Duffy and Pettorelli, 2012; de Boer *et al.*, 2013). The influence of NDVI on movement behaviours has also been reported, including home range size (Young, Ferreira and Van Aarde, 2009), randomness (Wittemyer *et al.*, 2008) and distance (Young and Van Aarde, 2010) of daily movements, and timings of seasonal migrations (Bohrer *et al.*, 2014). Vital demographic rates of elephants are also well predicted by NDVI time series, including oestrus and conception rates and timing (Rasmussen, Wittemyer and Douglas-Hamilton, 2006; Wittemyer, Ganswindt and Hodges, 2007; Wittemyer, Rasmussen and Douglas-Hamilton, 2007), and juvenile mortality (Wittemyer, 2011). In addition, NDVI has predictive ability regarding elephant diet composition and the switch from dry season browsing to wet season grazing (Cerling *et al.*, 2006, 2009; Wittemyer, Cerling and Douglas-Hamilton, 2009).

Given the growing body of support for the relationship between NDVI and animal, especially elephant, space use and demographic rates, NDVI was utilised here to drive individual-based models of elephant movement and population dynamics in the Amboseli ecosystem, Kenya. Critical to this is understanding how NDVI relates to the mechanistic drivers determining elephant abundance and distribution, which requires an understanding of the relationship between NDVI and food available to elephants. This chapter therefore aimed to establish the relationship between satellite-derived NDVI and on-the-ground measures of vegetative biomass in order to map the food available to the Amboseli elephants through time and space. The results inform models described in subsequent chapters of this thesis, which will ultimately act to provide improved insight into the factors determining elephant movements and population dynamics and may in turn aid conservation planning for elephants.

2.2 Methods

On-the-ground biomass

The Amboseli Elephant Research Project (AERP) has been collecting data on the herb-layer biomass of vegetation in the Amboseli National Park (ANP) since 1982 (Moss, Croze and Lee, 2011a). All surveying methods were designed by W.K. Lindsay and are further documented in (Lindsay, 1982).

Twelve vegetation plots were established in areas representative of the six major habitat types found in ANP (outlined in Table 2.1). Swamp edge habitats (SEG, PAX and YAX) are fed by ground water from the slopes of Kilimanjaro in the south and so have year-round potential for primary productivity, whilst dry woodland habitats (SS, TW and XW) rely on seasonal rainfall for plant growth. Where possible, plot locations were kept consistent over the years of the study but were relocated if the habitat type was deemed to have changed beyond its definition or if the area became inaccessible due to, for example, flooding, cattle grazing or fencing. If plots were relocated, they were moved within the minimum possible distance from the previous location to an area representing the intended habitat type.

Plots were surveyed biannually to coincide with the extremes of vegetative biomass: shortly following the onset of the long rains (roughly May) and the end of the long dry season (roughly October) each year. A slanting pin-frame with 10 pins was placed 50 times at two meter intervals along a 100 meter transect (McNaughton, 1979). The number of pins intercepting vegetation (out of a possible 10) and height of vegetation closest to the central pins was measured at each point to derive mean percent vegetation cover and height for the transect.

Predictive equations linking mean vegetation height and percent cover to dry biomass (g m^{-2}) were developed through calibration experiments (Lindsay, 1982) for swamp edge and dry woodland habitats:

$$\ln(HLB) = -0.899 + 0.81 \times \ln(ht) + 1.120 \times \ln(cov) \qquad \textbf{eqn 2a}$$

and

$$\ln(HLB) = 2.504 + 0.393 \times \ln(ht) + 0.459 \times \ln(cov) \qquad \textbf{eqn 2b}$$

where HLB is the herb layer biomass of swamp edge (eqn 2a) or dry woodland (eqn 2b) habitats in g m^{-2}, ht is the mean height of vegetation in cm and cov is the mean percent cover of vegetation along the transect.

We assumed that herb-layer biomass represented the food available to elephants in the Amboseli ecosystem since these elephants are predominantly grazers with woody vegetation, bark, fruit and flowers only constituting a small portion of their diet (Lee pers. comm.).

Table 2.1. The habitat types of Amboseli National Park - as described in (Lindsay, 1982).

Habitat	Code	Habitat type	Description
Date palm and fever tree swamp edge woodland	PAX	Swamp edge	Occurs in a small, isolated area around the central swamp in ANP. Woody layer comprised of low-growing date palms (*Phoenix reclinata*) and fever trees (*Acacia xanthophloea*). Canopy cover averages roughly 20%. Prolific growth of large, woody herbs (including *Aubutilon mauritianum*), with a grass and herb layer typical of SEG (see below).
Swamp edge grassland	SEG	Swamp edge	Occurs along edges of the permanent swamps, where water flows beneath the soil for much of the year. Herb layer dominated by dense layer of Bermuda grass (*Cynodon dactylon*) with few creeping herbs at ground level. Woody herbs and shrubs sparse but develop localised thickets where soil moisture is highest.
Young fever tree swamp edge woodland	YAX	Swamp edge	Occurs in scattered patches along swamp margins. Basically, SEG with fairly dense (about 15%) cover of young and maturing fever trees, which flourish in these areas of low soil salinity and permanent water.
Salvadora and *Suaeda* woodland	SS	Dry woodland	Formerly XW (see below), but now devoid of all but a few fever tree seedlings. Dominated by shrubs *Salvadora persica* and *Suaeda monoica*. Herb layer similar to that of YAX although species composition and biomass changed since disappearance of canopy.
Umbrella tree woodland	TW	Dry woodland	Occurs on volcanic and lacustrine soils of southern ANP. Woody layer dominated by umbrella tress (*Acacia tortilis*) with a variety of, mostly evergreen, woody shrubs and herbs in understory. Canopy cover variable but averages 4-5%. Herb layer dominated by palatable, productive grasses (*Cynodon plectostachyus* and *Sporobolus spp*).
Fever tree woodland	XW	Dry woodland	Survives on the deeper alkaline soils in isolated patches. Similar to TW but with fewer herb and shrub species, a *Sporobolus* dominated herb layer, and an exclusively *A. xanthophloea* tree layer in various states of size and health creating a canopy cover of about 2%. *Suaeda monoica* occurs as a major understory species.

Remotely-sensed vegetation indices

Remotely-sensed measures of vegetation were obtained from the Moderate Resolution Spectroradiometer (MODIS) mission launched on the Terra satellite in 1999. The satellite has a near polar orbit at an altitude of 705km to achieve daily global coverage with a repeat cycle taking 16 days, during which each area of the Earth's surface is viewed from a range of angles (NASA, 2018).

NDVI is derived from the MODIS reflectance data as 16-day composites. Composites are composed of the best daily, atmospherically-corrected, bidirectional surface reflectance on a pixel-by-pixel basis in the 16-day period, chosen to minimise cloud cover, optimise the solar and view angles, and have the best atmospheric correction (Huete, Justice and Van Leeuwen, 1999).

We obtained 250m resolution 16-day composites of Terra-MODIS NDVI from the Oak Ridge National Laboratory Web Service (Vannan *et al.*, 2011). Specifically we used the MOD13Q1 product (Didan, 2015). Data were filtered using QA flags so that only ‘good’ quality pixels were used in our calculations. Terra-MODIS was used rather than Aqua-MODIS because of the longer NDVI time-series available (Terra operational since 2000, Aqua since 2002).

Calibration

NDVI was obtained for dates and locations corresponding to vegetation surveys. Instances where ‘good’ quality NDVI values could not be obtained were excluded from analysis. Linear regression was used to determine the strength of correlations for each vegetation plot and habitat classification. The full NDVI time series (2000-2017) for each vegetation plot location was also obtained to further investigate the relationship between vegetative biomass and NDVI.

2.3 Results

Correlation between Biomass and NDVI

In all cases, biomass was positively correlated with NDVI. However, the strength and significance of the relationship varied with habitat type and plot. When all plots were grouped together biomass was positively associated with NDVI ($r = 0.56$, $df = 206$, $p < 0.001$). Association was maintained when dividing plots by habitat type (i.e. swamp edge and dry woodland habitats) but varied when plots were grouped by habitat with only PAX, SEG and SS correlated (Figure 2.1).

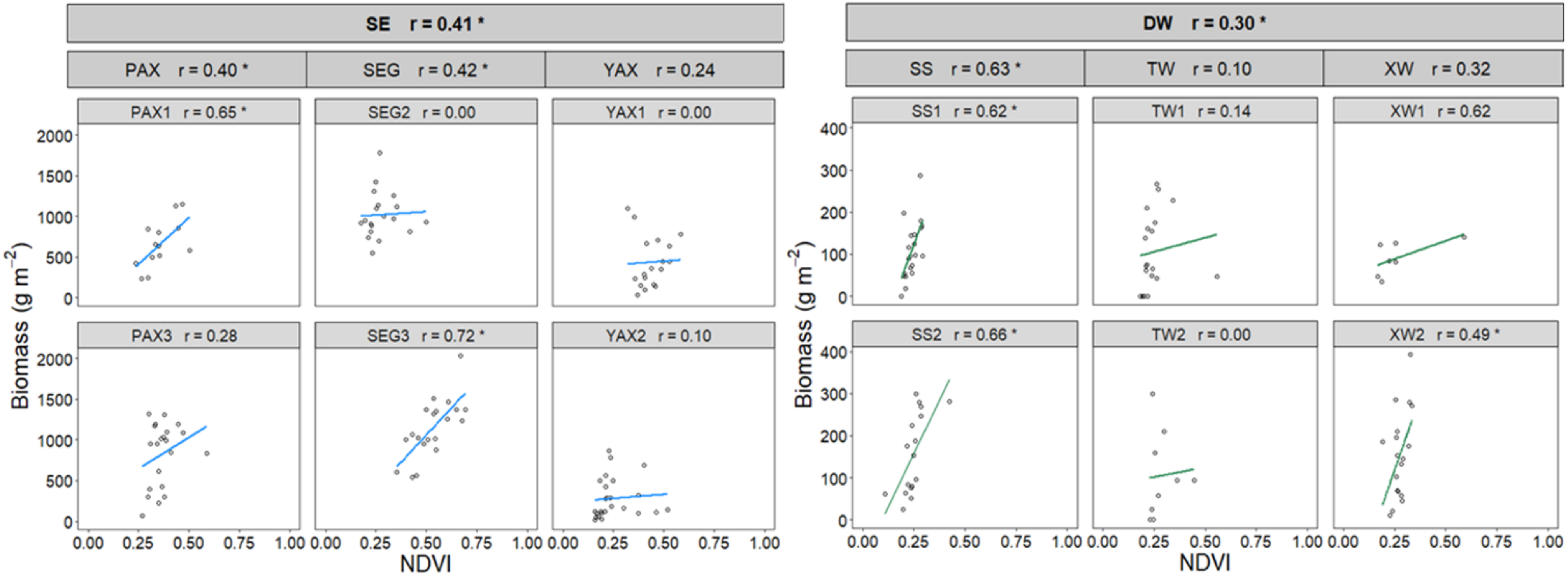

Figure 2.1. Correlations (coloured lines: blue = SE habitats, green = DW habitats) between satellite-derived NDVI and on-the-ground measures of herb-layer biomass (r = correlation coefficient; * indicates $p < 0.05$). Numbers after habitat codes refer to different plots of the same habitat.

Detailed Comparison of Biomass and NDVI Time-series

The biomass time-series derived from vegetation surveys is shown in Figure 2.2. Swamp edge habitats consistently had a higher biomass than dry woodland habitats. The biomass time-series shows peaks and troughs in vegetation biomass corresponding to wet and dry seasons respectively; wet season biomass was higher than previous and subsequent dry seasons except in 2008, 2009 and 2011 for both habitat types and 2002 for dry woodland. There was a significant drought beginning with poor rainfall in 2008 and continuing through 2009, when biomass was low in both habitat types.

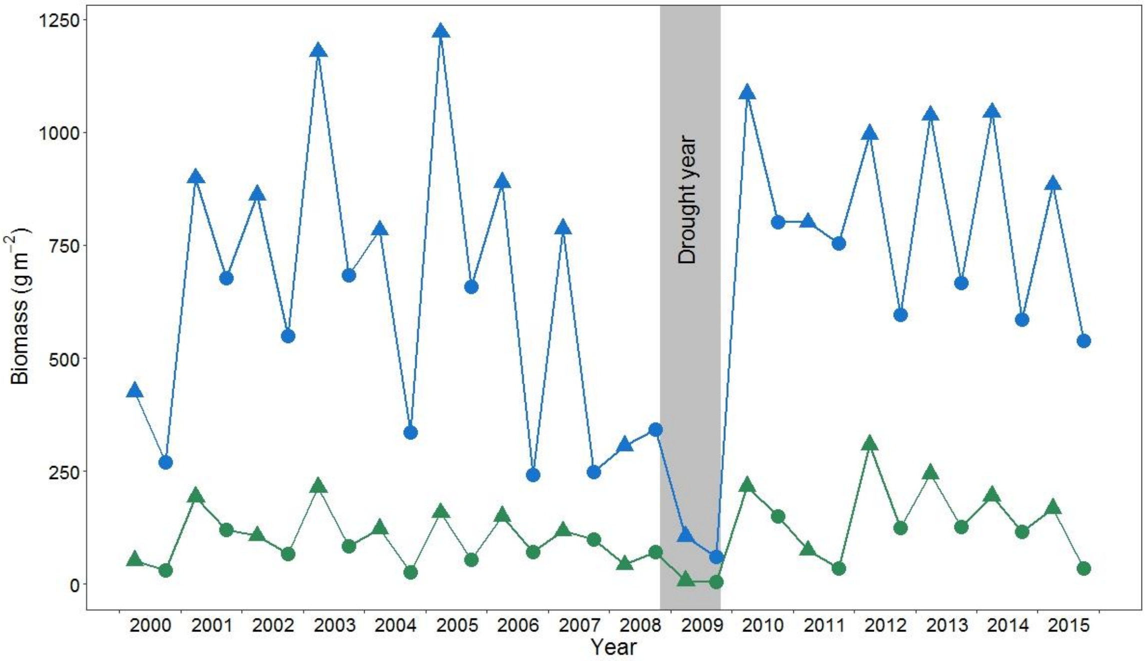

Figure 2.2. Mean herb-layer biomass time-series of swamp edge (blue) and dry woodland habitats (green). Measures recorded biannually to correspond to peak wet (triangles) and peak dry (circles) seasons. Years are calendar years. Grey shading indicates drought year.

Normalised NDVI and biomass time-series were compared on a plot-by-plot basis in order to identify reasons behind the variable correlation coefficients (Figure 2.3). The number of vegetation surveys varied by plot. Whilst some had a near-full time-series of biannual biomass from 2000 to 2017, the time-series of others was limited to just a few years (TW2, XW1 and XW2), reducing the ability to derive robust linear models.

Also notable were marked disparities between normalised NDVI and biomass values of plots SEG2, YAX1 and YAX2 throughout, and of plots TW1 and XW2 during wet seasons. Differences in normalised values suggests that either canopy interference or scale mismatch influenced results. Canopy interference arises when the canopy layer intercepts reflected radiation from the herb-layer. Here, this means that NDVI responded to canopy biomass rather than that of the herb-layer. Scale mismatch occurs when the spatial resolution of the RS data does not match the spatial extent of the ground-based measure (Kerr and Ostrovsky, 2003). In this case, the 250m resolution MODIS pixel considers a much wider spatial extent than that of the 100m biomass transect. Both canopy interference and scale mismatch can result in disparities between RS and ground-based data. Put simply, the RS data and vegetation transect recorded different things; ground-based surveys only measured herb-layer biomass along a 100m transect, whilst RS data recorded all vegetation within the 250m pixel. If the canopy layer or surrounding vegetation differed from vegetation on the transect, this variation would have been observed by the RS instrument but not reflected in the ground-based data. This was likely responsible for the limited correlations between RS and ground-based data.

The obvious step-change in NDVI values around 2013 for plots SEG2, YAX1, YAX2 and XW1 (i.e. the previous mean NDVI is markedly different to the subsequent mean NDVI) corresponds to the relocation of these plots (for reasons earlier described), which either reduced or increased the effects of canopy interference or scale mismatch.

On this basis, plots with insufficient biomass data (TW2, XW1 and XW2) and those suffering issues of canopy interference or scale mismatch (SEG2, YAX1, YAX2, TW1) were removed from the analysis. We also chose to remove both PAX plots (PAX1 and PAX3) due to high canopy cover, and both SS plots (SS1 and SS2) due to the prevalence of shrubs. The remaining plot (SEG3) had no canopy cover and was in a fairly homogeneous location thus minimising canopy interference and scale mismatch. The linear equation relating SEG3 herb-layer biomass (g m^{-2}) to satellite-derived NDVI showed a strong positive correlation ($r = 0.72$, $df = 18$, $p < 0.05$):

$$Biomass = 2666 \times NDVI - 270 \,, \qquad \textbf{eqn 3}$$

where $Biomass$ is the herb-layer biomass of SEG3 vegetation and $NDVI$ is the Terra-MODIS NDVI value for the corresponding date and location. This equation is used to estimate biomass, and thus food available to elephants, across the Amboseli ecosystem in subsequent chapters of this thesis.

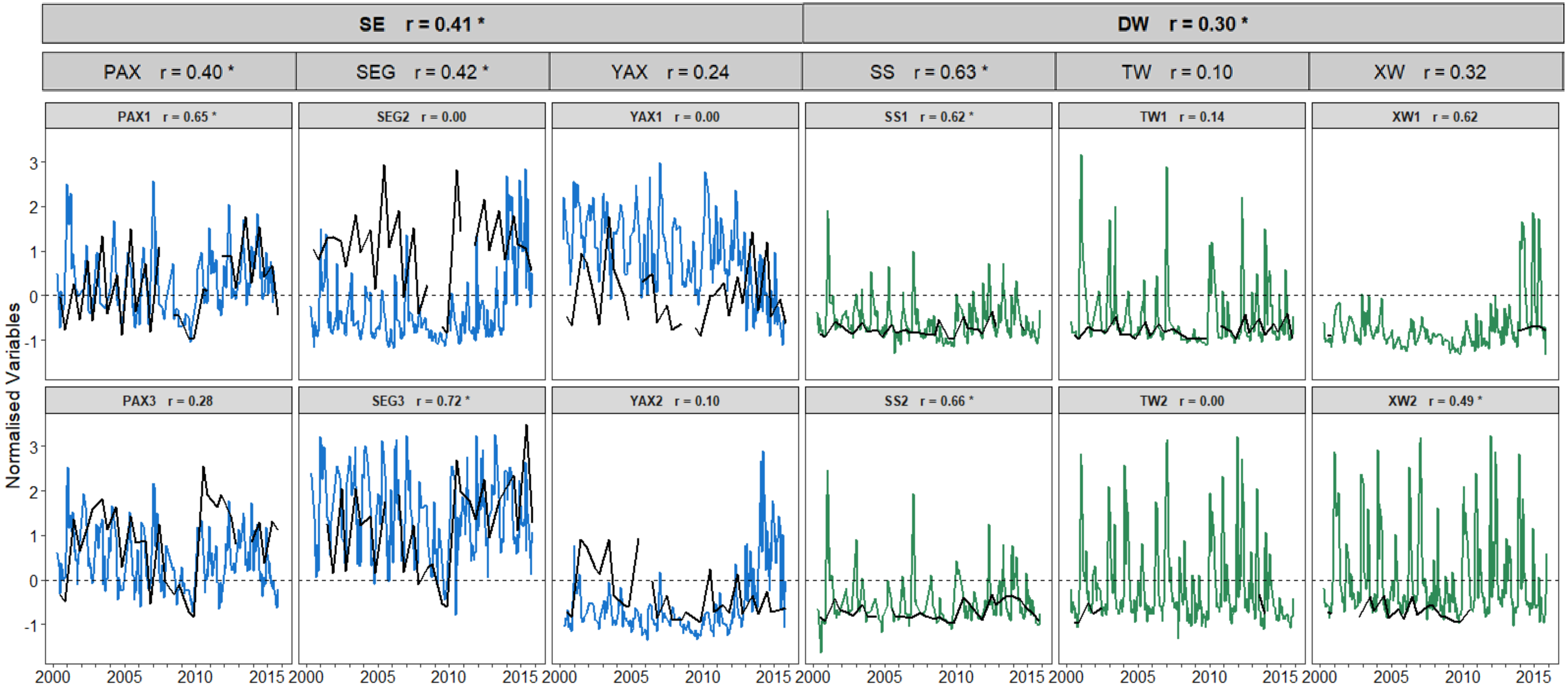

Figure 2.3. Normalised NDVI (coloured lines: blue = SE habitats, green = DW habitats) and biomass (black) time-series.

2.4 Discussion

Most vegetation plots proved unsuitable for the calibration of satellite-derived data to herb-layer biomass. Detailed investigation of NDVI and biomass time-series data revealed that insufficient biomass measures, scale mismatch and canopy interference were likely responsible for poor correlations. Few ground-based measures of biomass in some habitats prevented the derivation of robust linear models. In addition, the difference in the scale of ground-based surveys and RS data meant fluctuations in vegetation not accounted for by transects (i.e. trees, shrubs and surrounding vegetation) influenced NDVI. The two measures were thus reflecting different vegetation dynamics and caused poor correlations.

When unsuitable plots were removed, the herb-layer biomass of the single remaining plot (SEG3) was positively correlated to MODIS-NDVI. Whilst this relationship provides a strong basis for predicting SEG herb-layer biomass using NDVI, its ability to predict herb-layer biomass more widely must be carefully considered.

The application of this calibration exercise in subsequent modelling requires estimates of the relative herb-layer biomass rather than absolute values. The movement model presented in Chapter 3, predicts elephant movement decisions based on the relative food available in seasonal home ranges of elephant family groups. In Chapter 4, an energy budget model is driven by biomass over a 17-year period. Though the amount of biomass available in the environment determines the rates of survival and reproduction, calibration of model parameters means that relative food availability through time is enough to accurately predict elephant population dynamics after parameterisation. Absolute measures of biomass are therefore unnecessary in these models. Rather the relative availability of food through space and time determines movement decisions and population dynamics.

All swamp edge habitats in Amboseli (PAX, SEG and YAX) share a similar herb-layer, dominated by a dense layer of Bermuda grass (*Cynodon dactylon*) and few creeping herbs at ground-level (see Table 2.1 and Lindsay, 1982). Hence, it was expected that the herb-layer of these habitats relates similarly to NDVI but this relationship could not be established due to 15-20% cover of the date palm (*Phoenix reclinata*) and fever tree (*Acacia xanthophloea*) canopy. The herb-layer of dry woodland habitats (SS, TW and XW) differs from SEG3 in terms of species composition and biomass. The lower herb-layer biomass of dry woodland habitats is reflected in the lower mean NDVI when compared with swamp edge habitats (Figure 2.3). In the following chapters we therefore apply equation 3 to predict the herb-layer biomass – and thus food available to elephants – across the Amboseli ecosystem without concern for the propagation of error introduced in ground-truthing through this calibration exercise. We acknowledge however, that further work is required to produce precise estimates of herb-layer biomass using satellite data.

Biomass estimates are of increasing interest due to growing awareness of climate warming and the role that vegetative biomass plays in carbon sequestration (Kumar and Mutanga, 2017). Whilst direct ground-based measures of biomass are most accurate, the value of RS in estimating biomass over large spatial scales, in inaccessible locations and with reduced user effort has long been acknowledged. RS now presents the primary source for biomass estimation and there are a huge array of methods available (Lu, 2006). Briefly, these consist of optical, radar and LiDAR RS. Optical RS, relies on a range of techniques depending on the spatial scale of the RS product, including photo interpretation of vegetation characteristics at fine scales and vegetation indices at coarser scales. Photo interpretation of parameters including tree height, crown diameter and density, and stand area can provide accurate estimates of biomass but require extensive user effort and expensive high resolution datasets, which prevents the application of this method over larger areas (Lu, 2006). Vegetation indices have the advantage of removing variability in images caused by canopy geometry, soil backgrounds, atmospheric conditions and solar view angles, but the common occurrence of mixed pixels and the mismatch in the scale of RS and ground-based data means that not all indices correlate with biomass (Mutanga and Skidmore, 2004). Optical sensing offers long-term global coverage, repetitiveness and relative cost-effectiveness, but can be inhibited by cloud cover in some parts of the world. Radar RS presents the benefit of penetrating cloud cover and can detect properties of surface roughness, structure, moisture and geometry. Several radar RS parameters have shown correlations with measures of tree age, height, diameter at breast height, basal area and above ground biomass (Kasischke, Melack and Dobson, 1997). LiDAR RS uses pulsed lasers to measure the distance to the Earth surface and can generate precise three-dimensional information on the structure of the Earth’s surface. Its application in estimating biomass relies on precise measures of the vertical structure of vegetation and due to large current interest in this approach, LiDAR RS is increasingly applied in studies of vegetation dynamics (Lim *et al.*, 2003). The application of the various RS methods in estimating above-ground biomass is the focus of a special issue of Remote Sensing (*Remote Sens*., Volume 9, Issue 9, September 2017). In general, the chosen method for estimating biomass will depend on the user’s needs, the spatial extent of the study area, the characteristics of the RS data and economic support.

The process of calibrating satellite-derived NDVI to provide measures of food availability presented here may be applied to other herbivores and study systems where the aspects of vegetation that constitute food for a species are known and biomass of this vegetation can be quantified on-the-ground. As illustrated here, efforts should be made to minimise canopy interference and scale mismatch. Canopy interference is a common problem suffered by RS data especially under high biomass conditions where there are multiple layers of vegetation. Scale mismatch too regularly arises when calibrating RS data, caused by differing spatial extents of the RS and ground-based measures (Kerr and Ostrovsky, 2003). In highly heterogeneous habitats variation within a RS pixel (250x250m for MODIS) may not be identified by a single transect or smaller quadrat when measuring vegetation on-the-ground. The effects of both scale mismatch and canopy interference can be minimised by carefully designing ground-based data collection methods to suit the desired RS product (Hoffer, 1971): ground-based measures must be collected over an area comparable to the spatial resolution of the RS data and should ensure higher canopy layers do not cover the desired biomass metric. However, when using historically collected data as we did here, ground-based data are unlikely to have been designed for calibration of RS data and so a degree of 'retrofitting' is required: careful examination of both RS and ground-based data should reveal non-conformities which may then be removed from subsequent analyses.

Additional technological advances may improve the calibration of RS data. Satellites with increasingly high spatial resolution, such as the European Space Agency's Sentinel missions (Drusch *et al.*, 2012), may reduce the required spatial coverage of ground-based measures and minimise the influence of scale mismatch in heterogeneous habitats. Alternatively, unmanned aerial vehicles, or drones, are increasingly equipped with sensors able to collect the same information as those deployed on satellites. Drones also provide high resolution images and have the advantage of being programmable by the operator to observe only an area of interest.

The issue of too few ground-based biomass measures could obviously be addressed by increasing sampling efforts, but more importantly serves as a reminder as to the strengths of RS in collecting regular consistent measures of the Earth's surface with minimal user effort (Pettorelli *et al.*, 2014). Obtaining appropriate RS data is unlikely to be the limiting factor in these exercises given the increasing availability of freely available resources (Aroma and Raimond, 2015). Using the methods presented here, spatially and temporally consistent measures of food availability may be used to better understand aspects of animal energetics, movement behaviour and population dynamics over long time periods and large spatial extents.

Calibration of RS data more generally, is an important step in identifying and applying a suitable proxy for its intended purpose or question (Hoffer, 1971). Often RS measures are used as a proxy without fully understanding the mechanisms underlying the relationship (or lack of) between the RS measure and the response variable, limiting the value of these interpretations. Although calibration is not always possible due to inaccessibility of study areas (because of political instability, terrain or legislative issues for example), limited time and funding, or lack of appropriate methods for measure the desired variable, where possible ground-based data should correspond closely to the objectives of the research and problems involved. Given a good understanding of how RS measures relate to biophysical characteristics of the Earth's surface, RS can be widely applied to answer many questions and challenges faced in ecology and biodiversity conservation.

The calibration of satellite NDVI presented in this chapter allows the use of satellite NDVI to estimate food availability in the subsequent chapters of the thesis.

Chapter 3. Modelling large herbivore movement decisions: beyond food availability as a predictor of ranging patterns[1]

3.0 Abstract

The ability of animals to adapt to their changing environment will depend in part on shifts in their ranging patterns, but when and why individuals choose to move requires detailed understanding of their decision-making processes. We develop a simple decision-making model accounting for resource availability in habitually used ranges. We suggest that disparities between model predictions and animal tracking data indicate additional factors influencing movement decisions, which may be identified given detailed system-specific knowledge. The model was evaluated using movement data from satellite-tracked elephants (*Loxodonta africana*) inhabiting the Amboseli ecosystem in Kenya, moving from savannah areas with low quality but constant resource availability, to areas with temporally-constrained higher nutrient availability. Overall the model predictions represented the data well: there was a good correlation between predicted and observed locations for the combined data from all elephants, but variation between individuals in how well the model fitted. For those elephants where model predictions were less successful, additional factors likely to affect movement decisions, such as reproduction, anthropogenic threats, memory and perception, are suggested. This protocol for building and testing decision-making models should contribute to success in attempts to preserve sufficient space for large herbivores in their increasingly human-dominated ecosystems.

3.1 Introduction

In the face of a changing climate and the rapid conversion of natural habitats to human-dominated landscapes, the future of many species will depend on their ability to adapt to new circumstances. Adaptation may involve behavioural changes or innovations (Sol *et al.*, 2005), but geographical shifts in a species range (Laidre *et al.*, 2018) or in how a species moves through its existing range (Olden *et al.*, 2004; Tucker *et al.*, 2018) may allow it to cope with novel environmental conditions or constraints. Range shifts require animals to make the decision to relocate from one site to another and have often been predicted through the use of simple decision models (Bastille-Rousseau *et al.*, 2018). Whilst these shifts are largely guided by suitable climatic conditions and the provision of sufficient food and water, movement decisions are also likely mediated by other factors. The predicted shifts can be incorporated into conservation and management strategies for species of concern, but are unlikely to be accurate unless the full range of factors influencing movement can be taken into account.

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[1] This chapter has been published as follows: Boult, V.L., Sibly, R.M., Quaife, T., Fishlock, V., Moss, C. & Lee, P.C., 2018. Modelling large herbivore movement decisions: Beyond food availability as a predictor of ranging patterns. *African Journal of Ecology*, 57(1), 10–19.

Here we present a means of identifying factors other than simple resource-requirements which mediate movement decisions for large herbivores negotiating heterogeneous landscapes. Our method uses disparities between a simple model of resource-driven decision-making and animal tracking data to indicate the need to incorporate other factors that affect movement decisions. Given a detailed understanding of the study system, these factors can be identified using local knowledge (see also Bastille-Rousseau et al., 2018). Models were developed and evaluated using elephants (*Loxodonta africana*) inhabiting the Amboseli ecosystem in Kenya as a case study. Ensuring a future for elephants in this increasingly human-dominated landscape hinges on understanding how and why elephants use the landscape through space and over time.

Long-term monitoring of elephant populations and remote tracking studies have greatly improved our understanding of general patterns in elephant ranging behaviour (e.g. Wall et al. 2013). Elephants show large-scale, purposeful space use (Polansky, Kilian and Wittemyer, 2015) and so require large areas over which to roam to access heterogeneously distributed resources (e.g. Leuthold 1977; Lindeque & Lindeque 1991; Thouless 1996; Blake et al. 2003; Birkett et al. 2012). It is clear that elephants do not use the space available to them at random. Instead, elephants generally shift ranges seasonally (Western and Lindsay, 1984; Leggett, 2006; Loarie, Van Aarde and Pimm, 2009), searching for water (Chamaillé-Jammes and Valeix, 2007; de Beer and van Aarde, 2008; Redfern *et al.*, 2015) and the highest quality vegetation (Loarie, Van Aarde and Pimm, 2009; Bohrer *et al.*, 2014). This results in dynamic habitat and food type preferences (Cerling *et al.*, 2006; Shannon, Page, Slotow, *et al.*, 2006; Loarie, Van Aarde and Pimm, 2009).

We developed a simple decision-making model which tracked the food available within habitually-used ranges to satellite-tracked individuals from five family groups (representing the movements of over 220 elephants in the Amboseli population), whilst taking into account the daily need of individuals for water. The individuals had complete perceptual knowledge of resource availability in their home range and the model assumed that, when water availability allowed, individuals moved to maximise their nutrient intake rate and subsequent fitness (Okello *et al.*, 2015), as in optimal foraging theory (Stephens and Krebs, 1986; Roever, van Aarde and Chase, 2013; Bastille-Rousseau *et al.*, 2017; Vasconcelos, Fortes and Kacelnik, 2017). We assumed that individuals make daily choices whether to relocate to an alternative location or to stay in the current location (Petit and Bon, 2010). Where model predictions did not match those of tracking data, we used detailed knowledge of the elephants and ecosystem to identify additional factors, such as physiological or social needs, which depend *inter alia* on an individual's sex, age, reproductive status and body condition (Lindsay, 2011).

3.2 Materials and methods

Case study site information

The study was carried out in the Amboseli ecosystem (bounding coordinates: -2.02N, -3.28S, 38.03E, 36.67W), an area of approximately 8000km^2 straddling the border of southern Kenya and northern Tanzania, comprising the central Amboseli National Park (392km^2; ANP hereafter) and surrounding landscape (Croze & Lindsay, 2011; see Appendix A: Figure A.1). The habitat consists of semi-arid savannah that responds seasonally to highly variable rainfall. Rain predominantly occurs in two seasons; a short wet season (November and December) and the long rainy season (March through May; Altmann, Alberts, Altmann, & Roy, 2002). During dry seasons a series of swamps in the central basin provide the primary source of water, fed by groundwater flow from the slopes of Kilimanjaro in the south (Croze and Lindsay, 2011), though other perennial sources occur in the Selenkay Conservancy and in Kitenden, in the form of a borehole and two natural springs. Wildlife concentrates in the central basin during dry seasons and disperses following rain (Western, 1975). The Amboseli ecosystem is home to around 1700 individually known and monitored elephants (Lee *et al.*, 2013). Unlike most other African populations, the Amboseli elephants have been relatively undisturbed by human activities. However recent human population growth in Kenya and a lifestyle shift from nomadic pastoralism to sedentary farming (Western, Groom and Worden, 2009) presents growing challenges for the persistence of Amboseli's wildlife, especially for elephants.

Animal tracking data

GPS-GSM collars (@ Savannah Tracking) were fitted in July 2011 to five adult female elephants (Ida, Lobelia, Maureen, Vicky and Willow) from different family groups, representing locations of over 220 individuals (because families forage as units). Habitat heterogeneity around the central protected area affects ranging strategies and reproductive success, so not all dispersal directions are equal for Amboseli elephants. Target females were selected based on more than 40 years of observations to represent the known diversity in dispersal areas and foraging opportunities in Amboseli (which are largely inherited through generations unless disrupted by human disturbance; Croze & Moss, 2011; Moss, 1988) and to minimise risks to target elephants, family members and staff. Individual females were selected according to ethical and safety criteria, minimising the disturbance of each intervention. Target females were 1) not matriarchs, 2) without a calf aged <2 years and 3) closely bonded to matriarchs so shared the matriarch's movement patterns and therefore represented the maximum part of the family. Matriarchs were not collared due to the drastic potential impact of matriarch loss on families given the small but inherent risks of immobilisation, and the greater ease of managing non-target family members during immobilisations when they had a safe rallying point around their matriarch. Collars were fitted under the authority of the Kenya Wildlife Service, the Kenyan body regulating interactions with elephants, and with research clearance to Amboseli Trust for Elephants from the National Commission for Science, Technology and Innovation (NACOSTI/P/15/9605/5732).

GPS fixes were recorded at hourly intervals for roughly 12 months, giving in sum 43,728 location fixes. Collar data were summarised into daily presence or absence from ANP. Given the reliance of elephant families on water, an elephant was considered present in ANP on any day in which distance from the swamp was zero at any time during that day. Conversely if the distance from the swamp was never zero, the elephant was considered that day to have dispersed from ANP. The dispersal area of each female was identified as the 95% kernel density estimates of her locations outside the park boundary.

Resource-driven movement model

We developed a profitability index to indicate the resource availability of each dispersal area and of ANP, while taking into account the daily need of female elephants for water (Figure 3.1). Water was considered essential and elephants were only able to move to areas where water was available. The swamp edge habitat alone was used to indicate profitability for ANP, as elephants consistently return to the park to feed on the reliable and abundant swamp edge vegetation, as well as drink. Swamp edge was therefore used as representative of the resources drawing elephants back to ANP from their dispersal areas.

$$\underset{\textit{of specified area}}{\text{Profitability}} = \underset{\textit{Median NDVI}}{\text{Quantity of vegetation}} \times \underset{\textit{Protein content (\%)}}{\text{Quality of vegetation}} \times \underset{\textit{Binary}}{\text{Water availability}}$$

Figure 3.1. Profitability of each dispersal area and ANP, calculated daily. See 3.2 for definitions of vegetation quantity and quality. Water availability is a binary variable taking values of 1 or 0 depending on whether or not water is available in the specified area.

Vegetation quantity

Data on vegetation quantity were acquired using the Normalised Difference Vegetation Index (NDVI), which exploits the marked difference in reflectance in red and near infra-red wavelengths characteristic of healthy green vegetation (Huete *et al.*, 2002). We used 16-day composite values of NDVI retrieved from Terra-MODIS (Moderate Resolution Imaging Spectroradiometer) to infer time-specific values of vegetation quantity. Specifically we used the MOD13Q1 product accessed via the Oak Ridge National Laboratory Web Service (Vannan *et al.*, 2011). Median NDVI values were calculated for each individual’s dispersal area (i.e. 95% kernel density estimates outside ANP) and swamp edge for each 16-day interval. Data were filtered using the MOD13Q1 QA flags such that only ‘good’ quality NDVI observations were used in our calculations. For extended remote sensing methodology, see Appendix A.2.

Vegetation quality

Crude protein is an important limiting factor for herbivores inhabiting savannah ecosystems (Sinclair, 1975) and we therefore assessed vegetation quality by its protein content (%). The diet of Amboseli elephants is dominated by grasses, so we used grass protein content as our measure of vegetation quality. Protein content varies seasonally, peaking during the green-up of vegetation following the onset of rains (Georgiadis and McNaughton, 1990; Lindsay, 1994). Here we estimate protein content depending on whether or not it rained in the previous month. Lindsay (1994) measured the protein content of Amboseli swamp edge vegetation and rainfall throughout the course of a year. From these data, we assigned protein content of swamp edge vegetation as 11.8% or 8.4% depending on whether or not it rained in the preceding month. Georgiadis & McNaughton (1990) collected similar measurements in the broader Amboseli ecosystem outside the Amboseli swamps and found protein contents of 23.0% during the green-up following rains and 10.0% in the subsequent drying phases. We used the figure of 23.0% if the change in NDVI was positive, indicating green-up in the month after rains, at all other times 10.0%.

Water availability

Permanent water sources were available in ANP and in the dispersal areas of Vicky (Selenkay), and Ida and Lobelia (Kitenden). We deemed water available year-round in these areas. We used daily measures of rainfall from the rainfall gauge in the Amboseli Elephant Research Camp (-2.679S, 37.267E) to indicate rainfall across the entire Amboseli ecosystem since NDVI fluctuations across the ecosystem are generally synchronous. Rainfall contributed to surface water availability in all areas and so water was considered available across the entire basin for seven days following rain.

Movement-decision model fit

We assumed that if individual movement behaviour was governed by resource availability, individuals should move to maximise profitability throughout the year. Therefore when ANP profitability was greater than that of the dispersal area, the individual should be present in ANP on that day, and vice versa. If profitability for the two locations was very close (difference < 0.3) no prediction was made as to which provided the optimal foraging location.

The daily absence or presence of the elephants as predicted by profitability was compared to actual absence or presence indicated by the collar data. The correlation between predicted and observed presences and absences was calculated as a ϕ statistic (Conover, 1971). ϕ is the equivalent of Pearson’s correlation that is applicable to binary data. ϕ values were tested for significance using chi-square with 1 degree of freedom.

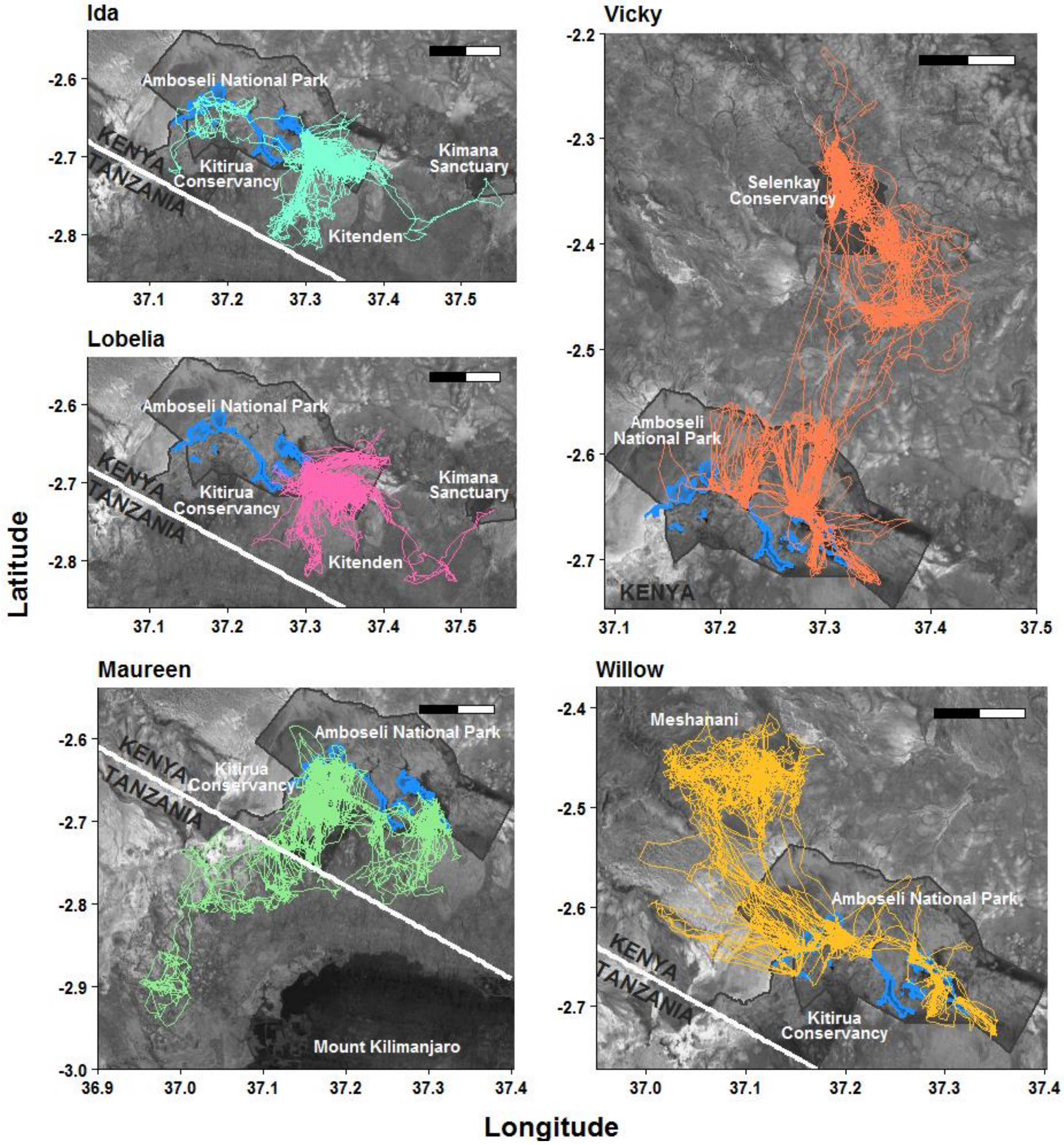

Figure 3.2. Tracks of five collared elephants displaying use of Amboseli National Park and dispersal areas (coloured lines: different colour for each female). Protected areas are indicated by grey boundaries, the international border between Kenya and Tanzania by the white line, and the central Amboseli swamps in blue. Scale bar represents 10km (divisions of 5km). Two females used the same dispersal area (Kitenden, southeast); other females ranged to the north, northwest and southwest when leaving ANP.

3.3 Results

Ranging behaviour

The ranging behaviour of the five collared elephants over a 12-month period is illustrated in Figure 3.2. Ida and Lobelia spent most of their time (~85%) in ANP, primarily in the southeast around the southern tip of the eastern swamp (Longinye; see Appendix A: Figure A.1 for detailed park map). From there both elephants regularly moved southwest into the Kitenden region and occasionally east to the Kimana Sanctuary. Maureen, Vicky and Willow spent about half their time in the park. Maureen used the eastern swamp and the area around and including the western swamp (Longolong). From there she dispersed south through the Kitirua Conservancy and then southwest across the foothills of Kilimanjaro into Tanzania. Vicky and Willow also used the eastern swamp, but additionally used the northern tip of the central swamp (Enkongo Narok). Within the park Vicky frequented the north and dispersed north to spend much time in the Selenkay Conservancy. Willow by contrast used the west of the park from which she dispersed northwest to the Meshanani region.

Profitability

Profitabilities calculated for the swamp edge and dispersal areas (Kitenden, Kitirua-Tanzania, Selenkay and Meshanani) captured spatial and temporal variation (Figure 3.3). Temporally, profitability generally increased following the onset of the rains and declined as the rains subsided. Spatially, areas differed in the precise timing and extent of increases and decreases in profitability. ANP profitability varied less than the profitability of the dispersal areas because in the dry seasons the swamps retained abundant green vegetation but did not experience the dramatic increase in protein content seen in dispersal area vegetation following rain. As a result, there was temporal variation in whether profitability was higher in ANP or in the dispersal area, predicting switches in the optimal foraging location between ANP and the dispersal areas. Generally, profitability indices predicted that elephants should be present in the national park during August, September and October 2011, January and February 2012 and from May 2012 onwards. At other times they were predicted to move out to their family dispersal areas.

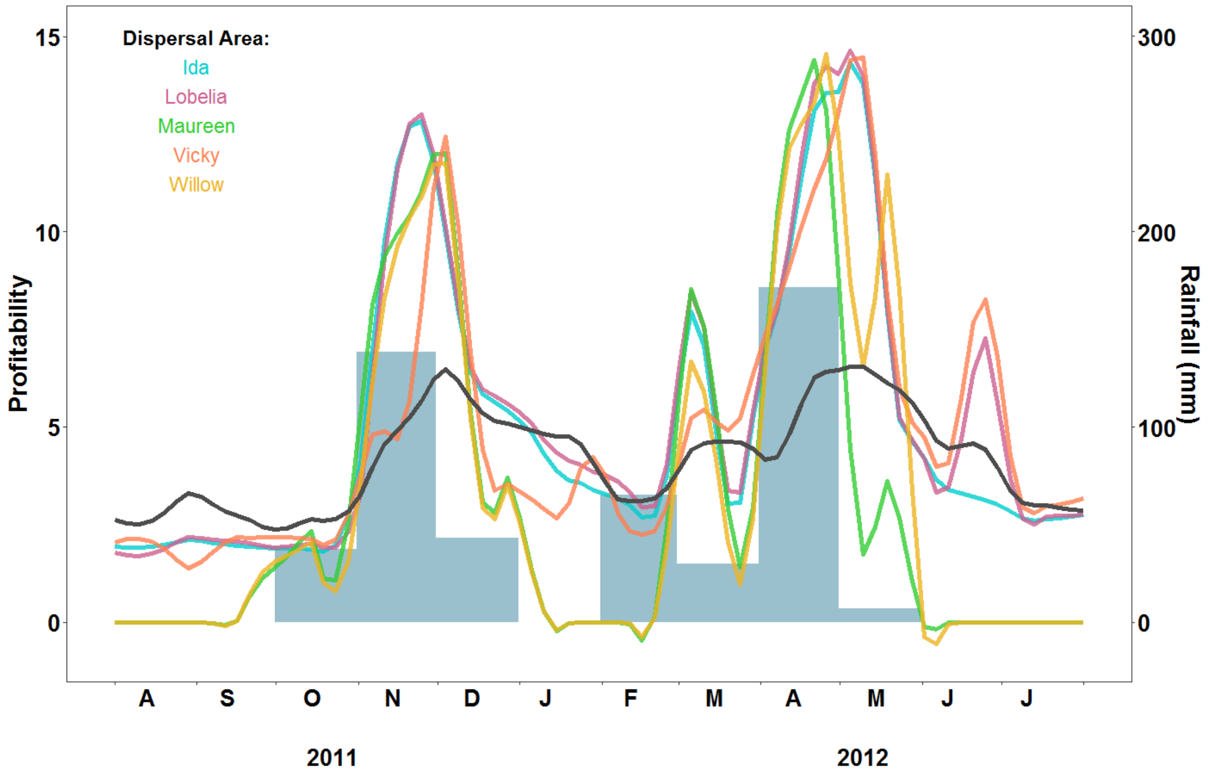

Figure 3.3. Response of profitability (lines: black = swamp edge, coloured = dispersal areas), the product of the quantity and quality of vegetation, and water availability, to monthly rainfall (bar: blue).

Movement-decision model fit

Overall the model predictions replicated the location data well: there was good correlation between predicted and observed presences and absences for the combined data from all five elephants (ϕ = 0. 37, *p*<0.001), but there was variation between elephants in how well the model fitted (Breslow-Day test, χ^2_4 = 67.4, *p*<0.001, Figure 3.4). The locations of Vicky were well predicted by the model (ϕ = 0.60, *p*< 0.001, Figure 3.4) though the model was unable to predict Vicky's brief excursions between August and October 2011, nor her absence from the park in May to June 2012. The model was moderately successful in predicting the locations of Ida, Lobelia, Maureen and Willow (ϕ = 0.42, 0.27, 0.39 and 0.46 respectively, *p*< 0.001 for each), but failed to predict the regular presence of Ida and Lobelia in ANP throughout both wet seasons. Maureen was regularly absent between August and October 2011 and in June and July 2012 when the model assumed presence throughout. The timings of Maureen's major excursions from the park were also slightly ahead of those predicted by the model. Willow's movements were well predicted with the exception of brief excursions during August and September 2011 and of her continued absence from the park during June and July 2012.

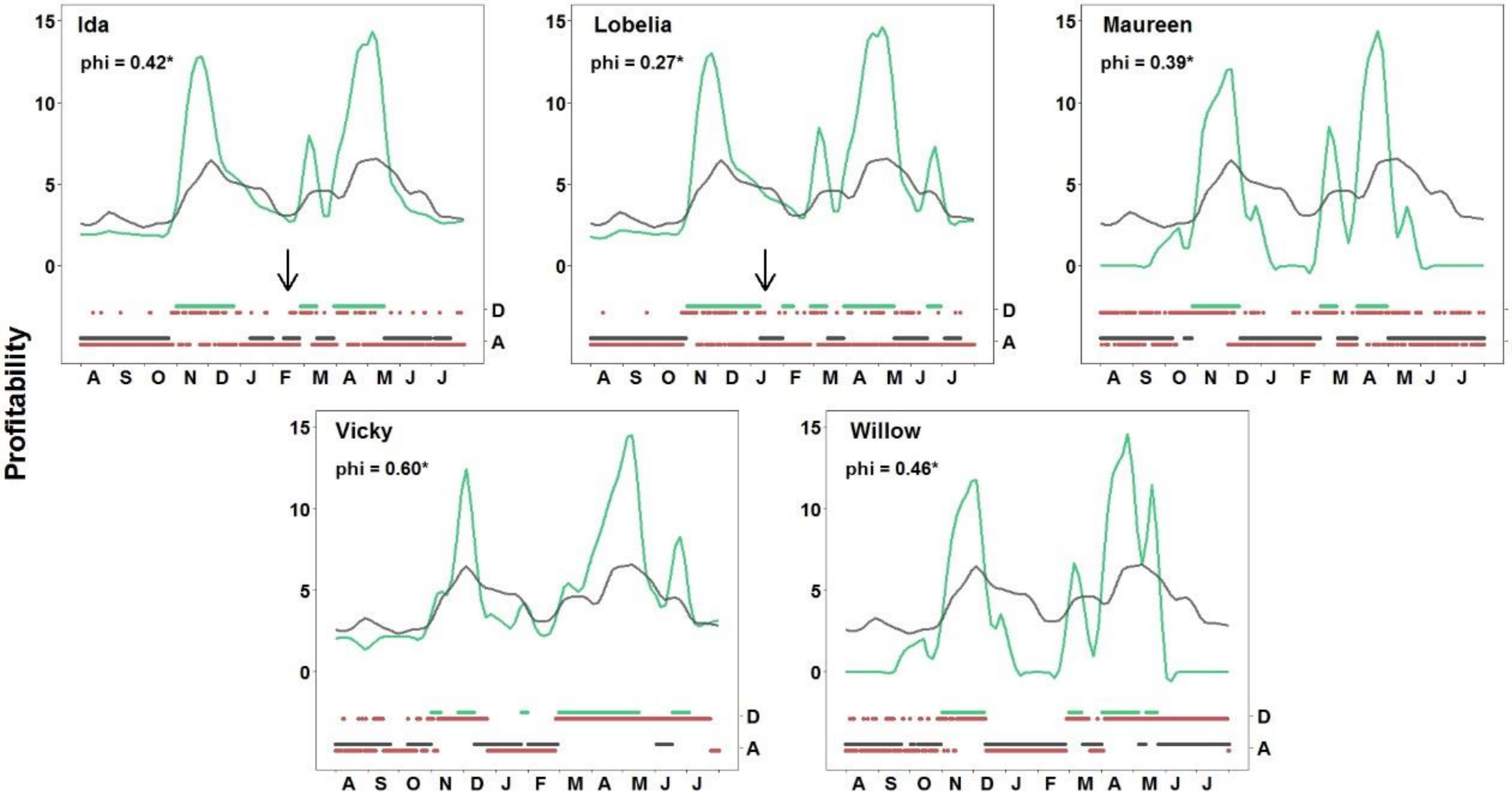

Figure 3.4. Profitabilities of swamp edge (black curve) and dispersal area (green curve) for each collared individual. Horizontal lines at bottom of each panel indicate model predictions (black, A = Amboseli National Park; green, D = dispersal area) and collar data (red). No predictions were made if profitabilities were within 0.3 of each other. Arrows indicate parturition events for Ida and Lobelia. Phi coefficients (ϕ) indicate correlation between model predictions and collar data; * indicates significance of this relationship (Chi-squared: $p < 0.001$).

3.4 Discussion

By modelling the profitability of the traditional foraging areas of each of the five elephant families while taking account of their daily need for water, we predicted the timings of their shifts in optimal locations. The shift timings were similar despite the different dispersal areas used by the collared elephants (Figure 3.3). In general, ANP offered the highest rate of nutrient intake during the dry seasons until the onset of rains, at which point the dispersal areas provided better foraging locations provided that water was available. While the model fitted the data well overall, there was variation among elephants in the ability of the model to correctly predict park absence and presence. Predictions and observations were correlated for all five individuals, but while the correlation was good for Vicky and Willow, it is likely that other factors also influenced the movement decisions of Ida, Lobelia and Maureen. Given an in-depth knowledge of the study system (AERP long term data), we now attempt to identify these factors and suggest how they can be incorporated into future movement models for elephants.

The sustained residency of Ida and Lobelia in ANP is likely due to the fact that both females gave birth during the 2012 short wet season (January-February). Elephants usually seek safe areas as parturition approaches and for some time after as new-born calves are vulnerable to disturbance and predation (Ruggiero, 1991) and limited in their travel capacity. For family units experiencing recent parturition events, the motivation to remain in ANP increases because it is perceived as a relatively safe area. During the period of sampling, Ida and Lobelia's dispersal areas of Kitenden and Kimana were relatively high risk because a number of elephants were killed or injured as a result of human interactions (Big Life Foundation/AERP long term data). In elephants, risks in the form of anthropogenic threats are known to deter long-term elephant habitat use (Roever, van Aarde and Chase, 2013) and alter the daily locations of resting sites (Wittemyer *et al.*, 2017). Risks affect animal decision-making more widely when animals sacrifice optimum nutrient intake to minimise the risks of predation (Barnier *et al.*, 2014; Bastille-Rousseau *et al.*, 2017). Including the risks associated with human-elephant interactions should improve the model fit. Relative risk could be measured in terms of the number of negative human-elephant interactions (injuries or mortalities) over a specified period, land use type (pastoralist vs. agricultural vs. wildlife zones) or human density in an area (which is also a function of land use type). Over the longer-term, periods of drought could also be used as an indirect predictor of human-associated risk, because competition for water sources and high-quality food patches increases contact between humans and elephants (Chiyo *et al.*, 2005) and the economic threats of livestock loss erode tolerance for wildlife (Western, Nightingale, Sipitiek, Mose, & Kamiti, pers. comm.).

Behavioural differences between conspecifics can be viewed as evidence of personality; consistent differences in the behavioural responses of individuals across various spatial and temporal contexts (Beekman and Jordan, 2017). Here therefore, we may alternatively consider the residency of Ida and

Lobelia could be to be due to their ‘wary’ personalities, whilst Vicky is more ‘bold’ (Jolles *et al.*, 2017). Personality has been reliably demonstrated for elephants (Lee and Moss, 2012; Seltmann *et al.*, 2018) but has yet to be systematically sampled across the subject families and is only speculative at this point. However, AERP’s long-term observations suggest that personality is shaped by family members (particularly the matriarch) and by experiences, especially those early in life. It can be proposed that, as seen in many other bird, fish and mammal species (Weiss, 2018), personality may both shape and be shaped by exposure to risk.

Maureen displayed much lower use of ANP than predicted by the model, suggesting she was less reliant on the swamps for dry season water as she had access to an alternative water source in the Kitirua Conservancy. Elephants share this water point with livestock and people, often at high concentrations, but this area also showed high tolerance for wildlife during the study period. The model was also unable to predict the timing of Maureen’s location shift, consistently predicting a later dispersal than seen in the collar data. The dispersal area used by Maureen in Tanzania is characterised by mature Acacia woodlands rather than the open bushed savannah associated with the majority of the ecosystem. Acacia flower ahead of the onset of rains and Maureen’s early excursions may coincide with this phenological event, rather than the NDVI observed green-up. Flowering in bushlands might be associated with higher sugar and other nutrient transport in Acacia stems, which are desirable elephant foods (Lindsay, 1994). Incorporating nutrient fluxes that are independent of vegetation green-up will require both phenological monitoring of the timing of flowering and quantifying the associated nutrient benefits. The remotely sensed measures of greenness used here are insensitive to the spectral changes associated with flowering, thus suitable alternative remote sensing techniques are needed for a more comprehensive accounting for foraging movements.

While we can suggest other factors that operate in combination with nutrient intake to affect movement decisions, the behavioural mechanisms underlying movement patterns remain poorly understood (Bolger *et al.*, 2008); indeed whether movement decisions are guided by animals’ perceptions of current environmental conditions or predictions based on memory is uncertain. The capacity of elephants to remember the spatial locations of out-of-sight individuals (Bates *et al.*, 2008) and the purposeful movement to water resources beyond the senses of sight or smell (Polansky, Kilian and Wittemyer, 2015) shows that elephants have a keen spatial memory. Despite this, data show that decision points (Polansky, Kilian and Wittemyer, 2015) coincide with the onset of the rains, suggesting that the onset of rains may be used as a key environmental cue to instigate range shifts (Prins, 1996; Holdo, Holt and Fryxell, 2009). Also relevant to this question are several brief excursions by Vicky and Willow to their respective dispersal areas prior to their longer-term range shifts. This ‘scouting’ behaviour (Bracis and Mueller, 2017) suggests sampling of the conditions at their destination before committing to the final range shift. Both of these factors suggest perception-guided movement. However, rainfall across the Amboseli ecosystem is perhaps more temporally and spatially variable than accounted for here, meaning elephants cannot rely on the same rules each year. Memory alone is likely to be less effective in such a patchy environment, and so individuals will use both immediate perception and memory when making movement decisions. Although memory is important in defining the destination of movements based on previous experiences of improved nutrient intake rate, perception is crucial in remaining flexible to local environmental changes in climatic conditions and risk.

We have introduced a simple decision-making model of the resource-driven factors affecting key decisions of where individuals go and when. Where the model predictions replicated individual locations well, a key benefit of movement over an ecosystem is indicated, which is to maximise nutrient intake rates. That the model does not perfectly fit the locations of elephants suggests that other factors need to be included in combination with nutrient intake rates. High residency of elephants that disperse to the eastern part of the ecosystem suggests that individuals and families make movement decisions based on trade-offs between the resource-related benefits of dispersal and the associated risks (see also Chiyo et al., 2014). For Ida and Lobelia, it is hard to determine whether perceived risks resulted from human-elephant interactions, the dangers involved with moving new-born calves over long distances, or the limited travel speed of those vulnerable calves. More data characterising risks and associated movements are important (Nielsen, Stenhouse and Boyce, 2006; Roever, van Aarde and Chase, 2013) and necessary before these factors can be reliably included in an enhanced model of movement decision-making. Male elephants were not considered here due to differences in resource requirements. Males are less reliant on water than females and forage less selectively, prioritising quantity over quality (Shannon, Page, Duffy, *et al.*, 2006b). When in musth, male elephant movement is largely focused on the pursuit of oestrous females, with little consideration for food (Poole, 1987). Previous work in Amboseli has demonstrated the importance of both food (NDVI) and social needs (Chiyo *et al.*, 2014; Fishlock, Caldwell and Lee, 2016) on male ranging, so it is expected that this model could be extended to non-musth males but would need further modification to take into account the energy demands of musth, which is a topic for future study. Further development of the model will ultimately provide a basis for robust prediction of elephant movements under a variety of environmental and physiological conditions.

Here, it is argued that simple resource-driven movement models based on easily accessible resource availability data in combination with animal tracking studies will be useful in identifying additional features influencing movements in well-studied systems, where additional supporting data types can add to understanding movement decisions. This will allow conservationists and wildlife managers to better understand how large herbivore movements might respond to management scenarios (e.g. fences, new roads) and future environmental changes (e.g. shifting rainfall patterns), and in this way can help challenges for human-wildlife coexistence.

Chapter 4. Individual-based modelling of elephant population dynamics using remote sensing to estimate food availability[2]

4.0 Abstract

Strategies for the conservation and management of many wild species requires an improved understanding of how population dynamics respond to changes in environmental conditions, including key drivers such as food availability. The development of mechanistic predictive models, in which the underlying processes of a system are modelled, enables a robust understanding of these demographic responses to dynamic environmental conditions. We present an individual-based energy budget model for a mega-herbivore, the African elephant (*Loxodonta africana*), which relates remotely measured changes in food availability to vital demographic rates of birth and mortality. Elephants require large spaces over which to roam in search of seasonal food and thus are vulnerable to environmental changes which limit space use or alter food availability. The model is constructed using principles of physiological ecology; uncertain parameter values are calibrated using approximate Bayesian computation. The resulting model replicates observed population dynamics data well. The model has critical value in being able to project elephant population size under future environmental conditions and is applicable to other mammalian herbivores with appropriate parameterisation.

4.1 Introduction

Elephants are simultaneously a species of conservation concern and problem for coexisting humans (Hoare, 2000; Evans and Adams, 2018). The recent spike in elephant poaching fuelled by the ivory trade continues to threaten the persistence of elephant populations (Blanc, 2008; Chase *et al.*, 2016), whilst the rapid growth of the human population and associated conversion of elephant habitat to human dominated landscapes increases interactions between humans and elephants, where elephant behaviours (e.g. crop foraging and infrastructure damage) may compromise coexistence (Wittemyer, 2011; Browne-Nunez, Jacobson and Vaske, 2013). Although poaching and human-elephant interactions (HEI) can alter elephant demographics and cohort survival (Jones *et al.*, 2018), it is widely accepted the population dynamics are governed by the distribution and abundance of food and water (Rasmussen, Wittemyer and Douglas-Hamilton, 2006; Wittemyer, Rasmussen and Douglas-Hamilton, 2007); when resources are limited, animal draw on their energy reserves, female reproductive capacity is reduced, animals starve and eventually die (Sinclair, 1975). Changes in habitats and vegetation – and thus food available to elephants – owing to climate change and land use strategies, will have large scale implications for the future of elephant populations, which may act to counter or to exacerbate

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[2] This article has been published as follows: Boult, V.L., Quaife, T., Fishlock, V., Moss, C.J., Lee, P.C. & Sibly, R.M, 2018. Individual-based modelling of elephant population dynamics using remote sensing to estimate food availability. *Ecological Modelling*, 387, 187-195.

the effects of poaching and HEI. Ensuring a future for elephants will therefore rely on understanding how elephant population dynamics respond to food availability.

To incorporate this heterogeneity into a model requires an individual-based approach (Grimm and Railsback, 2005), in which responses to food availability vary between individuals depending on their age, sex and reproductive state. Such models can combine known and projected patterns of food availability with the cohort dynamics apparent in age-structured populations to improve our mechanistic understanding of the processes underlying population dynamics as well as predicting responses to future environmental change (Evans *et al.*, 2013; Stillman *et al.*, 2015; Wood, Stillman and Hilton, 2018). Individual-based models (IBMs) have been widely used to model population dynamics in spatiotemporally heterogeneous environments; individual responses to a spatially explicit environment and interactions with other individuals are modelled in detail, allowing population dynamics to emerge from the sum of individual characteristics (DeAngelis and Mooij, 2005; Grimm and Railsback, 2005; Railsback and Grimm, 2012).

The inclusion of energy budgets in IBMs aiming to capture population dynamics is essential if populations are to respond accurately to food availability; this inclusion allows reproductive opportunities and deaths from starvation to be properly related to the energy available in the environment (Sibly *et al.*, 2013). Energy budgets rely on equations describing the process of energy intake and allocation to energy-expending processes. These equations are broadly applicable to a wide variety of taxa, but parameters controlling these relationships vary interspecifically. Occasionally, these parameters have been empirically determined for a species, but more often than not this information is lacking. Empirical studies to estimate values are not always feasible due to funding and time constraints, lack of appropriate methods and equipment, or ethical considerations. Elephants, like many mega-herbivores, are a species for which empirical determination of some physiological parameters is intrinsically difficult: elephant physiology does not lend itself to laboratory studies nor can physiological parameters be readily determined in the field. Estimation of parameter values is however possible using inverse modelling if, as here, data to hand include records of key drivers (food availability) and resulting population dynamics.

Here we construct a model of individual energy budgets based on current understanding of physiological ecology, with parameters specifying energy allocation between the vital life processes of maintenance, growth and reproduction. Each individual in the IBM has its own energy budget and lives in a population in an environment for which food availability is known from remotely-sensed measurements. Emergent population dynamics are compared to observed rates of reproduction and mortality, and parameter values are obtained through calibration using approximate Bayesian computation (ABC; Van Der Vaart et al., 2015) – an example of inverse modelling. Our aim is to develop a mechanistic model with good predictive qualities that can serve to forecast future population dynamics in response to climate change and alternative management scenarios.

4.2 Materials and methods

Study system

The Amboseli ecosystem (bounding coordinates: -2.02N, -3.28S, 38.03E, 36.67W) covers an area of approximately 8000km^2, straddling the southern border of Kenya and the northern border of Tanzania. It comprises the central Amboseli National Park (ANP; 392km^2) and surrounding landscape (Croze and Lindsay, 2011).The habitat consists of semi-arid savannah and bush, with permanent swamp vegetation present within ANP (Figure 4.1). Fluctuations in vegetation availability and quality are driven by two wet seasons: the short-rains (November-December) and the long-rains (March through May; Croze & Lindsay, 2011). The basin is home to ~1700 individually-known and monitored elephants (Lee *et al.*, 2013). The population has remained largely undisturbed by poaching, although human population growth and a shift from nomadic pastoralism to sedentary farming poses a significant threat to the future of Amboseli elephants (Western, Groom and Worden, 2009), as elephant habitats become increasingly human-dominated and human responses to elephants become shaped by local political and cultural dynamics (Okello, 2005).

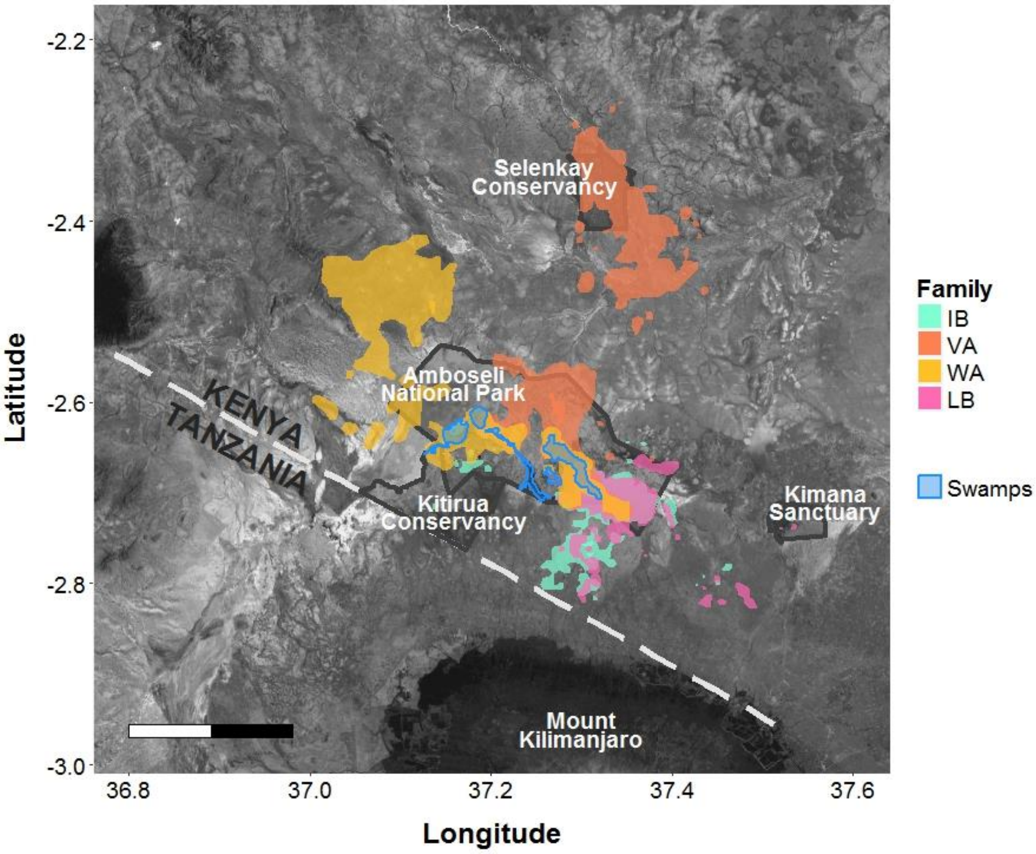


Figure 4.1. The home ranges (coloured polygons) of elephant family groups (IB, LB, VA and WA) included in the model. This represents the spatial extent of NDVI used to calculate time-specific food availability. Protected areas are indicated by dark grey boundaries, the international border between Kenya and Tanzania by the dashed white line, and the central Amboseli swamps in blue. Scale bar represents 10km (divisions of 5km).

Elephant population dynamics

The Amboseli Elephant Research Project (AERP) has monitored more than 3,300 individually-known elephants from over 60 family groups in the Amboseli ecosystem since 1972. Elephants are identified by means of a photo recognition file illustrating unique identifying features; calves are identified through association with their known mothers (Moss, Croze and Lee, 2011b). Censuses are attempted on a monthly basis for all family groups noting individuals present and those missing. By tracking individuals in this manner throughout their lives, birth and death dates are recorded.

Births: New-born and young calves are aged based on body size and proportions, skin colouration, motor coordination, and behaviour of both mother and calf (Moss, 1988). Since 1978, when the last family unit was identified, age estimates are mostly within 1 month (see Appendix B.3). The age of individuals born prior to start of the study was estimated using techniques including hind foot length (Western, Moss and Georgiadis, 1983; Lee and Moss, 1986, 1995), tooth eruption and wear (Laws, 1966), tusk length (Moss, 1988, 1996) and circumference at the lip (Pilgram and Western, 1986), and shoulder height and back length (Croze, 1972; Laws, Parker and Johnstone, 1975; Lee and Moss, 1995; Moss, 1996; Shrader *et al.*, 2006; Trimble *et al.*, 2011). Age was backdated to give an estimate of birth date for all individuals and has been validated by collection of lower jaws post-mortem whenever possible (Lee *et al.*, 2012).

Deaths: Determining date of death for individual elephants has proven more difficult. In family groups, if an adult female was absent but her youngest calves present, the family was monitored closely. If her absence was prolonged for more than a week, while the rest of the family were sighted with her youngest offspring, she was assumed dead. For calves under three years old, absence whilst their mother was present suggested the calf had died. If a juvenile female or an adult female with her calves was missing, these individuals were assumed dead if not sighted for a month with their family. Once it was concluded an individual had died, the death date was recorded as the midpoint between when the individual was last seen alive and when they were first noted as missing. Rarely (<5% of records), mortalities were more directly monitored due to illness or injury, or when carcasses were found and identified. For the purposes of model analysis, we defined ‘calf’ mortality as deaths occurring in individuals less than two years of age and ‘adult and juvenile’ mortality as deaths occurring in individuals two years or older. This reflects the differing energetic thresholds controlling mortality in these groups: calf mortality occurs when mothers' stores (fat) reaches zero; adult and juvenile mortality occurs beyond this point, when all non-essential structural tissues (muscles) have also been depleted.

For the purposes of model development and calibration, we modelled the population dynamics of four family groups (IBs, LBs, VAs and WAs). These families were chosen due to regular monitoring providing good confidence in birth and death dates, and good understanding of movement patterns owing to GPS collars fitted to females in these families (Boult, Sibly, *et al.*, 2018). Individual demographic records were used to initiate the model elephant population (n = 126 on 1st March 2000; see Appendix B: Table B.5) and provided annual records of elephant population dynamics for model calibration (on 1st October 2000-2016; see *Calibration* below).

Estimating food availability

We estimated food availability using 16-day composite values of the Normalised Difference Vegetation Index (NDVI; MOD13Q1 product; Didan, 2015). NDVI is a general measure of the greenness of the top layer of the Earth's surface and generally correlates well with ground-based measures of vegetation biomass, primary productivity and leaf area index, and has been widely used in models of animal performance and movement (reviewed in Pettorelli et al., 2011, 2005). We obtained measures of NDVI from the NASA Terra-MODIS (Moderate Resolution Imaging Spectroradiometer) mission accessed via the Oak Ridge National Laboratory web service (Vannan *et al.*, 2011). Terra-MODIS was used rather than Aqua-MODIS because of the longer NDVI time-series available (Terra operational since 2000, Aqua since 2002). We chose not to combine the two MODIS sensors given that cloud cover was not a particular issue for satellite observation of Amboseli. Data were filtered using the MOD13Q1 QA flags so that only 'good' quality NDVI observations were considered in our calculations. NDVI values were calibrated using on-the-ground measures of herb-layer biomass, collected biannually in ANP since 1982 (Lindsay, 1982, 1994, 2011; see Appendix B.3). A single median NDVI value was calculated for the combined home ranges of family groups (95% kernel density estimates; Figure 4.1; Shannon et al., 2006a) for each 16-day composite and converted to biomass (kg m^{-2}) in the model. The decision to use a single median NDVI value at each time step was taken firstly, because of uncertainty as to where each family was in its range and secondly, to reduce model run time.

Model description

The model relates spatiotemporal variation in food availability to changes in vital demographic rates through individual energy budgets. Individuals forage on locally available food and the assimilated energy is allocated to the energy-expending processes of life; from this population dynamics emerge (Railsback and Grimm, 2012; Sibly *et al.*, 2013; Johnston *et al.*, 2014). In the future the model may be applied as a tool for predicting the response of elephant populations to projected variation in food availability resulting from climate change or land use management strategies.

In Appendix B, we provide a TRACE document ("TRAnsparent and Comprehensive model Evaludation"; Augusiak and Van den Brink, 2014; Grimm et al., 2014, 2010; Schmolke et al., 2010) containing evidence that our model was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose. This includes a complete model description in the standard Overview, Design concepts and Details format (ODD; Grimm et al., 2010).

State variables and scales

The modelled environment represents the combined home ranges of the four family groups as a single patch (Figure 4.1), characterised by the time-specific median NDVI, resulting biomass, and energy content of its vegetation. The elephant population in the model comprises the individuals in four family groups – adult females and their immature offspring of both sexes (males become independent of their natal group at 12 years old). These four families comprised 126 individuals at the time of model initiation (1st March 2000). Elephants are characterised by variables describing their physiology in terms of age, sex, mass, energetic processes and reproductive states. Each individual experiences life through its own energy budget, the details of which depend on its age and sex. The model runs in daily time steps from the 1st March 2000 until the 20th November 2016 – the time period for which Terra-MODIS NDVI data were available.

Model schedule

Elephants in the model execute procedures to update their energy budget once a day. The energy budget model follows that described by Sibly *et al.* (2013; Figure 4.2). Each individual begins with the intake of energy if food is available in the environment. The assimilated energy along with energy in storage tissues (fat) make up the 'energy reserves', and are available for use in energy expending processes: maintenance takes priority, after which come growth and/or reproduction depending on age, sex and energy reserves. Following maintenance, if energy reserves remain, sexually immature individuals (females <9 years old and males <19) grow. Growth in elephants is prolonged (Karkach, 2006; Shrader *et al.*, 2006; Hollister-Smith *et al.*, 2007), and individuals continue to grow beyond sexual maturity if energy is available after paying the costs of reproduction. Only females reproduce in the model as males disperse prior to sexual maturity. If energy remains following maintenance, sexually mature females proceed through the reproductive cycle. Assimilated energy is always utilised first and energy from stores is used only if required. If maintenance costs cannot be met by reserves, individuals enter starvation and metabolise non-essential structural tissues (muscles). If these tissues are depleted, an individual dies. Background mortality accounts for stochastic mortality events.

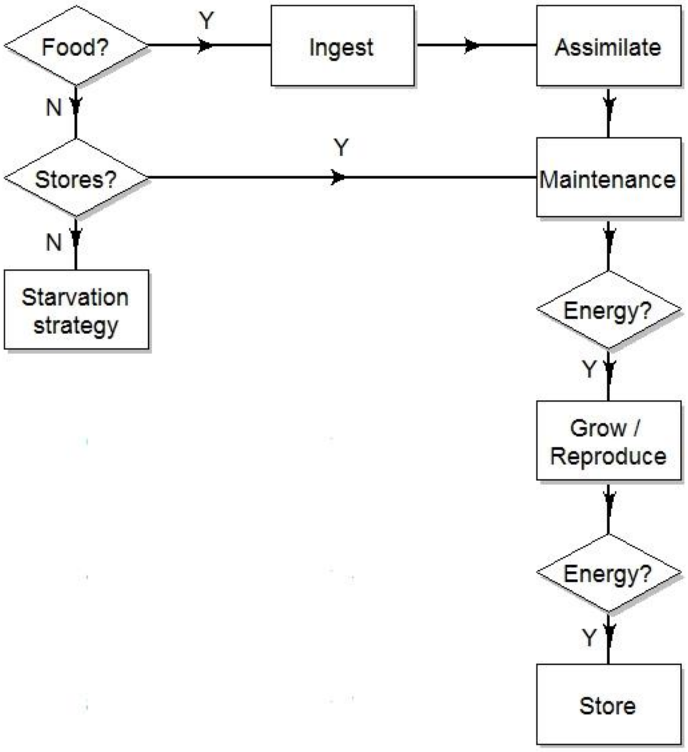


Figure 4.2. Overview of the daily updating of each individual's energy budget. If energy is available through reserves, an individual will utilise this energy in maintenance, growth and reproduction. If insufficient energy remains to cover costs of maintenance, individuals enter starvation. These energy budgets cause births and deaths from which over time the population dynamics emerge.

The energy budget of an individual therefore responds to the energy available from food in the environment. When food is abundant, as in wet seasons, energy intake exceeds energy-expenditure, and individuals may allocate energy maximally to all processes and accumulate stores. When food is limited, as in dry seasons or dry years (droughts), energy expenditure may outweigh energy intake, and individuals must utilise stores in order to maintain growth and reproduction. Thus, as food availability cycles through abundance and limitation, an individual’s energy balance fluctuates between positive and negative, and body composition (see Appendix B.4) responds accordingly (Figure 4.3).

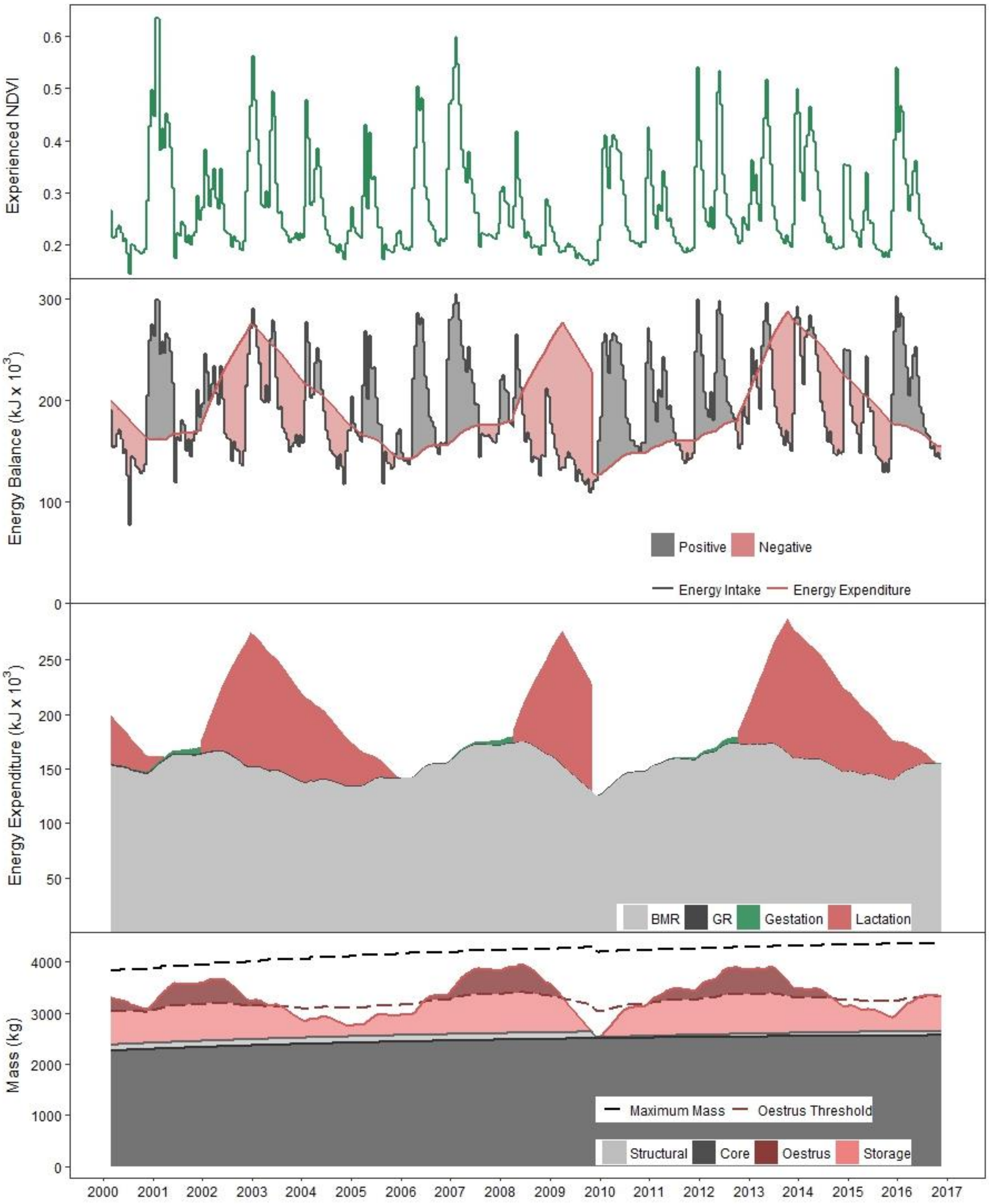


Figure 4.3. Energy balance and resulting body composition of adult female elephant, Ilka, throughout the model period 2000-2016. The top plot shows the NDVI experienced by Ilka. NDVI is used here as a proxy for food availability, peaking during the biannual wet seasons and declining as the dry seasons progress. The energy balance plot compares energy expenditure with energy assimilated (red and grey lines, respectively). The resulting energy balance indicates whether energy intake was greater or less than energy expenditure (grey and red shading, respectively), and broadly coincides with peaks and troughs in NDVI. The energy expenditure plot further breaks down expenditure into BMR, gestation, growth and lactation. Lactation is energetically costly and results in a period of net negative energy balance. Due to the fluctuating energy balance, body composition changes: storage tissues increase when the balance is positive but are depleted during times of negative balance. Structural tissues may be depleted during starvation, as seen here in 2009-2010.

Sub-models

Full details of each procedure, including equations and parameter derivation, are described in the TRACE document.

Energy intake: Ingestion rate (IR; kg day^{-1}) depends on body size (scales to the ¾ power; Brown *et al.* 2004), age, food density (biomass) and consumer (elephant) density. In terms of age, elephants less than a year old obtain all energy through the ingestion of milk; individuals are milk-dependent until two years of age but begin supplementing milk intake with vegetation after a year; between the ages of one and four, decreasing milk ingestion is supplemented with increasing vegetation intake; at four years old elephants are weaned and feed entirely on vegetation. Suckling individuals first ingest milk from their mother then, if over a year old, will ingest vegetation. The maximum vegetation IR is reduced by the rate of ingestion already achieved through suckling. Food density (kg m^{-2}) also influences vegetation ingestion, following a Holling type II functional response (Holling 1959; Lindsay 1994). This is adjusted according to a Beddington-DeAngelis functional response to account for consumer-density dependent ingestion rate (Beddington, 1975; DeAngelis, Goldstein and O'Neill, 1975). If no food is available, IR is zero. IR is converted to energy given the energy content of food (KJ kg^{-1}). Only a proportion of energy ingested in milk or vegetation is available for energy expending processes following assimilation efficiencies.

Maintenance: Basal metabolic rate (BMR; KJ day^{-1}) scales allometrically to the ¾ power with total body mass and accounts for the standard costs of maintenance essential for survival, so has first call on energy reserves (Sibly *et al.*, 2013). If insufficient reserves remain to cover BMR, an individual enters starvation and non-essential structural tissues (muscles) may be metabolised to cover these costs (Atkinson, Nelson and Ramsay, 1996). If all non-essential structural tissue is depleted, an individual dies.

Growth: After birth male and female elephants follow von Bertalanffy growth curves (Lindeque and van Jaarsveld, 1993) resulting in the sexual dimorphism in stature observed in elephants. Parameters of the von Bertalanffy growth curve fitted to shoulder height in the Amboseli elephants were taken from Lee and Moss (1995) and the equation adapted to describe growth in mass rather than length (Sibly *et al.*, 2013). Daily growth rates depend on current structural mass and energy available. The energy required to fuel maximum growth fuels both the synthesis and the energy content of new tissue (KJ day^{-1}). If insufficient energy is available to grow maximally, growth may continue more slowly. Any growth achieved is added to structural mass (kg).

Reproduction: Only female reproductive processes are represented in the model as males disperse prior to sexual maturity. If energy remains following maintenance, sexually mature females proceed through the reproductive cycle: oestrus, conception, gestation, parturition and lactation. Sexually mature females experience oestrus and conceive if not already pregnant or lactating a milk-dependent calf (<2 years), provided they have sufficient storage tissue (Bronson and Manning, 1991; Wittemyer, Rasmussen and Douglas-Hamilton, 2007). Gestation typically lasts ~660 days (Poole *et al.*, 2011) during which time a female commits energy to foetal growth. If insufficient reserves remain to cover the energetic costs of foetal growth (the synthesis and energy content of new tissue) the mother miscarries. Parturition occurs at the end of gestation. Mother and calf are linked to relate the energy budget of a calf to that of its mother. The sex of the calf is determined at random with equal probability of becoming a female or male. The new-born calf has age zero and no energetic reserves. The mother lactates until the calf is weaned at four years old, but the energy required for lactation varies throughout this period (Oftedal 1985). Before the calf is a year old, milk forms the sole energetic intake so fully covers the costs of maintenance and growth. Lactation peaks when the calf is a year old. For the first two years of life, the calf is milk-dependent and so dies if its mother does, but after peak lactation, the amount of milk supplied by the mother decreases at a constant daily rate as the calf increasingly supplements this diet with vegetation. From two to four years of age the calf suckles at a decreasing rate and is no longer dependent on milk, and can survive without its mother. The mother lactates maximally if her energy reserves allow, but otherwise provides as much milk as her reserves allow. Calves over a year of age may make up for this deficit by consuming more vegetation. If a mother dies or enters starvation, lactation stops and the fate of the calf depends on its age and food availability. If a calf dies, the mother stops lactating.

Energy reserves: If assimilated energy remains following all expenditure it is stored as fat until a maximum is reached.

Mortality: In addition to mortality events described above, background mortality is included to account for deaths arising from stochastic events such as poaching, predation, disease or injury. When storage tissues remain, background mortality occurs at a constant rate for all individuals. This rate increases during starvation to account for the increased susceptibility of starving individuals to disease and risk-taking behaviour (Foley, Papageorge and Wasser, 2001).

Analysis

Calibration

Eleven parameters were deemed uncertain and thus required calibration to accurately predict population dynamics (see Appendix B.6). We calibrated these parameters using rejection approximate Bayesian computation (ABC; Van Der Vaart *et al.* 2015): parameter values were sampled randomly from uniform prior distributions ranging from roughly half to double the reference values; the model was simulated 100,000 times; the 30 simulations which best fitted the data (annual population size, birth and mortality rates on 1st October 2000-2017) were accepted. We chose to accept the 30 best fitting runs as a compromise between including only well-fitting runs and the need to produce posterior distributions (van der Vaart *et al.*, 2015). Simulations were run in parallel through R 3.3.1 using the R package *RNetLogo* (Thiele, Kurth and Grimm, 2012; Thiele, 2014).

Local sensitivity analysis

Local sensitivity analysis identified relative sensitivities of population size, birth rates, adult and juvenile mortality, and calf mortality rates to changes in calibrated parameter values. Changes in outputs were averaged over a 10% increase and decrease in each parameter, and over ten repeated simulations to account for stochasticity in the model. While one parameter was tested all others were kept at their calibrated values.

Validation

To validate the model we compared model outputs to independent data from families not used in model calibration for the time period 2000- 2016. We used the 30 parameter sets accepted in the ABC to simulate the population dynamics of six intensively recorded Amboseli elephant family groups (AAs, FBs, GBs, JAs, KB2s and OBs; n = 105 initially on 1st March 2000). These families spend more time in Amboseli National Park and thus use a different area to that used in model calibration (Remelgado *et al.*, 2017). However, the ranging patterns of these families have only been recorded within ANP. Therefore, median NDVI was extracted from the 95% density kernels of known ranging within ANP and the model was used to estimate the total area used by these families (see Appendix B.4). The model was initialised for these individuals (population on 1st March 2000; see Appendix B: Table B.6) and run with the adjusted NDVI input data.

Hypothetical range loss scenarios

To demonstrate the potential of the model to estimate elephant population size under environmental change scenarios, we implemented two hypothetical range loss scenarios representing a 10% and 50% reduction in home ranges. We assumed that the median NDVI was unaffected by range loss. Increasing human populations in the Amboseli ecosystem could result in elephant range loss through the conversion of elephant habitats to cropland, over-grazing by livestock, the installation of fences or transport links which may prevent movement across the ecosystem, or increasing HEI and resulting avoidance of these areas by elephants. We ran each scenario with the 30 parameter sets accepted in the ABC.

4.3. Results

Calibration

We determined goodness of model fit to data using R^2 coefficient of determination. Model fits to the population dynamic data are shown in Figure 4.4. Adult and juvenile mortality rates were well predicted by the model, which accurately replicated low levels of background mortality and captured the high mortality rate associated with a drought in 2009. Modelled calf mortality also matched observations well, again capturing background and drought-related rates, although the prediction for

2005 was too high. Birth rates were well replicated throughout the simulation period, including low birth rates following the 2009 drought and the subsequent ‘baby-boom’ in 2012, with the exception of under-prediction in 2014 and 2015. As a result of model fit to birth and death rates, overall predictions of population size were good, with slight under-prediction from 2014 onwards owing to the lower than observed birth rates.

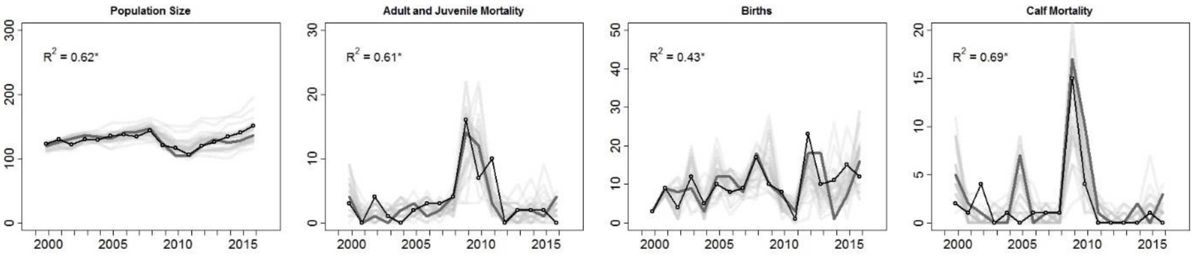


Figure 4.4. Population size, births and deaths for modelled families in Amboseli years 2000 – 2016. Black lines and points show the data, the thick grey line is the best fitting simulation. Light grey lines show the 30 best fitting simulations indicating the uncertainty in model outputs that result from uncertainty in the values of parameters. Amboseli years run October to September. R^2 of best fitting simulation presented on plot. * indicates significance with $p < 0.05$.

Sensitivity analysis

Sensitivities of key variables to model parameters are shown in Table 4.1 as the % change in the variable relative to 10% changes in parameter values. Adult and juvenile mortality was the least and calf mortality the most sensitive variable. Calf mortality was especially sensitive to parameters controlling energy intake from milk (AE_{milk} and E_0) as expected given that milk provides the primary source of energy for calves, and to B_0 which controls metabolic rate, the main source of energetic expenditure for elephant calves. All population variables were relatively sensitive to parameters controlling energy intake (hsc, $maxIR_{scaling}$ and AE_{veg}).

Table 4.1. Sensitivities of population size, total number of births and mortalities, presented as % change in output for a 10% change in parameter (mean and standard error over ten repeated simulations and for changes above and below parameter value).

Parameter	Pop. size	Births	Adult and Juv. Mort.	Calf Mort.
$stor_{scaling}$	-0.07 ± 3.02	0.02 ± 2.14	-0.14 ± 9.83	-0.31 ± 2.26
Hsc	-2.30 ± 3.19	-1.30 ± 2.81	0.70 ± 12.39	0.94 ± 1.66
$maxIR_{scaling}$	4.76 ± 4.09	2.69 ± 3.26	-0.63 ± 15.91	-3.98 ± 1.68
AE_{veg}	4.34 ± 4.87	2.38 ± 3.38	-0.38 ± 15.88	-4.28 ± 2.16
AE_{milk}	-0.42 ± 2.82	-3.39 ± 4.57	0.70 ± 13.33	-14.93 ± 3.9
B_0	-3.71 ± 3.59	0.63 ± 3.9	0.18 ± 17.13	15.95 ± 2.83
E_0	-0.52 ± 3.37	-3.48 ± 5.71	0.74 ± 11.5	-15.00 ± 4.32
E_{PL}	-1.82 ± 2.59	-0.89 ± 2.64	0.86 ± 12.34	0.88 ± 2.14
MR_{back}	-0.15 ± 2.65	-0.14 ± 2.16	-0.05 ± 11.06	0.02 ± 1.09
$MR_{scaling}$	0.08 ± 1.95	0.05 ± 1.97	0.09 ± 10.38	-0.12 ± 2.36
DD	-1.19 ± 3.07	-0.67 ± 3.21	0.32 ± 10.88	0.65± 1.92

Validation

The model with its calibrated parameter values was validated by comparing its predictions with independent data from a different family groups utilising a different area (Figure 4.5). Model predictions match these data well though the peak in birth rates was predicted a year late following the 2009 drought.

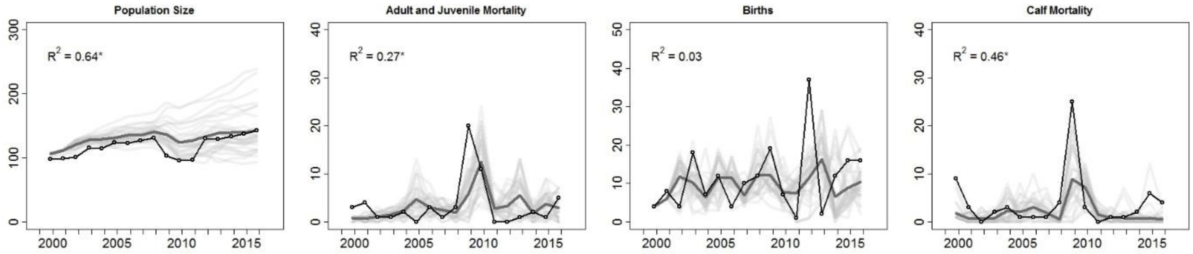


Figure 4.5. Validation of model fit. Population size, births and deaths for families not used in model calibration. Black lines and open points show the data, light grey lines show the 30 simulations indicating the uncertainty in model outputs that results from uncertainty in the values of parameters. R^2 of mean simulation presented on plot. * indicates significance with $p < 0.05$.

Hypothetical range loss scenarios

To demonstrate the model's potential application, we modelled the population size of the four family groups (IBs, LBs, VAs, and WAs) given hypothetical reductions of 10% and 50% of their home ranges (Figure 4.6). Over the time period for which the model was calibrated, a 10% reduction in range had little impact on the population size predictions throughout, whilst a 50% range loss predicts the end population size was generally below 100 individuals, compared to 151 in reality.

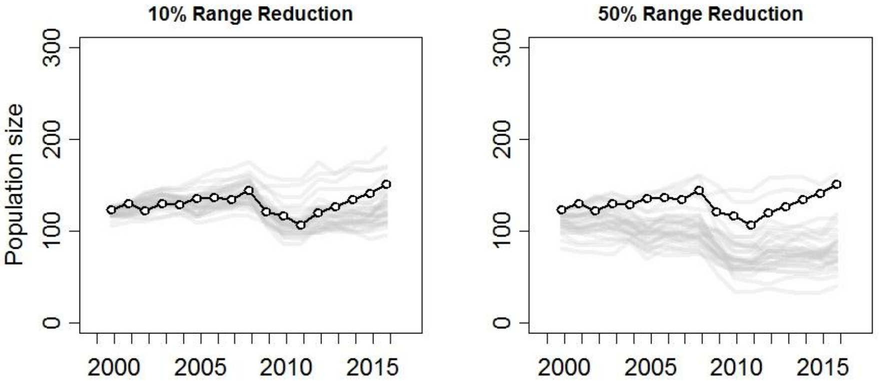


Figure 4.6. Population size for modelled families in Amboseli years 2000 – 2016 given hypothetical scenarios of 10% and 50% range loss. Black lines and open points show the observed population size data, light grey lines show the 30 simulations indicating the uncertainty in model outputs that result from uncertainty in the values of parameters.

4.4 Discussion

Following calibration, the model predictions generally replicate the data well and in particular predicts the critical events induced by the 2009 drought. The Amboseli elephant population as a whole declined by 25% during the drought; in our modelled families 16 adults and 15 calves died. Starving adult females struggled to meet the demands of reproduction, resulting in the deaths of young calves and failure of pregnancies. Despite the drought breaking at the end of 2009, the 22-month gestation period of elephants meant there was a two-year lag in births with low numbers of births occurring in 2010 and 2011, but since drought acts to synchronise female reproduction there was a 'baby-boom' in 2012. Such drought-induced population dynamics are critical in the natural regulation of population size and are captured by the model, as indicated by the high R^2 values.

Elevated calf mortality predicted by the model in 2005 was the result of low median NDVI during this period. In contrast to the 2009 drought, we believe elephants were able to buffer this period of low productivity in 2005 by being more selective in their foraging locations and retreating to the fairly constant source of food in the ANP swamps, hence mortality rates are low. This was not possible during the 2009 drought, which began with a prolonged period of low rainfall in 2008, meaning 'fall-back' resources such as the swamps were already depleted by the time the official drought occurred in 2009. This resulted in the high mortality rates of both adults and calves in 2009. The under-prediction of birth rates in 2014-2015 in both the calibration and validation of the model is possibly because densities of other grazers are not considered in the model. The number of grazers in the Amboseli ecosystem remained low for a prolonged period following the drought, limiting competition for food for elephants. Incorporation of interspecific competitor density would be expected to improve model fit to birth rates post-2009, as elephants access more food and reproduce more readily. The under-prediction of population size from 2014 onwards results from under-prediction of birth rates in this period.

The sensitivity analysis provided further support that the model was working accurately. The robustness of adult and juvenile mortality to changes in parameter values reflects generally low mortality rates in adult elephants whose large body size and substantial energy reserves allow them to buffer fluctuations in energy intake and expenditure. Calf mortality on the other hand is extremely sensitive, indicative of the vulnerability of young elephants to environmental changes (Foley, Pettorelli and Foley, 2008; Woolley, 2008; Wato *et al.*, 2016). The overall sensitivity of all model outputs to parameters controlling energy intake confirms that food availability is the key driver of elephant population dynamics. This endorses the use of mechanistic approaches in modelling the bottom-up processes controlling population dynamics.

Given the success of the model in predicting observed elephant population dynamics, we demonstrated how this model may be applied to predict the response of elephant population size to changes in their range. A range reduction of 50% caused the population size of modelled families to decline, indicating that less absolute space would support fewer elephants. Whilst these scenarios were hypothetical, the model may be easily adapted to simulate range reduction resulting from specific land-management strategies such as the installation of fences or conversion of elephant habitats into human-dominated landscapes, both of which are possible scenarios for the elephants of Amboseli and elsewhere in Africa. The food availability input data may also be altered to simulate changes in median NDVI resulting from, for example, climate change, provided the relationship between NDVI and climatic variables is known. The use of NDVI here to represent herb-layer biomass could be replicated in other open, grass-dominated ecosystems following calibration. Calibration is crucial in order to exclude unintended land-cover types and identify any features which may influence satellite-derived observations. By these means the model may also be readily applied to other elephant populations whose ranging patterns are known, or to other mammalian herbivores inhabiting grass-dominated ecosystems following re-parameterisation of the model. When considering application to species with finer-scale movements, it may be necessary to utilise a remote sensing product with higher spatial resolution, such as Landsat or Sentinel. Improvements in the estimation of biomass or food availability may perhaps be possible using alternative sensors, such as LiDAR, or alternative variables, such as the enhanced vegetation index (EVI) or net primary productivity (NPP).

With the increasing demand for predictive modelling of population responses to environmental change (Wood, Stillman and Hilton, 2018), we believe mechanistic models which relate key drivers to population dynamics are appropriate for improving understanding of the processes underlying demographics and for providing robust predictions under novel environmental conditions. We have presented a model which relates elephant population dynamics to food availability and may be applied to understanding how elephants will cope given projected climate change scenarios, land use change and management strategies. We hope that this will be used as a tool to aid the conservation and management of elephant populations and the ecosystems they inhabit, and may be applied to other species of interest to wildlife managers.

The individual-based model linking food availability to population dynamics developed here is applied in the next chapter to identify key threats facing the Amboseli elephants.

Chapter 5. Human-driven habitat conversion is a more immediate threat to Amboseli elephants than climate change

5.0 Abstract

Global change presents a major challenge to biodiversity conservation, which must identify and prioritise the most critical threats to species persistence given limited available funding. Mechanistic models enable robust predictions under future conditions and can consider multiple stressors in combination. Here we use an individual-based model (IBM) to predict elephant population size in Amboseli under a range of environmental scenarios incorporating climate change and anthropogenic habitat loss. Conversion of natural habitats to human-dominated landscapes reduces the food available to wildlife, while climate change is expected to alter the quality of food in remaining habitats. The IBM uses estimates of food availability under future environmental scenarios as a key driver of elephant population dynamics and relates variation in food availability to changes in vital demographic rates through an energy budget. Habitat loss, rather than climate change, represents the most significant threat to the persistence of the Amboseli elephant population. Our study highlights the importance of collaborations and agreements that preserve space for Amboseli elephants to ensure the population remains resilient to environmental stochasticity.

5.1 Introduction

African elephants (*Loxodonta africana*) face an array of threats, from ivory poaching to negative human-elephant interactions, habitat loss and climate change. Poaching has been responsible for the drastic reduction of elephant populations across Africa, from an estimated one million in 1970 (Douglas-Hamilton, 1987) to around 400,000 in 2016 (Chase *et al.*, 2016). Although poaching continues to pose a threat, the sharing of space between people and elephants in the face of environmental change is of growing concern.

In 2009 Africa's human population hit one billion, having doubled since 1982, and it is expected to double again by 2050 (UNDESA 2017). The associated conversion of natural habitats into human-dominated landscapes squeezes wildlife into smaller and increasingly isolated pockets of land, where resource availability is reduced and dispersal is limited. Habitat fragmentation due to human encroachment also increases interactions between humans and wildlife (Hoare, 1999), where undesirable elephant behaviours reduce tolerance by people (Dickman, 2010; Browne-Nunez, Jacobson and Vaske, 2013). As the absolute space available to wildlife declines, climate change may alter the quality of remaining habitats: rising global temperatures and shifts in the amount, distribution and timing of rainfall are expected to alter vegetative communities, with implications cascading up the trophic web (Walther, 2010). Given elephants' large body size and range requirements, elephants are expected to be amongst the hardest hit by these environmental changes (Martínez-Freiría *et al.*, 2016).

Food availability is a key bottom-up driver of elephant population dynamics (Rasmussen, Wittemyer and Douglas-Hamilton, 2006; Wittemyer, Rasmussen and Douglas-Hamilton, 2007; Boult, Quaife, *et al.*, 2018) and movement behaviour (Loarie, Van Aarde and Pimm, 2009; Bohrer *et al.*, 2014; Boult, Sibly, *et al.*, 2018), but is expected to change as environmental conditions shift. Here we estimate the food available to elephants inhabiting the Amboseli ecosystem in Kenya under projected climate change and anthropogenic habitat loss scenarios. Projected food availability is used to drive an individual-based model (IBM) which predicts vital elephant demographic rates through an energy budget. IBMs present a powerful tool for future scenario modelling as their process-based approach maintains the predictive ability of IBMs under novel environmental conditions (Stillman *et al.*, 2015) and can capture the cumulative impacts of multiple environmental changes (Nabe-Nielsen *et al.*, 2018). Projected elephant population size emerges from IBM simulations, providing vital information on the potential outcomes of environmental change scenarios. Results are used to identify scenarios which pose the greatest threat to the Amboseli elephants and will aid in prioritising land management policy and conservation efforts.

5.2 Methods

The individual-based model

We previously developed an IBM relating temporal variation in food availability to elephant life histories through individuals' energy budgets (Boult, Quaife, *et al.*, 2018). The model incorporates females of all ages and males prior to dispersal from their natal family at 12 years old. Elephants were assumed to use the area available to them evenly. Food available to elephants was estimated as a single mean value across the ecosystem using remotely-sensed measures of vegetation (normalised difference vegetation index; NDVI). Energy is taken from food available in the environment and allocated by each individual in the model to the energy expending processes of life (Sibly *et al.*, 2013). When food is abundant, energy is allocated maximally to maintenance, growth and reproduction, and storage tissues are accumulated. When food is limited, maintenance takes priority and growth and reproductive rates reduce. If the costs of maintenance cannot be met, individuals die. In this way birth and death rates, and ultimately population size, emerge.

The model was re-calibrated by fitting to historic (2000-2016) data of Amboseli elephant demographic rates, using approximate Bayesian computation (ABC; van der Vaart, Beaumont, Johnston, & Sibly, 2015) to describe the uncertainty in parameter values (Appendix C: Figure C.1). The uncertainty arising from unknown parameters in the IBM was propagated to population projections in scenarios below by running the model for each of the 30 parameter sets that best fitted historic data. Full details of the IBM development, parameterisation and validation are presented in Boult, Quaife *et al.* (2018).

Habitat loss scenarios

The risk of loss of a habitat is not equal across ecosystems and some areas are more susceptible to anthropogenic conversion than others. We developed six possible scenarios of habitat loss for Amboseli based on empirical data and stakeholder opinion (Figure 5.1). We divided the ecosystem into administrative units and ranked each unit based on change in human population density (from 1989 and 2009 Kenyan censuses; CBS 1994; KNBS 2013; Figure 5.1b), incidences of negative human-elephant interactions (HEI; 2014-2018; Big Life Foundation data; Figure 5.1c), stakeholder opinion ranking administrative units based on the likelihood that elephants would have continued access to the area (Figure 5.1d; stakeholders listed in Appendix C: Table C.1) and conservation area status (KWCA 2017; Figure 5.1e and 5.1f). We believe these metrics give a good indication of possible habitat loss: change in human population density is closely related to habitat conversion and infrastructural development; in conservation areas people are committed to protecting wildlife, supported by economic benefits; frequency of non-crop-foraging HEI affects (and predicts) human tolerance for wildlife and may align with areas that, although not physically lost to elephants, are avoided due to perceived risks (Roever et al. 2013; Wittemyer et al. 2017). We excluded crop-foraging because occurrence coincides with crop areas near areas of high human population growth, which is covered in figure 5.1b, and which is geographically fairly limited in the ecosystem.

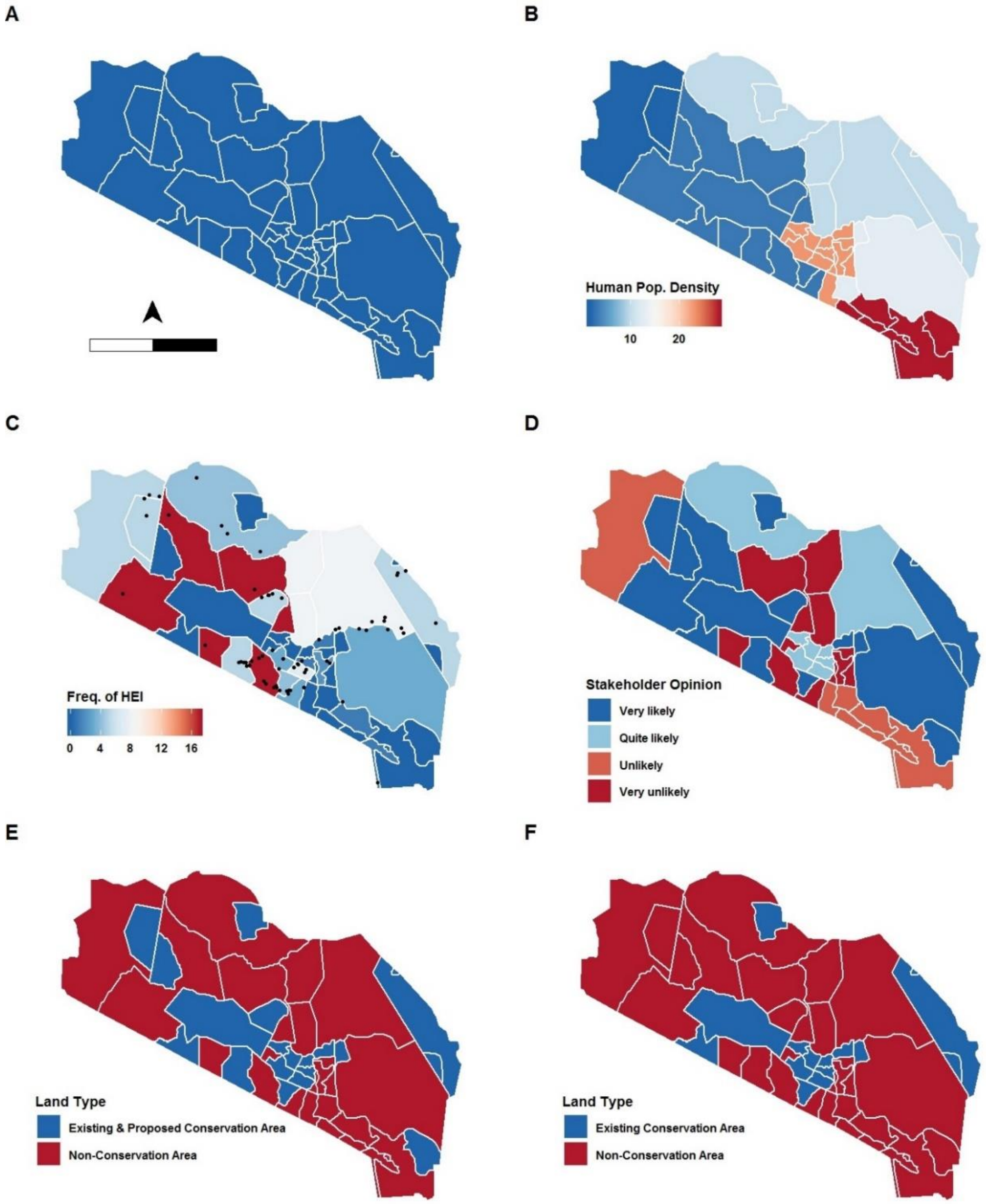


Figure 5.1. Predicted Amboseli habitat loss scenarios. Scenarios were based on empirical data and stakeholder opinion. In each scenario, the red and orange areas are lost. A) The full-area scenario: elephants have access to the full extent of the ecosystem. B) Areas which have experienced the greatest increase in human population density (additional number of people per km^2) could be converted to non-habitat and become inaccessible to elephants. C) Areas with the highest frequency of non-crop-raiding human-elephant interactions (black points) may be avoided by elephants due to perceived risks. D) Habitats thought by stakeholders to be unlikely or very unlikely to remain suitable elephant habitats are lost. E) Only existing and proposed conservation areas remain suitable, accessible habitats for elephants. F) Only existing conservation areas remain suitable, accessible habitats for elephants. We assumed that elephants could move through lost habitats, but that these areas no longer represented forging opportunities. Arrow = north. Scale bar represents 20km (divisions of 10km).

Climate change scenarios

We used climate change simulations supplied by the ISI-MIP 2b project, developed to provide information about the impacts of different greenhouse gas (GHG) emissions scenarios in different sectors on different scales (Warszawski *et al.*, 2014). The ISI-MIP 2b simulations incorporate four general circulation models (GCMs; GFDL-ESM2M, HadGEM2-ES, IPSL-CM5A-LR and MIROC-ESM-CHEM) and two representative GHG concentration pathways (RCP2.6 and RCP6.0). The RCP2.6 pathway is designed to be broadly consistent with the United Nations Paris Agreement targets to limit global temperature rise, and RCP6.0 produces a roughly 3°C rise in global temperatures above pre-industrial levels by 2100. The ISI-MIP dataset covers 2006-2099 at a 0.5° × 0.5° resolution. The projected data are bias-corrected to provide long-term agreement with observed historic data (Hempel *et al.*, 2013).

Combined stressor scenarios

Since aspects of environmental change interact and may have additive or antagonistic effects on elephant demographics, we also considered the impacts of climate change and habitat loss in combination. We simulated the IBM under both HadGEM2-ES emissions scenarios (RCP2.6 and RCP6.0) for each habitat loss scenario. We chose to only use HadGEM2-ES as all GCMs showed good agreement in elephant population projections, but HadGEM2-ES projected the largest difference between RCPs and thus represented the greatest uncertainty.

NDVI projections

To determine future food available to elephants, we projected NDVI under our climate and habitat scenarios. We first established the historic relationship between NDVI and rainfall in Amboseli. We classified historic Amboseli years 2000-2016 by rainfall collected at the Amboseli Elephant Research Camp gauge (coordinates: 2.68S, 37.27E) using the standard precipitation index (SPI; Mckee, Doesken, & Kleist, 1993). Amboseli years run from October to September to align with the annual rainfall cycle (i.e. Amboseli year 2000 runs October 1999 to September 2000; Croze & Lindsay 2011). Each Amboseli year was classified by its SPI as follows: ≥2 = very wet, (1, 2) = wet, (-1, 1) = normal, (-2, -1) = dry and < -2 = drought.

Historic NDVI values were obtained for the area available to elephants under each habitat loss scenario from the Terra-MODIS (Moderate Resolution Imaging Spectroradiometer) mission (Didan, 2015), using the MOD13Q1 product accessed via the Oak Ridge National Laboratory web service (Vannan *et al.*, 2011). For each SPI class, we calculated a median NDVI value per month for each area available to elephants. These values were used to construct monthly NDVI time series for the projected period (2007-2099) under scenarios of habitat loss only, climate change only and their combined effects.

For habitat loss scenarios, we assumed a stable average climate throughout and used monthly NDVI values from ‘normal’ SPI years only. For climate scenarios, we first calculated the SPI of Amboseli years for the projected period using monthly precipitation totals from the eight ISI-MIP climate scenarios (four GCMs and two RCPs). Using monthly NDVI values from habitat scenario A assuming no habitat loss, we arranged monthly NDVI values by projected SPI. In combined scenarios, monthly NDVI was projected according to HadGEM2-ES RCPs and all habitat loss scenarios.

Model simulations

For all simulations, we assumed the Amboseli elephant population used the area available to them evenly. Under scenarios of habitat loss, we assumed that elephants could move through lost habitats, but that these areas no longer represented foraging opportunities for elephants. Therefore, where our scenarios include habitats only accessible via converted habitats, our projections may be conservative.

For all scenarios, the IBM was simulated from 2007 until 2099 for each of the 30 best calibrated parameter sets to indicate uncertainty arising from parameter uncertainty in the IBM. The IBM was initiated with the known elephant population on the 1st January 2007. Under habitat loss and combined scenarios, the *area* parameter in the IBM was adjusted at model initiation to indicate the habitat remaining (Appendix C: Table C.2) and population size was recorded at the end of 2099. In climate simulations, elephant population size was recorded at the end of each Amboseli year (30th September).

5.3 Results

Habitat loss projections

Scenario A, in which current ecosystem limits remain unchanged, shows the elephant population remains stable around its current size. Habitat loss inevitably reduces the number of elephants supported by the ecosystem, as seen in Figure 5.2, though elephant numbers are not directly proportional to the amount of area lost (Appendix C: Table C.2). Scenario B, where habitat is lost to human population growth, supports fewer elephants than scenario C, where areas become avoided due to risks associated with HEI, despite the amount of area lost being similar. In scenario F, where only existing conservation areas remain accessible, the model predicts a ~80% reduction in elephant numbers.

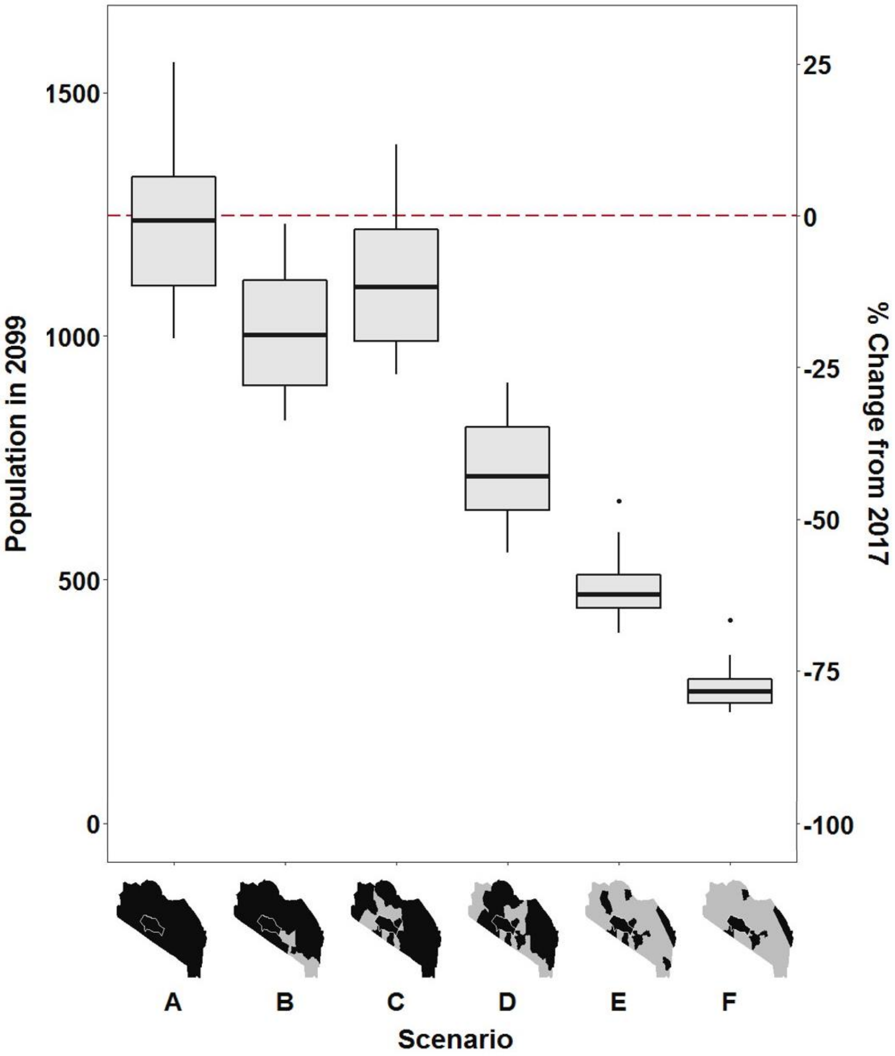


Figure 5.2. Projected elephant population size in 2099 and percent change from the 2017 population for habitat loss scenarios (A-F) assuming 'normal' climates (see Methods). Boxplots (median and interquartile ranges) indicate uncertainty arising from parameters used in the IBM. Points show outliers. Dashed line = elephant population size in 2017 (n =1247). Maps: black polygons = remaining elephant habitats; grey polygons = lost habitats.

Climate change projections

The four GCMs agreed closely on projected precipitation changes throughout the simulation period although the timing and frequency of projected droughts varied (Appendix C: Figure C.2). Overall, RCP2.6 GHG scenarios project constant or slight declining trends in absolute precipitation whilst the higher emissions scenario RCP6.0 projected an increase in precipitation (Appendix C: Figure C.3). 'Drought' years as defined by SPI were more frequently projected in the first half of the 21st century in RCP6.0 scenarios, but this trend was reversed for RCP2.6 scenarios with droughts mostly occurring in the latter half of the century (Figure 5.3: arrows).

In all climate scenarios, the IBM projected an increase in the initial elephant population of 1099 individuals in 2007, with early growth (2007-2015) slowing and stabilising around 1250 elephants. The elephant population is thus not expected to deviate much from the current population size under any climate scenario. Droughts intersperse the time-series and generate population crashes as vegetation availability limits survival and reproduction. Interquartile ranges for projections indicate that some uncertainty arises due to parameter values used in the IBM.

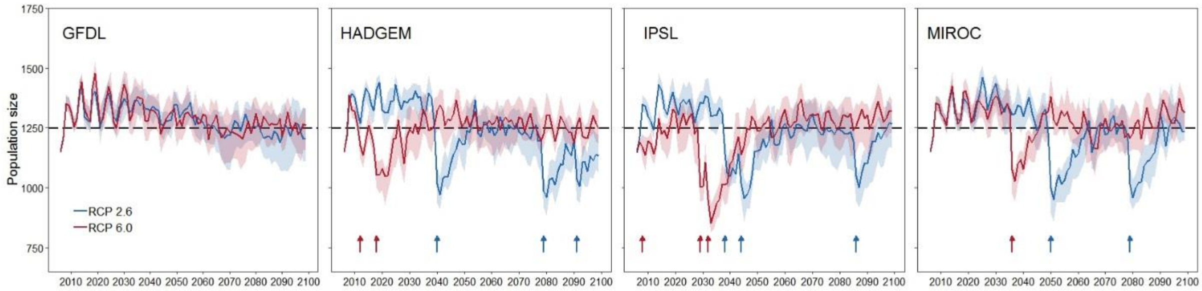


Figure 5.3. Elephant population projections given expected scenarios of climate change. Four GCMs (GFDL, HadGEM, IPSL and MIROC) and two GHG emissions scenarios (RCP2.6 and RCP6.0; blue and red lines, respectively) are included to account for uncertainty in climate projections. Lines = median, shading = interquartile range indicating uncertainty arising from parameters in the IBM, arrows = drought years. The dashed line shows elephant population size in 2017 (n = 1247).

Combined stressor projections

The combined effects of habitat loss and climate change (HadGEM2-ES) are shown in Figure 5.4. In all habitat scenarios, the higher emission climate scenario (RCP6.0) projected a larger elephant population than the low emission scenario but these differences were smaller than the differences between habitat scenarios. Even in habitat scenario A and RCP 6.0, the elephant population does not deviate dramatically from the current population size.

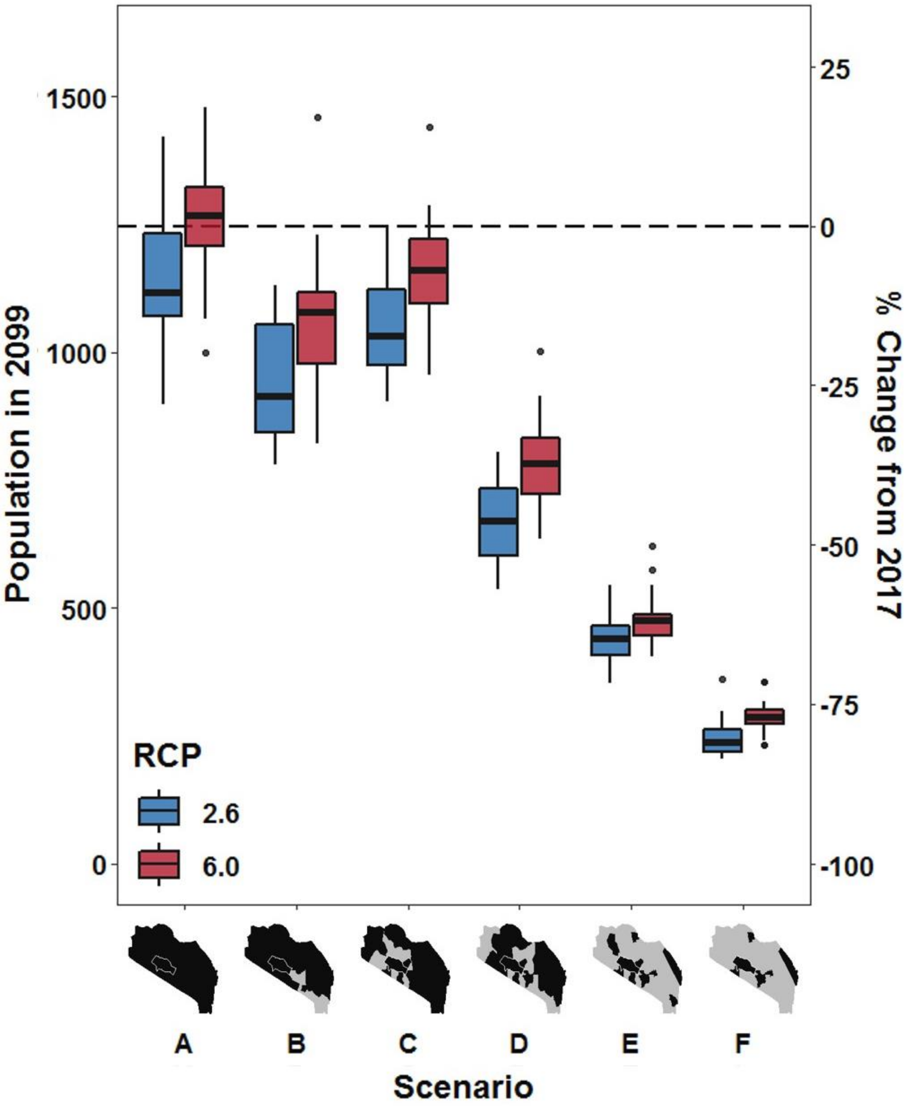


Figure 5.4. Elephant population size in 2099 and percent change from 2017 under combined climate change and habitat loss scenarios. For each habitat scenario (A-F), the IBM was simulated with RCPs 2.6 (blue) and 6.0 (red). Boxplots (median and interquartile ranges) indicate uncertainty arising from parameter uncertainty in the IBM. Points show outliers. The dashed line shows elephant population size in 2017 (n = 1247). Maps: black polygons = remaining elephant habitats; grey polygons = lost habitats.

5.4 Discussion

Models suggest that habitat loss, rather than climate change, is the most significant immediate threat to the Amboseli elephants. The elephant population declines under all scenarios of habitat loss, though declines are not directly proportional to the amount of area lost since areas vary in vegetation quantity and quality, and so in importance to elephants. Despite the areas lost due to human population growth and HEI (scenarios B and C) representing roughly the same total space, our IBM predicted bigger losses of elephants resulting from human population growth rather than HEI. This is likely because HEI generally occurs where people and livestock share space with elephants. Livestock grazing tends to occur on drier land where crop production is difficult; in contrast, human population growth is usually concentrated around highly productive areas. This underscores the problems posed by agricultural encroachment into key foraging areas for the Amboseli elephants and highlights the need for landscape-scale planning of human development.

Like many areas, Amboseli faces increasing pressure on the space and resources available to people and wildlife. With growing competition for space, the government has encouraged people to settle and farm, resulting in the widespread subdivision of land, the expansion of irrigated and rain-fed agriculture, and the emergence of many unplanned developments (Croze, Moss and Lindsay, 2011; Schüßler, Lee and Stadtmann, 2018). Community choices and human tolerance will shape Amboseli's conservation success, and our model has begun to identify how these choices would impact elephants. Scenario E, representing the accessibility of only existing and proposed conservation areas, suggests that conversations to promote human-elephant coexistence beyond the boundaries of conservation areas may be worth ~800 elephants, or ~60% of the current population. Models predict a ~80% decline, to ~300 elephants supported by the ecosystem if elephants were confined to existing conservation areas alone (scenario F). Such small elephant populations are vulnerable to stochastic perturbations including demographic and environmental stochasticity, and natural disasters (Shaffer, 1981). Fewer elephants may also decrease tourism revenues (Naidoo *et al.*, 2016) which represent a key component of successful balance between biodiversity conservation and socio-economic development in many African landscapes.

Local community decisions are hugely important for the future of Amboseli's elephants, limiting habitat conversion and mitigating HEI to ensure continued accessibility of the ecosystem for all wildlife. Amboseli stakeholders are already well aware of these needs. Land management planning is a new part of the Kenyan constitution, and Amboseli's ecosystem management plan was the first to be formally gazetted (but is already due for renewal). Amboseli has several projects in place to ease HEI, including Amboseli Elephant Research Project's livestock loss consolation scheme (Sayialel and Moss, 2011) and Big Life Foundation's elephant-proof fence to prevent crop foraging by elephants and the further expansion of agriculture (Big Life Foundation, 2017). More broadly, Amboseli is developing community-led multi-stakeholder initiatives under the Amboseli Ecosystem Trust, to promote evidence-based and transparent landscape planning in order to balance human and wildlife needs.

Whilst variation in food availability resulting from climate change does not appear to present a significant direct threat to the Amboseli elephants, we advise caution based on potential interactions between climate change and human behaviour which may indirectly impact elephants. For example, more rainfall in the area may draw more people seeking to expand and intensify agriculture to the region. In addition, we have only considered the four GCMs which participated in the ISI-MIP 2b experiments, and these may not be fully representative of the broader set of more than 40 different GCMs which participated in the underlying Coupled Model Intercomparison Project, phase 5 (CMIP5) from which the ISI-MIP simulations were selected (Appendix C: Figure C.3). We note that if these simulations under-represent the frequency of droughts then the assessed effect of climate change on Amboseli elephants would be too small. Another issue not addressed here is the impact of rising atmospheric CO_2; it is well established that increased CO_2 makes vegetation more tolerant to droughts, and hence the impact of low rainfall on available food may be less than suggested here. It is also important to note that the impacts of climate change on elephant populations will vary by location given disparities in projected rainfall across African elephant range states. In southern Africa in particular, climate projections suggest rainfall will decline (Serdeczny *et al.*, 2016), resulting in reduced vegetation productivity and potential food limitations for elephant populations.

We also acknowledge limitations with the IBM used in these projections. Firstly, the IBM considers only food limitation as a stressor impacting elephant energetics and demography. Rather, additional stressors are likely to emerge from environmental changes. Warming climates are expected to increase physiological stress in elephants (Mumby *et al.*, 2015). More directly, the expansion of human activities will bring people and elephants into closer contact, likely competing for the same resources, potentially increasing elephant mortality rates as a result of negative human-elephant interactions. Alternatively, elephants may access additional high-quality food sources in the form of crops. Second, the IBM assumes elephants use the ecosystem evenly. In reality, some areas are used more heavily by elephants than others. Inclusion of more explicit elephant space use may alter results if areas lost to habitat conversion are more or less heavily used than assumed in our model. While these factors are likely to be important in determining the response of elephants to future environmental change and thus may influence our model predictions, the mechanisms by which these stressors act, and the quantification of their impacts are yet to be determined. Future modelling efforts should attempt to include a wider suite of stressors to improve the accuracy of predictions in uncertain future conditions.

Our results suggest that while most of the uncertainty about the future stems from different potential scenarios of habitat loss, there is significant uncertainty stemming from unknown parameters in the IBM. The latter will hopefully reduce as improved methods are developed in data assimilation, an active area of research (see, e.g., Van Der Vaart et al. 2018). Further improvements to the model may be made by addressing the assumption that elephants use the space available to them evenly. Rather, elephants utilise established home ranges and move seasonally to maximise resource availability. Inclusion of spatially explicit ecosystem use may allow our model to identify elephant families most at risk from change and further pinpoint critical areas for elephants. Future efforts should also consider adult males, who occupy different ecological niches that vary their needs and interactions with humans (Shannon, Page, Duffy, *et al.*, 2006a), and the impacts of other global change scenarios, such as variation in livestock density or demand for ivory, which may act to exacerbate or alleviate the impacts of habitat loss and climate change.

The approach used here relies on the general mechanistic relationship between food availability and demographic rates. How food availability is influenced by environmental change is estimated and underlies IBM predictions of elephant population size. We believe IBMs present a strong solution for improving our ability to predict the responses of animal populations to combined stressors and novel environmental conditions (Stillman *et al.*, 2015; Nabe-Nielsen *et al.*, 2018). The IBM employed here uses a general energy budget framework, calibrated to the Amboseli elephants, and could be readily adapted for other elephant, or mammalian herbivore, populations. We therefore see that this approach provides the basis for the development of a broader toolkit for use by stakeholders in assessing the relative importance of different policy decisions for animal populations.

Chapter 6. Discussion

In the face of rapid global change, the need for predictive models which can identify current and future threats facing species and ecosystems is becoming ever more evident (Wood, Stillman and Hilton, 2018). Realistic models which remain robust under novel conditions and can incorporate the combined effects of multiple stressors in combination are required to simulate predicted global change and its impacts on biodiversity so that limited available resources can be targeted at tackling the most critical threats (Evans, 2012). The aim of this thesis was to develop such models, which are here applied to identify the major threats facing the elephants of Amboseli. Food availability was considered a key driver of animal population dynamics and fitness-maximising behaviours were assumed throughout (Sibly *et al.*, 2013). The ability of models based on these fundamental principles alone to fit the observed demographic rates and movement patterns of Amboseli elephants has confirmed the importance of food availability in driving animal populations, whilst deviation of observations from predicted responses has illuminated additional factors mediating the ability of elephant to maximise fitness. The culmination of this thesis was the identification of key threats facing the Amboseli elephants in the 21st century and recommendations for the management of the ecosystem.

In this final chapter, I summarise the findings of each chapter in turn, then discuss the implications of the work for the management of the Amboseli ecosystem. I also emphasize the generality of the approach adopted and thus its potential application to a broad range of study species and systems. I hope that the work presented here will generate further use of individual-based models (IBMs) in conservation biology and in turn contribute to biodiversity conservation.

6.1. Thesis overview

The need for predictive modelling in ecology and conservation is addressed in **Chapter 1**, with particular attention paid to the opportunities offered by IBMs (Grimm and Railsback, 2005). Importantly, the challenges presented by the added complexity of IBMs are introduced, including the difficulties in developing, analysing and communicating IBMs, and the data required to inform the increasing number of parameters, leading to greater uncertainty in predictions (Grimm and Railsback, 2005). These challenges have been tackled throughout the thesis. The potential for remote sensing to provide data on key environmental drivers at across large scales with spatial and temporal consistency is introduced. Here, RS has provided information on the dynamics of food available to elephants through space and time (Chapter 2), which is used to drive the models presented in Chapters 3 and 4. Through collaboration with the Amboseli Elephant Research Project (AERP), data to calibrate and validate the IBM has been readily available, highlighting part of the value of long-term individual-based field studies. In later chapters, the IBM is calibrated using approximate Bayesian computation with the number of runs maximised to minimise the uncertainty in parameter values and model predictions (van der Vaart et al. 2016; Chapter 4). Remaining uncertainty is carried forward to scenario simulations to acknowledge the uncertainty in projections made in Chapter 5. Finally, efforts were made to document the development, calibration and analysis of the IBM in line with current best-practise in the field (Grimm *et al.*, 2014).

In Chapter 1, the system which has provided the focus of modelling efforts is also introduced. The Amboseli elephants are world renowned, but their future is increasingly uncertain due to the pressures of human population growth, changing human behaviours and resulting environmental change. Questions surrounding the future of Amboseli elephants have guided the design and application of models presented here, and have highlighted the potential value of process-based approaches for informing biodiversity conservation.

Having established the need for information on key drivers of animal population dynamics and behaviours, in **Chapter 2** the potential of RS data to estimate food available to elephants was examined. NDVI was selected as an appropriate proxy for vegetative biomass (Pettorelli, Vik and Mysterud, 2005) and thus food available to elephants. To understand how NDVI relates to vegetation dynamics in Amboseli, measures of on-the-ground biomass were compared to NDVI values across the habitats of ANP and over time. Results were hindered by common limitations of RS, including mismatches between the scale of satellite and ground-based measures, and interference from non-food vegetation types (Kerr and Ostrovsky, 2003). However, a relationship was established, confirming NDVI as a proxy for vegetative biomass, and proved useful in subsequent chapters for estimating the relative food available to elephants, accurately predicting movement patterns and demographic variation.

The full potential for the integration of RS data in IBMs has yet to be achieved. RS presents opportunities to not only drive IBMs as here, but also the potential to calibrate and validate model predictions. RS can provide information on key environmental variables such as climate, vegetation dynamics and land cover, and can monitor changes in these variables over time (Kerr and Ostrovsky, 2003; Turner *et al.*, 2003). Such variables could be incorporated as drivers of processes, allowing some pattern of interest to emerge, or could themselves be the emergent property of a model, meaning RS could provide data to test model predictions. As RS data become increasingly accessible (Turner *et al.*, 2015), software and expertise for its use develop, and the need for consistent data over large spatiotemporal scales grows, the integration of RS in IBMs will likely increase, encouraged by successful examples like that presented here.

In **Chapter 3**, a simple decision-making model using resource availability to predict the seasonal range shifts of elephants was developed and tested using satellite tracking data for five individuals. Resource availability was considered to be a combination of water and food availability, and was estimated in the seasonal home ranges of elephants over the course of a year. Based on relative resource availability in seasonal home ranges, the model predicted whether elephants would be located in ANP or their respective dispersal areas. Predictions were based on fundamental fitness-maximising behaviour, that is, elephants would move to maximise the resources available to them. The model predicted shifts in the locations of all individuals, but the ability of model predictions to replicate tracking data varied. Where the model matched individual data well, they highlighted a key benefit of seasonal range shifts, which is to maximise resource availability. Where individual locations differed from model predictions, detailed knowledge of the study individuals and ecosystem was used to identify additional factors, such as reproductive state and perceived risk (Ruggiero, 1991; Roever, van Aarde and Chase, 2013; Wittemyer *et al.*, 2017), for consideration in predicting elephant movement patterns. It was argued that the combination of a simple decision-making model based on fundamental principles of fitness-maximising behaviour, animal tracking data and detailed local knowledge can be used to identify factors guiding movement decisions of individuals.

Such an approach would be appropriate for a wide number of applications. As earlier discussed, data on key environmental drivers are now readily available via RS and can be used to model expected patterns of animal space use assuming fitness-maximising behaviours. The availability of animal movement datasets is also increasing in terms of the number of studies, locations and taxa, with much data becoming freely accessible through platforms such as Movebank (Wikelski and Kays, 2018). Utilising such data and the mechanistic approach employed here, an improved understanding of the factors influencing animal movement decisions can be gained. This understanding will aid conservation practitioners in identifying the potential responses of animal space use to environmental change and management decisions.

An IBM relating food availability to the population dynamics of elephant family groups through an energy budget was developed in **Chapter 4**. Again, the model assumed that individuals would act to maximise fitness: energy intake from the environment was maximised and energy expenditure was prioritised to improve survival and reproductive rates. The energy budget was based on a general framework described in Sibly et al. (2013). Parameters controlling the processes of energy intake and expenditure were derived from the literature and uncertain parameters were calibrated using approximate Bayesian computation (van der Vaart *et al.*, 2015) to fit the vital demographic rates (births and deaths) underlying population dynamics. The ability of the model to replicate both calibration and validation data of elephant population dynamics highlighted the importance of food availability as a key driver of elephant populations.

The fundamental fitness-maximising principle upon which the IBM is based, and the use of a general energy budget framework and freely available estimates of food availability, allows this approach to be widely applied to a range of taxa and ecosystems. Already this approach has been applied in marine systems, utilising RS of phytoplankton to drive the population dynamics of mackerel (*Scomber scombrus*; Boyd et al. 2018), and models are currently being developed following this approach for red deer on the Isle of Rum (*Cervus elaphus*) and sea bass in UK waters (*Dicentrarchus labrax*) by members of the University of Reading. Further applications of this modelling framework are examined below (see 6.3).

The IBM developed in Chapter 4 was applied to simulate the effects of environmental change scenarios on Amboseli elephants in **Chapter 5**. Continuing with the general principle that food availability drives animal population dynamics, NDVI (our proxy for food available to elephants) was projected under scenarios of climate change and habitat loss in the Amboseli ecosystem. Relationships between NDVI and rainfall, and how this varied across different spatial aspects of the ecosystem were established using historical observations. Standardised scenarios of climate change (Warszawski *et al.*, 2014) predicted stable or slight increases in the amount of rainfall, and therefore had no real impact on the number of elephants supported by the ecosystem. There is currently little consensus on the best means to quantify the likelihood of habitat conversion, though the field of predictive ecology and conservation would benefit from a standardised approach to allow for comparison across studies. Here, habitat loss scenarios were developed using empirical data and stakeholder opinion and predicted significant losses in Amboseli's elephant population size. Declines were not however directly proportional to the amount of area lost owing to the spatial heterogeneity in NDVI and food availability. Projections identified habitat lost to human population growth as disproportionately important foraging resources for elephants and has highlighted the need to manage human development and expansion in highly productive areas. More importantly, loss of all but protected habitats resulted in an 80% loss of elephants in Amboseli. There is an urgent need to find solutions guaranteeing continued elephant access to the ecosystem beyond the boundaries of protected areas. The ecosystem stakeholders are well aware of this, but require tools, like this model, to evaluate alternative land use choices and community decisions. Human-wildlife coexistence strategies will thus be key to the successful conservation of the Amboseli elephant population in the 21st century.

In summary, models based on the fundamental principles of fitness-maximisation and food availability as a key driver (Sibly *et al.*, 2013) have accurately predicted the population dynamics and movement decisions of elephants inhabiting the Amboseli ecosystem (Boult, Quaife, *et al.*, 2018; Boult, Sibly, *et al.*, 2018). The process-based approach used in these models has allowed for the robust predictions (Stillman *et al.*, 2015) of the implications of potential environmental change scenarios for Amboseli elephants and in doing so has highlighted the value of these approaches in informing conservation and management decisions (Wood, Stillman and Hilton, 2018). By adopting an individual-based approach throughout, models have accounted for, rather than ignored, individual variation and in doing so, have identified intraspecific differences in responses to environmental drivers which will be important to consider when predicting the impacts of global change on species more generally.

Whilst emphasising the values of a process-based approach, the challenges in adopting such approaches have been acknowledged and addressed. The need for measures of key drivers

(Uchmański and Grimm, 1996) was addressed through the integration of RS data and made relevant through calibration with ground-based measures of biomass. Uncertain parameters controlling the energy budget model were calibrated using recent advances in approximate Bayesian computation to minimise uncertainty in model predictions (Grimm and Railsback, 2005). The large datasets required to calibrate and validate IBMs (Grimm and Railsback, 2005) were provided through collaboration with the Amboseli Elephant Research Project, who have collected valuable data on the life histories of Amboseli's individual elephants since 1972 (Moss, Croze and Lee, 2011a).

Here, models focused on Amboseli elephants, in part due to the practicalities addressed by the rich dataset and in part because of the interest in elephants as a species of conservation concern, highlighting the value of the approach to answer real-world questions. However, the fundamental principles guiding model development mean that methods employed here may be easily applied to study the impacts of future environmental change on other species and study systems. I now go on to explain the implications of this research for Amboseli elephants and their ecosystem, then discuss the potential application of this approach to other study systems.

6.2. Implications for Amboseli

The results presented here have shown that: 1) it is possible to construct IBMs which accurately reflect population dynamics for female African elephants and 2) this generates the possibility of data-driven discussions about Amboseli's future for non-technical specialists and policy-makers who are charged with decisions.

Amboseli is not unique in its mosaic of protected and non-protected areas (Newmark, 2008), nor in the sharing of these spaces between wildlife and people. In the past, designation of protected areas for the sole use of wildlife and the exclusion of human activity was considered the only way to effectively conserve species (Pimbert and Pretty, 1995). However, with controversies over the exclusion of local people from areas upon which they relied (Brockington, Igoe and Schmidt-Soltau, 2006) and growing concerns that protected areas are not 'future-proof' (Hannah *et al.*, 2007), focus has turned towards community-based conservation (Hackel, 1999), in which land is managed for the mutual benefit of people and wildlife.

In Amboseli, roughly 80% of the ecosystem falls beyond the boundaries of conservation areas. In these areas human and livestock populations have grown, agriculture has proliferated around key water sources and on productive soils, and infrastructure has been developed with no planning or ecological risk assessments (Croze, Moss and Lindsay, 2011; Schüßler, Lee and Stadtmann, 2018). In conjunction, there is high unemployment – especially of young people – around Amboseli, livelihoods are unstable and rely heavily on climatic conditions, so poverty is common (World Bank Group, 2018). The need to develop strategies which ensure human-wildlife coexistence is well understood by Amboseli's stakeholders, forming a central part of the existing ecosystem management plan (Kenya Wildlife Service, 2008) and ongoing discussions for renewal of the plan.

Historically, efforts to aid coexistence have been largely reactive and were criticised for being too slow and inconsiderate of social intricacies, leading to distrust between local people and the conservation sector. In response, Kenya Wildlife Service (KWS) and the Amboseli Ecosystem Trust (AET) established the Human Wildlife Coexistence Committee (HWCC) in 2016 to coordinate the efforts of the conservation community operating in Amboseli with the aim of increasing the rapidity of responses to incidents of HEI and becoming more proactive. At present, operational coexistence strategies in Amboseli include, but are not limited to: Amboseli Trust for Elephants' consolation scheme for livestock killed by elephants; Big Life Foundation's compensation scheme for livestock killed by predators; the installation of lion-proof bomas by Born Free Foundation; Lion Guardians' lion tracking scheme to monitor the movements of lions and advise communities about lion presence and measures to avoid lion interactions; the installation of 80km of elephant-proof fencing to protect smallholders from elephant crop foraging; scholarships for local children to attend school and university (probably more than 100 scholarships are provided by the numerous organisations operating in the ecosystem); the International Fund for Animal Welfare's livelihood support initiatives, especially for women, to improve literacy and income stabilisation. Further, the HWCC is establishing standardised response protocols for dealing with HEI incidences, outlining the steps to be taken and the intersection between stakeholder responsibilities. The implementation of such initiatives requires cooperation between community leaders, numerous NGOs and KWS, who actively participate in developing and approving protocols. These initiatives and protocols will also form part of the conservancy management plans and the 2018-2028 Ecosystem Management Plan, which is to be gazetted under both wildlife and environmental laws providing the power to prevent further land conversion in Amboseli.

The combination of better legislation to prevent further land conversion, active management of the human-wildlife interface and sustainable livelihood diversification presents a promising outlook for future coexistence between people and wildlife in Amboseli. Results presented here will contribute to an existing knowledge base to inform data-driven protocols and the IBM could be incorporated into decision-making structures (see 6.3) to assess how individual livelihood choices will affect elephants and the ecosystem services they provide.

6.3. Further development and future applications

As introduced in Chapter 1, there is a growing need for predictive models in conservation and ecology to identify future changes to the abundance and distribution of species. Here, the approach is developed and applied to inform conservation priorities for Amboseli elephants, but could be easily adapted to provide insight for other species of interest. Such species may be those of conservation concern, those of important economic or functional value to humans, or those which threaten human livelihoods. This thesis has demonstrated the use of process-based approaches based on general principles and freely accessible data to answer questions of importance biodiversity conservation and ecosystem management.

Adaptation for alternative applications

Models presented here have assumed fitness-maximising behaviour throughout (Sibly, 2002). That is, individuals act to maximise their reproduction, growth and survival by moving to maximise resource availability and energy intake. Energy is obtained from food available in the environment. An energy budget links variation in food availability to vital demographic rates (Sibly *et al.*, 2013). These principles apply not only to elephants, but across the spectrum of taxa.

Model inputs largely consisted of freely accessible data. The availability of food was estimated using RS data and made relevant to Amboseli through a simple calibration exercise (Chapter 2). RS proxies can even been related to the population dynamics of higher trophic levels (Pettorelli *et al.*, 2011), and so application is not limited to herbivores. Parameters controlling the energy budget model were derived where possible from published literature, whilst uncertain parameters were estimated using allometric equations or through parameter sharing with similar species, then calibrated using approximate Bayesian computation (Chapter 4). Climate models were accessed through the freely accessible ISI-MIP platform and had already undergone required pre-processing (Chapter 5; Warszawski et al. 2014). These input data are freely available for other study systems or species, allowing relative ease of model adaptation. All model programming and analysis presented in this thesis was also carried out using freely available software (NetLogo and R) and all scripts have been provided: https://github.com/vlboult93. The only data used here which is not freely accessible was the longitudinal demographic data used in model initiation and analysis. Studies boasting such rich datasets are established globally for a wide range of taxa (Hayes and Schradin, 2017). Collaboration with these studies may allow access to such valuable data, though research using such data should seek to answer questions of interest to the study. The partnership with AERP which underpinned the success of this project should act to encourage collaborations between long-term studies and researchers developing novel approaches to conservation.

Given the general principles underlying model design and the use of freely accessible model input data, the approach presented here could be easily adapted to provide information on the responses of other elephant or species population dynamics to environmental change scenarios. Those wishing to do so would simply need to adjust the RS measure of food availability, change the energy budget parameters to suit the species of interest, and extract climate projections for the desired area. Additional scenarios of environmental change or management plans may be developed and incorporated into the IBM depending on the needs of the user. In this way, the process-based approach developed here can be applied broadly to answer questions of conservation and management significance.

Future developments

There is potential to not only adapt the models constructed here for other animal populations, but also to further develop them to include more realism. In this case, the models presented here should act as first, null models, assuming elephant movement decisions and population dynamics are only driven by food availability. Future modelling efforts can then compare outputs to null model results and identify developments which improve the models' predictive ability.

The first potential improvement will likely come from the incorporation of spatially explicit foraging. Whilst the IBM used spatially explicit estimates of food availability and climate change, the space use of elephants was assumed to be equal across the ecosystem. Rather, elephant family groups use specific home ranges and some aspects of the ecosystem host more elephants than others (Croze and Moss, 2011). This means that whilst current model predictions replicate population-level demographics well, disparities may emerge when considering demographics on a family-by-family basis, as family groups have access to different foraging resources. The effects of different food availability to families is most evident in times of food limitation, when families with access to more abundant or better-quality resources survive and reproduce more readily than others. Space-use also has important implications when considering the impacts of environmental change. Where habitats support more elephants than assumed by the IBM, loss of these habitats will have a greater impact on the elephant population as a whole than projected by the IBM. On the other hand, where habitats are less utilised by elephants, projections may exaggerate impacts on elephants. To incorporate spatially explicit ranging into the model would require either data on the distribution of Amboseli's elephants through time or a better mechanistic understanding of the factors driving elephant distributions. Distribution data is not currently available for the wider Amboseli elephant population beyond the boundaries of the national park, but in Chapter 3 we started to identify the mechanisms driving elephant movements using GPS tracking data for five families. Food availability was one of many factors determining seasonal elephant movements and suggested the inclusion of additional factors to improve predicted elephant locations. Future integration of spatially explicit space-use or mechanistic movement processes will provide more accurate projections of elephant population dynamics and will be important in determining the impacts of environmental change.

The IBM also excluded independent males. Male elephants are larger, tend to be less reliant on water and high quality vegetation (Stokke and du Toit, 2000, 2002), engage in 'risky' behaviours (Chiyo, Lee, *et al.*, 2011) and may be disproportionately targeted by poachers due to their larger tusks (Jones *et al.*, 2018). Males may therefore respond differently to environmental change and future inclusion of males in the model could prove enlightening.

If adding model complexities through spatially explicit ranging behaviour or inclusion of independent males, exploration of more efficient model calibration techniques may be worthwhile. Rejection-ABC was used here (van der Vaart *et al.*, 2015), but advances in ABC techniques, such as SMC-ABC (Sisson, Fan and Tanaka, 2007) and error-calibrated-ABC (van der Vaart, Prangle and Sibly, 2018), offer the ability to further reduce uncertainty in parameter values while requiring fewer model simulations.

The IBM in its current form has provided information of interest to stakeholders. However, stakeholders increasingly appreciate the availability of software and app-based tools for use in their work (Chapron, 2015). There is thus potential and demand to develop the IBM into a software application. This should be an interactive tool which allows the user to 'implement' potential scenarios of habitat conversion based on current discussions of land management, run the model and receive results quickly. Such a tool would be of great value to discussions and workshops, and may guide land management planning in the ecosystem.

6.4. Concluding remarks

With the current rate of global change threatening species persistence and ecosystem function, ecology and conservation must foresee arising challenges in order to move from reactive management strategies, where we begin 'on-the-back-foot', towards a more pre-emptive approach. The ability of traditional methods to remain robust under novel conditions and when considering multiple stressors in combination has long been questioned, resulting in calls for more process-based approaches. Research presented here has demonstrated the value of process-based models based on general principles and freely available data to answer real-world questions. This framework presents a useful toolkit for predictive modelling in ecology and conservation, and readily adaptable to address concerns facing other animal populations. Standardised climate scenarios make model predictions comparable to other climate impact studies, and standardised approaches to predicting other aspects of global change – such as habitat loss, species invasions and human behaviour change – would be of great value to practitioners. Focusing modelling efforts on the elephants of Amboseli has proved fruitful is establishing robust methods, but has also provided information to guide land management practises in the ecosystem. Further development of the IBM into an interactive tool for use by Amboseli's stakeholders will aid local communities in making evidence-based choices about land management and will confirm the role that human choices play in the conservation of Africa's elephants.

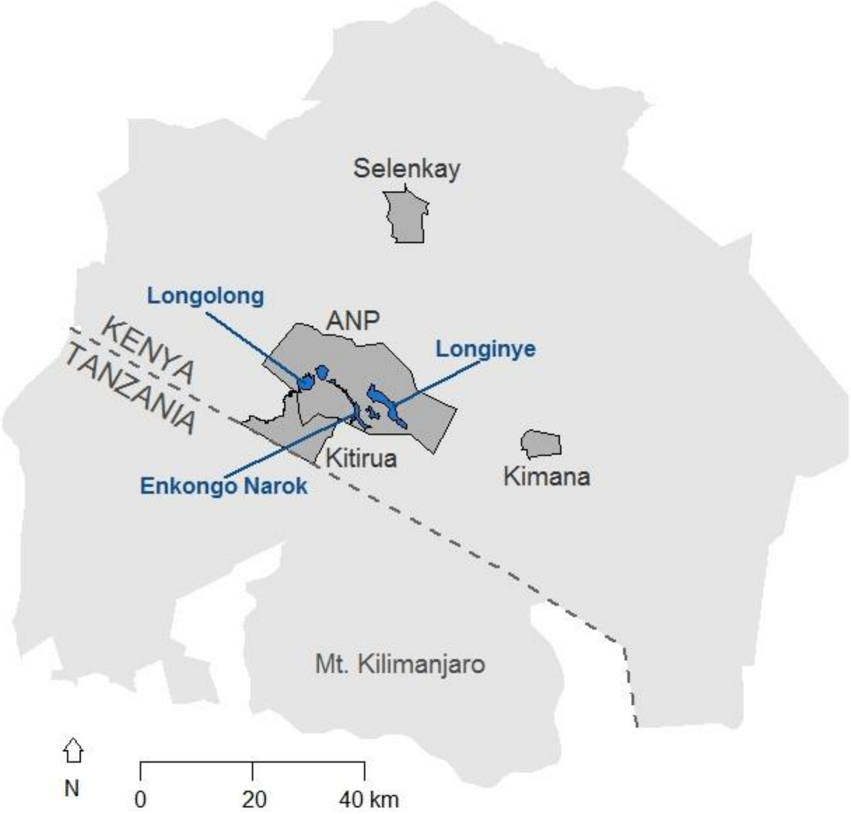
Appendices

A. Supplementary material for chapter 3

Figure A.1. Map of Amboseli ecosystem A) in context of Kenya (Amboseli ecosystem in pale red and Amboseli National Park, darker red) and B) showing spatial distribution of protected areas (dark grey polygons), swamps (in blue) and international border between Kenya and Tanzania (dashed line).

A)

B)



A.2 Extended remote sensing methodology.

The Terra-MODIS NDVI dataset was chosen for use in this manuscript for several reasons. Firstly, MODIS provides near-daily coverage of the entire Earth's surface and so presents a high temporal resolution which we deemed important for monitoring in real-time, changes in vegetation which may influence the movement choices made by elephants. The 250m spatial resolution of the MODIS NDVI dataset also provided sufficient spatial accuracy. The Terra-MODIS mission was chosen over the Aqua-MODIS mission (which provides the same dataset but is retrieved from a different satellite) because in a previous analysis by VLB not presented here, Terra-MODIS NDVI was found to relate more closely to ground-based measures on vegetative biomass in the Amboseli Ecosystem.

Terra-MODIS NDVI data were accessed via the Oak Ridge National Laboratory Web Service (Vannan *et al.*, 2011) and retrieved as 16-day composites (MOD13Q1). Composite images represented the 'best' daily image retrieved by the instrument within the given 16-day time period, taking into account quality, cloud and viewing geometry. Thus, a cloud-free, nadir view pixel with no residual atmospheric contamination, where available, represents the best image. NDVI pixels were further filtered using the MOD13Q1 QA flags so that only those marked as 'good' quality NDVI values were used in our calculations.

We retrieved NDVI values from across the Amboseli ecosystem every 16 days throughout the collaring period (July 2011 – August 2012) for location -2.651S, 37.359E and a spatial extent of 100km around this, meaning that each NDVI image covered just over 40,000km^2 and encompassed the entire extent of the Amboseli ecosystem.

From these NDVI images of the whole ecosystem, shapefiles of the swamp edge and dispersal areas (defined as the 95% kernel density estimates of elephant location fixes outside Amboseli National Park) were used to define the region within which to extract median NDVI values for each 16-day period. Occasionally due to cloud cover or QA filtering, no NDVI values were obtained for a given area. Where this was the case, missing daily NDVI values were filled with that of their nearest temporal neighbour. The script for this procedure is publicly available on GitHub (https://github.com/vlboult93/EleMovement.git).

B. Supplementary material for chapter 4: TRACE document

This is a TRACE document ("TRAnsparent and Comprehensive model Evaludation") which provides supporting evidence that our model presented in:

Boult, V.L., Quaife, T., Fishlock, V., Moss, C.J., Lee, P.C. & Sibly, R.M, 2018. Individual-based modelling of elephant population dynamics using remote sensing to estimate food availability. *Ecological Modelling*, 387, pp. 187-195.

was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

The rationale of this document follows:

Schmolke A, Thorbek P, DeAngelis DL, Grimm V. 2010. Ecological modelling supporting environmental decision making: a strategy for the future. *Trends in Ecology and Evolution* 25: 479-486.

and uses the updated standard terminology and document structure in:

Grimm V, Augusiak J, Focks A, Frank B, Gabsi F, Johnston ASA, Kułakowska K, Liu C, Martin BT, Meli M, Radchuk V, Schmolke A, Thorbek P, Railsback SF. 2014. Towards better modelling and decision support: documenting model development, testing, and analysis using TRACE. *Ecological Modelling*

and

Augusiak J, Van den Brink PJ, Grimm V. 2014. Merging validation and evaluation of ecological models to 'evaludation': a review of terminology and a practical approach. *Ecological Modelling*.

B.1. Problem formulation

This TRACE element provides supporting information on: The decision-making context in which the model will be used; the types of model clients or stakeholders addressed; a precise specification of the question(s) that should be answered with the model, including a specification of necessary model outputs; and a statement of the domain of applicability of the model, including the extent of acceptable extrapolations.

Summary:

- Elephant populations are threatened by poaching and human-elephant conflict, but environmental change affecting food available to elephants arguably presents a greater concern for their long-term persistence
- Understanding the relationship between food availability and elephant population dynamics is therefore vital
- The model presented here relates vital demographic rates to changes in food availability via an energy budget
- Application of the model will predict elephant populations respond to projected environmental change and will aid stakeholders in effectively managing elephant populations

Elephants are simultaneously considered a species of conservation concern and problem for coexisting humans (Hoare, 2000; Lee and Graham, 2006). The recent spike in elephant poaching fuelled by the ivory trade continues to threaten the persistence of elephant populations (Blanc, 2008; Chase *et al.*, 2016), whilst the rapid growth of the human population and associated conversion of elephant habitat to human dominated landscapes increases interactions between humans and elephants, where elephant behaviours (e.g. crop raiding and infrastructure damage) may compromise coexistence (Wittemyer, 2011; Browne-Nunez, Jacobson and Vaske, 2013).

Whilst poaching and human-elephant conflict (HEC) can alter elephant demographics (Jones *et al.*, 2018), elephant population dynamics are naturally governed by the distribution and abundance of their food (Rasmussen, Wittemyer and Douglas-Hamilton, 2006; Wittemyer, Rasmussen and Douglas-Hamilton, 2007). Changes in habitats and vegetation- and thus food available to elephants- owing to climate change and land management strategies, will have large scale implications for elephant populations, which may act to counter or add to the effects of poaching and HEC. Ensuring a future for elephants will therefore rely on understanding how elephant population dynamics respond to food availability.

The model presented here relates variation in food availability to changes in vital demographic rates through an energy budget. Food available to elephants is estimated using remotely sensed measures of vegetation. Energy is taken from the environment and allocated to the energy expending processes of life, allowing population dynamics and structure to emerge (Railsback and Grimm, 2012; Sibly *et al.*, 2013; Johnston *et al.*, 2014). This TRACE document provides details of model development and calibration.

The model is intended to accurately relate food availability to elephant population dynamics, and may be applied to predict the response of elephant populations to future environmental scenarios and allow stakeholders- including government officials who design policy regarding wildlife and natural resources, to reserve managers and charitable organisations who implement and fund management procedures- to effectively conserve and manage elephant populations.

B.2. Model description

This TRACE element provides supporting information on: The model. Provide a detailed written model description. For individual/agent-based and other simulation models, the ODD protocol is recommended as standard format. For complex submodels it should include concise explanations of the underlying rationale. Model users should learn what the model is, how it works, and what guided its design.

Summary:

Here we present the model description following the ODD (Overview, Design concepts and Details) protocol for describing Individual Based Models (IBMs; Grimm et al., 2006). The model is implemented in NetLogo 6.0.2 (Wilensky, 1999).

Purpose

The model relates spatiotemporal variation in food availability to changes in vital demographic rates through an energy budget and may be applied as a tool for predicting the response of elephant populations to future variation in food availability resulting from climate change or land management strategies.

State variables and scales

The modelled environment represents the combined home ranges of four elephant family groups (IBs, LBs, VAs, and WAs) inhabiting the Amboseli ecosystem, Kenya (Figure B.1), as a single patch, characterised by the time-specific food availability and energy content of vegetation. The elephant population comprises individuals of the four family groups: adult females and their immature offspring of both sexes (males become independent of their natal group at 12 years old). These four families comprised 126 individuals at the time of model initiation. Elephants are characterised by variables describing their physiology in terms of age, sex, mass, energetic processes and reproductive states (Table B.1). Each individual experiences life through their own energy budget, the details of which vary based on age and sex. The EEB runs from the 1st March 2000 until the 20th November 2016 (representing the availability of remote sensing data; see B.3) and proceeds in daily time steps.

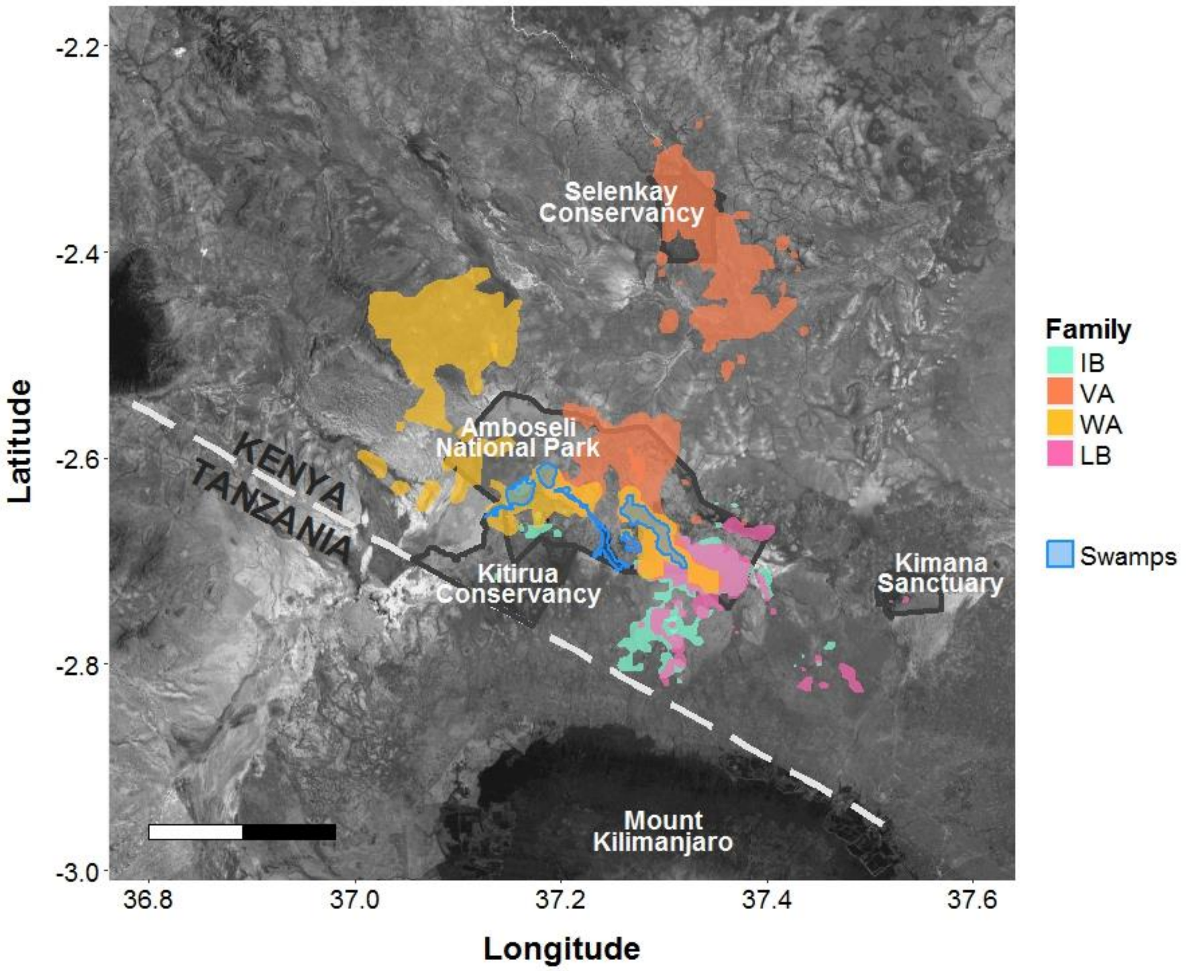


Figure B.1. The home ranges of four elephant family groups inhabiting the Amboseli ecosystem, Kenya (coloured polygons; 95% kernel density estimates; see B.4). This represents the spatial extent of the model and determines the remotely-sensed measures of vegetation used to calculate time-specific food availability (see B.3).

Table B.1. All elephants in the model are characterized by state variables describing their physiology in terms of age, sex, mass, energetic processes and reproductive states.

	Variable	Units	Description
All elephants	$age_{years} + age_{days}$	years + days	Age of individual in years and days
	BMR	KJ day^{-1}	Basal metabolic rate
	E_{assim}	KJ	Energy assimilated from food during the current time step
	E_{milk}	KJ day^{-1}	Energy ingested in milk
	E_{stor}	KJ	Energy available in storage tissues (fat)
	GR_{max}	kg day^{-1}	Maximum growth rate
	GR	kg day^{-1}	Growth rate
	IR	kg day^{-1}	Achieved ingestion rate
	IR_{max}	kg day^{-1}	Maximum ingestion rate
	$mort$	probability day^{-1}	Per capita mortality rate owing to stochastic events
	M_{core}	kg	Mass of core structural tissues (cannot be depleted for energy)
	M_{stor}	kg	Mass of storage tissues
	M_{struct}	kg	Mass of structural tissues
	M_{tot}	kg	Total mass of structural and storage tissues
	sex		Male or female
	$stor_{max}$	kg	Maximum mass of storage tissues
Female-only	E_{lact}	kJ day^{-1}	Energetic expenditure through lactation
	F_{GR}	kg day^{-1}	Foetal growth rate
	F_{mass}	kg	Mass of foetus
	L	true or false	Lactating?
	L_{count}	days	Days since parturition of calf
	O	true or false	Oestrus cycling?
	O_{count}	days	Days since individual last became receptive
	P	true or false	Pregnant?
	P_{count}	days	Days since conception

Process overview and scheduling

Elephants in the model execute procedures to update their energy budget once per time step (Figure B.2). The order of updating individuals is randomized by NetLogo at each time step. The energy budget model follows that described by Sibly *et al.* (2013).

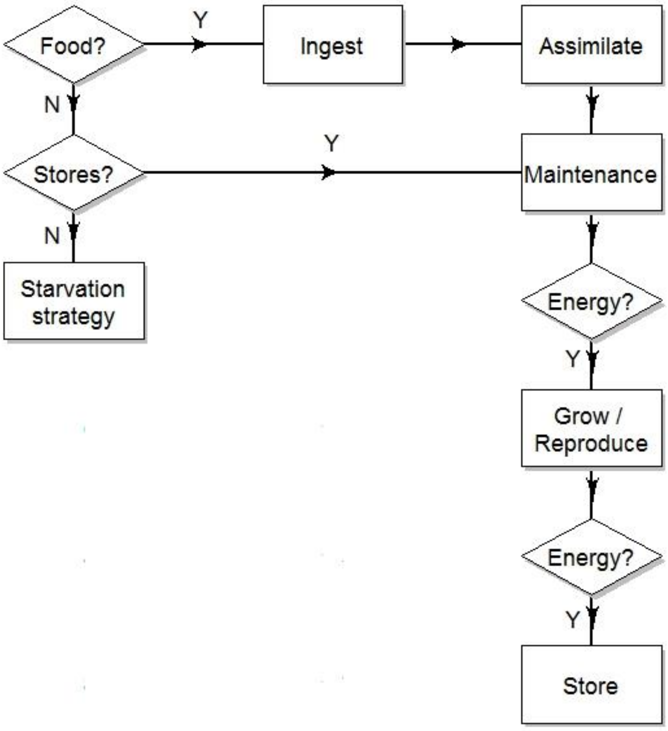


Figure B.2. Daily energy budget process overview carried out by each individual at each time step. If energy is available through food and/or stores, an individual will utilise this energy in maintenance, growth and reproduction. If insufficient energy remains an individual enters starvation during which time some non-essential structural tissues may be metabolised to cover the costs of maintenance only. If this also proves insufficient, the individual dies. This energy budget causes births and deaths, and will ultimately lead to the emergence of population dynamics.

Each individual begins with the intake of energy if it is available in the environment. The assimilated energy, along with energy in storage tissues (fat), make up the energy ‘reserves’, and are then available for use in energy expending processes. Maintenance takes priority and is followed by growth and/or reproduction depending on age, sex and energy remaining. Following maintenance, if energy reserves remain, sexually immature individuals (females <9 years old and males <19) will grow. Growth in elephants is prolonged (Karkach, 2006; Shrader *et al.*, 2006; Hollister-Smith *et al.*, 2007), so growth in some skeletal and mass components continues beyond sexual maturity if sufficient energy reserves remain following the costs of reproduction. Only females reproduce in the model as males disperse prior to sexual maturity. If energy remains following maintenance, sexually mature females proceed through the reproductive cycle. Left over energy is incorporated into the individual’s stores at the end of each time step. Assimilated energy is always utilised first and stored energy only if needed. If no energy reserves remain, the individual enters starvation and will cease growth and reproduction, but may metabolise some structural tissues to cover the costs of maintenance (Atkinson, Nelson and Ramsay, 1996). Individuals die at a background rate (accounting for stochastic mortality events) or if all non-essential structural tissues are depleted.

The energy budget of an individual therefore responds to the energy available from food in the environment. When food is abundant, such as in wet seasons, energy intake exceeds energy expenditure, and individuals may allocate energy maximally to all processes and accumulate stores. When food is limited, such as in dry seasons or drought years, energy expenditure may outweigh energy intake, and individuals must utilise stores in order to maintain growth and reproduction. Thus, as food availability cycles through abundance and limitation, an individual’s energy balance fluctuates between positive and negative, and body composition (see B.4) responds accordingly (Figure B.3).

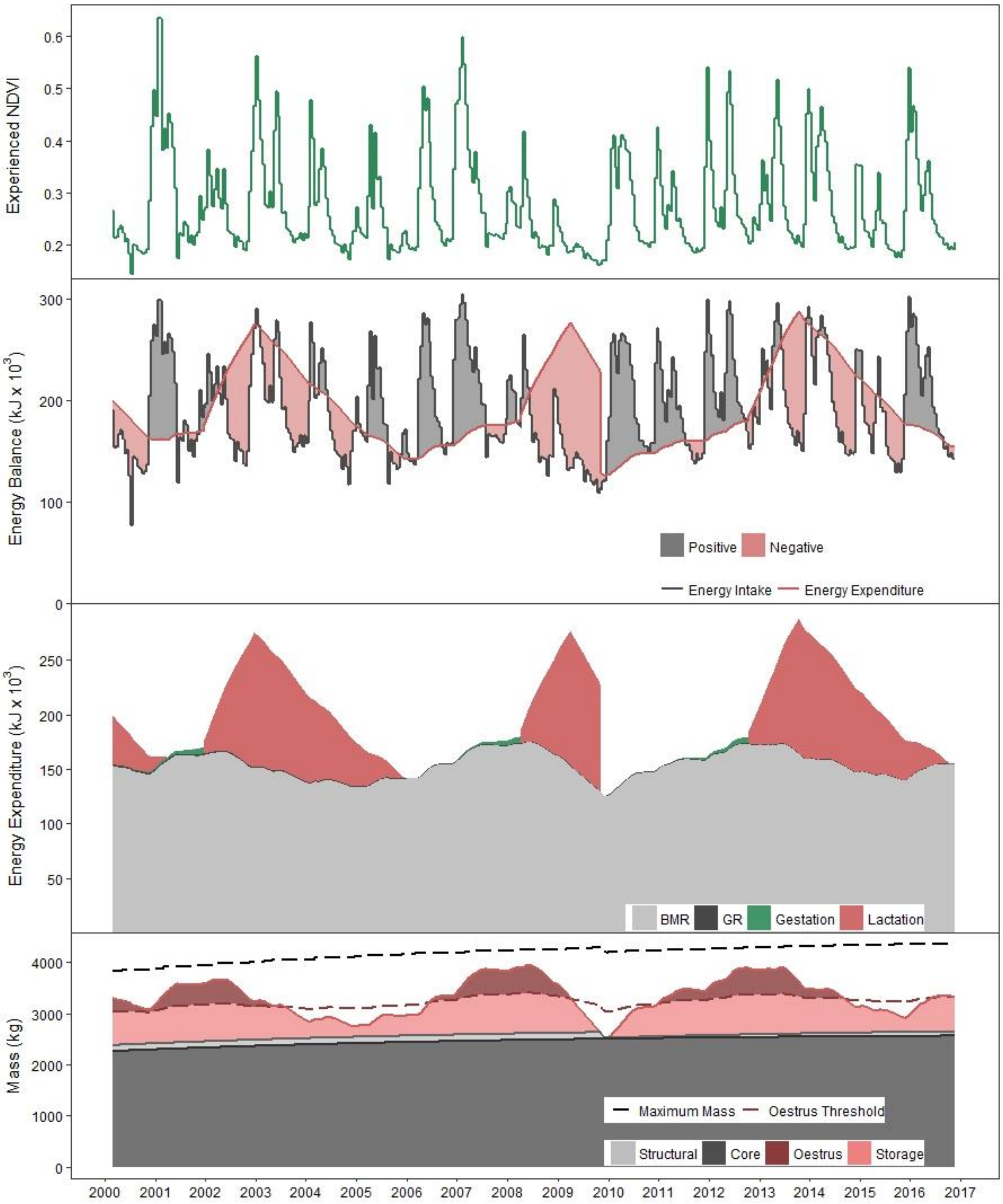


Figure B.3. Energy balance and resulting body composition of adult female elephant, Ilka, throughout the model period. The top plot shows the NDVI (Normalised Difference Vegetation Index) experienced by Ilka. NDVI is used here as a proxy for food availability (see B.3), peaking during the biannual wet seasons and declining as the dry seasons progress. The energy balance plot compares energy expenditure with energy assimilated (red and grey lines, respectively). The resulting energy balance indicates whether energy intake was greater or less than energy expenditure (grey and red shading, respectively), and broadly coincides with peaks and troughs in NDVI. The energy expenditure plot further breaks down expenditure into BMR, gestation, growth and lactation. Lactation is energetically costly and results in a period of net negative energy balance. Due to the fluctuating energy balance, body composition changes: during positive balance storage tissues increase, whilst these stores are depleted during times of negative balance. Structural tissues may be depleted during starvation, as seen here in 2009-2010.

Design concepts

Emergence: The key outputs of the model are births and deaths, which together with population size emerge from the ability of individuals to meet their energetic demands given the food available and background mortality.

Fitness: Individuals always intake the maximum possible amount of energy and distribute maximally to all energy expending processes in order of priority. By this means, individuals maximise survival and reproduction.

Sensing: To link the energy budgets of mothers and suckling calves (those under 4 years old), mothers and calves can detect the deaths of one another so that the death of the mother will result in the death of a milk-dependent calf (those under 2 years old) and the death of a calf will cause the mother to cease lactation.

Interaction: Mothers and suckling calves interact to link the energy budget and fate of the calf to that of the mother.

Stochasticity: Stochasticity is introduced into the model in three ways. Firstly, individuals are initialised with a random amount of storage tissue within the bounds of maximum storage (see B.4) following a uniform distribution, since data measuring storage tissues are lacking. Second, the sex of a new born calf is determined at random with equal chances of becoming a male or female. This influences the outcome of the model since females contribute more to population growth than males. Background mortality from stochastic events such as disease, predation, poaching or human-elephant conflict, occurs randomly (see Equation B.5 and Figure B.6).

Observation: Key outputs from the model are annual numbers of births and deaths, and overall population size. These are used as summary statistics in the calibration of the model (see B.6). Outputs are extracted annually to coincide with the end of each Amboseli year. Amboseli years run from the 1st October (Julian day 274) until 30th September (Julian day 273) the following year and relates to annual cycles of rainfall and vegetation in the Amboseli ecosystem (Croze and Lindsay, 2011).

Initialisation

The model is initiated with 126 individuals comprising the four family groups (IBs, LBs, VAs, and WAs) on 1st March 2000. The reproductive states of females at this time were derived from birth dates of their previous and subsequent calves (see B.3) and used to link mothers to the relevant calves and determine reproductive energy expenditure. The environment is initiated with time-specific food availability derived from remotely-sensed measures of vegetation (see B.3).

Input

Time-specific food availability is derived from remotely-sensed measures of vegetation (see B.3).

Submodels

The following submodels describe in detail the processes carried out at each time step. Parameter definitions and values used in submodels are presented in Table B.2.

Table B.2. Parameter definitions and values. Parameters were derived initially from the literature (see B.3). Uncertain parameters were then calibrated using approximate Bayesian computation (see B.6; indicated by *).

Parameter	Definition	Value	Eqn	Source
Body composition				
$stor_{scaling}$	Storage scaling coefficient = coefficient for scaling storage tissue maximum with total mass	0.08*	7	Reference value 0.06 (Pitts and Bullard, 1968)
core_prop	Core proportion = core structural mass as proportion of structural mass; cannot be depleted to cover costs of energy expenditure	0.951		(Atkinson, Nelson and Ramsay, 1996)
E_{flesh}	Energy content of flesh = energy in structural tissues	7000 KJ kg^{-1}	3b	(Sibly and Calow, 1986a)
E_{fat}	Energy content of fat = energy in storage tissues	39300 KJ kg^{-1}		(Schmidt-Nielsen, 1997)
E_{syn}	Energetic costs of synthesis = energetic cost of producing structural tissues	7000 KJ kg^{-1}	3b	(Sibly and Calow, 1986a)
Energy intake				
Hsc	Half saturation coefficient = food density at which half maximum ingestion rate is achieved	0.317 kg m^{-2}*	1b	Reference value 0.21 kg m^{-2} (Lindsay, 1994)
$maxIR_{scaling}$	Max IR scaling coefficient = coefficient for scaling maximum ingestion rate with body mass	0.334*	1a	Reference value 0.255 (Lindsay, 1994)
AE_{veg}	Assimilation efficiency of vegetation = proportion of ingested vegetation that is assimilated as energy	0.2*		Reference value 0.27 (Wiegert and Evans, 1967; Rees, 1982)
AE_{milk}	Assimilation efficiency of milk = conversion efficiency from mother's energy reserves to calf assimilated energy	0.95*		Reference value 0.84 (Agricultural Research Council, 1980)
DD	Density dependence coefficient = coefficient to adjust ingestion rate depending on density of elephants	710131*	1b	
Maintenance				
B_0	Taxon-specific normalisation constant = constant used to scale BMR with body size	351*	2	Reference value 293 (Peters, 1983)
Growth				
GRm *GRf*	Growth constants (male/female) = constant used to calculate the maximum daily addition of mass	0.07134 0.12763	3a	(Lee and Moss, 1995)
M_0_m M_0_f	Birth mass (male/female) = average mass at birth	120 kg 100kg		(Lee, 2011)

M_{∞}_m	Maximum structural mass (male/female) = average asymptotic mass of Amboseli elephants	4690 kg	3a	(Lee, 2011)
M_{∞}_f		2740 kg		
Reproduction				
o_cycle	Oestrus cycle = length of single oestrus cycle	112 days		(Moss, 1983)
r_days	Receptive days = length of time receptive during single oestrus cycle	4 days		(Moss, 1983)
oest_on	Oestrogen onset threshold = body fat threshold at which female may enter oestrus	0.2		(Bronson and Manning, 1991)
gest_period	Gestation period = length of pregnancy	661 days		(Poole *et al.*, 2011)
Fg	Foetal growth constant = daily addition of mass to growing foetus	0.0069	4a	(See B.3; Lee pers. comm.)
E_0	Energetic demand of lactation on day 0 = energy required to cover lactation on first day following parturition	11008 KJ day^{-1}*		Reference value 11886 KJ day^{-1} (see B.3)
E_pl	Energetic demand of peak lactation = energy required to cover lactation at peak (365 days following parturition)	123253 KJ day^{-1}*		Reference value 112170 KJ day^{-1} (see B.3; Oftedal 1985)
Mortality				
MR_{back}	Background mortality rate = daily rate of mortality owing to stochastic events (e.g. disease, injury, poaching etc.)	2.8×10^{-5} day^{-1}*	5	Reference value 2.74×10^{-5} (see B.3*;* Lee *et al.* 2011)
$MR_{scaling}$	Mortality rate coefficient = coefficient for relating mortality rate to body condition during starvation	8375*	5	Reference value 15000 (see B.3)
Biomass				
Multiple	NDVI conversion multiple = multiple used in equation to convert NDVI to biomass	2665.7	6	See B.3
Intercept	NDVI conversion intercept = intercept of straight line relationship between NDVI and biomass	-269.9	6	See B.3
Area	Total area of spatial extent = area represented by model	637142163 m^2		See B.4

Energy intake: Ingestion rate (IR; kg day-1) depends on body size (Brown *et al.* 2004), age, food density (biomass) and consumer (elephant) density. In terms of age, elephants less than a year old obtain all energy through the ingestion of milk; individuals are milk-dependent until two years of age but begin supplementing milk intake with vegetation after a year; between the ages of one and four, decreasing milk ingestion is supplemented with increasing vegetation intake; at four elephants are weaned and feed entirely on vegetation. Suckling individuals first ingest milk from their mother then if over a year old, will ingest vegetation. The maximum vegetation IR is reduced by the rate of ingestion already achieved through suckling. Food density (kg m^{-2}) also influences vegetation ingestion, following a Holling type II functional response (Holling 1959; Lindsay 1994). This is adjusted as per the Beddington-DeAngelis functional response to account for consumer-density dependent ingestion rate (Beddington, 1975; DeAngelis, Goldstein and O'Neill, 1975). If no food is available, IR is zero. IR is converted to energy given the energy content of food (KJ kg^{-1}). Only a proportion of energy ingested in milk or vegetation is available for energy expending processes following assimilation efficiencies (AE_{veg}, AE_{milk}).

Equation B.1a.

$$IR_{max} = \mathrm{maxIR}_{scaling}\ M_{struct}{}^{3/4}$$

where $\mathrm{maxIR}_{scaling}$ = scaling coefficient (see B.3)

M_{struct} = structural mass (kg)

Equation B.1b.

$$IR = IR_{max} \times \frac{biomass}{biomass + (hsc * p) + (DD * pop)}$$

where IR_{max} = maximum ingestion rate (kg)

$biomass$ = biomass (kg patch^{-1})

hsc = half saturation coefficient (kg m^{-2}; see B.3)

p = total area of represented in model (m^2; see B.4)

DD = coefficient of density dependence (see B.3)

pop = total number of individuals in the model

Maintenance: Basal metabolic rate (*BMR*; KJ day^{-1}) accounts for the standard costs of maintenance essential for survival, and so has first call on energy reserves (Sibly *et al.*, 2013). BMR scales with body mass according to Equation B.2 (note that for homeotherms, the Arrhenius term presented as part of this equation in Sibly *et al.* (2013) is unnecessary since body temperature is constant and its value can be subsumed into the normalisation constant; Gillooly *et al.* 2001; Brown *et al.* 2004).

Equation B.2.

$$BMR = B_0 M_{tot}{}^{3/4}$$

where B_0 = taxon-specific normalization constant (see B.3)

M_{tot}= total mass (kg)

If sufficient energy is assimilated (E_{assim}; KJ) through ingestion, this energy reserve is depleted to cover the costs of BMR. If insufficient, energy stores (E_{stor}; KJ) may be utilised to cover the additional costs. If both energy reserves (E_{assim} + E_{stor}) are exhausted, the individual is considered to be in starvation. During starvation, non-essential structural tissues (M_{struct}; kg; corresponding to muscle depletion during starvation) may be metabolised to cover the costs of maintenance only until a point at which the individual dies (M_{core}). Metabolising these tissues requires energetic expenditure in itself (Sibly *et al.*, 2013) so the total required energy is twice BMR.

Growth: Following maintenance, if energy reserves (E_{assim} + E_{stor}) remain, sexually immature individuals (females under nine years of age and males under 19) grow. Growth in male and female elephants is prolonged (Karkach, 2006; Shrader *et al.*, 2006; Hollister-Smith *et al.*, 2007), so growth continues beyond sexual maturity, but only if sufficient energy remains following the reproduction.

Both male and female elephants follow the von Bertalanffy growth curve (Lindeque and van Jaarsveld, 1993) but have different growth constants, birth and maximal masses (see B.3; Lee & Moss 1995). Daily maximal growth rates (*maxGR*; kg day^{-1}) are calculated using Equation B.3a (Sibly *et al.*, 2013) and depend on current structural mass.

Equation B.3a.

$$maxGR = \frac{3GR}{365} \times \left(M_{\infty}^{\frac{1}{3}} M_{struct}^{\frac{2}{3}} - M_{struct} \right)$$

where M_{struct} = structural mass at time t (kg)

M_{∞} = maximum structural mass (kg)

GR = von Bertalanffy growth constant (kg day^{-1}; see B.3)

The energy needed to fuel maximum growth (E_{GR}; KJ day^{-1}) is calculated as per Equation B.3b. If insufficient energy is available to cover maximum growth, growth continues at a suboptimal level. Any growth achieved is added to structural mass (M_{struct}; kg).

Equation B.3b.

$$E_{GR} = maxGR \times (E_{flesh} + E_{syn})$$

where $maxGR$ = maximum growth rate (kg)

E_{flesh} = energy content of structural tissue (KJ kg^{-1})

E_{syn} = energy costs of synthesis (KJ kg^{-1})

Reproduction: Only females reach sexual maturity in the model as males disperse beforehand (at age 12). Following maintenance, if energy reserves (E_{assim} + E_{stor}) remain, sexually mature females (those nine years or older) will assign energy to reproductive processes.

The reproductive cycle comprises several components: oestrus cycling, conception, gestation, parturition and lactation (Figure B.4). The full oestrus cycle of a female elephant lasts 112 days (about 16 weeks; Wasser et al., 1996), during which females are only receptive for about four days at the beginning of each cycle (Hildebrandt *et al.*, 2011). A female may only cycle through oestrus if she is not currently pregnant or lactating to a milk-dependent calf (under 2 two years old), and has sufficient energy stores (E_{stor}) to pass a proportional threshold ($oest_{on}$) and enter oestrus (Bronson and Manning, 1991; Wittemyer, Rasmussen and Douglas-Hamilton, 2007). If these conditions are met, the female will enter oestrus and conceive.

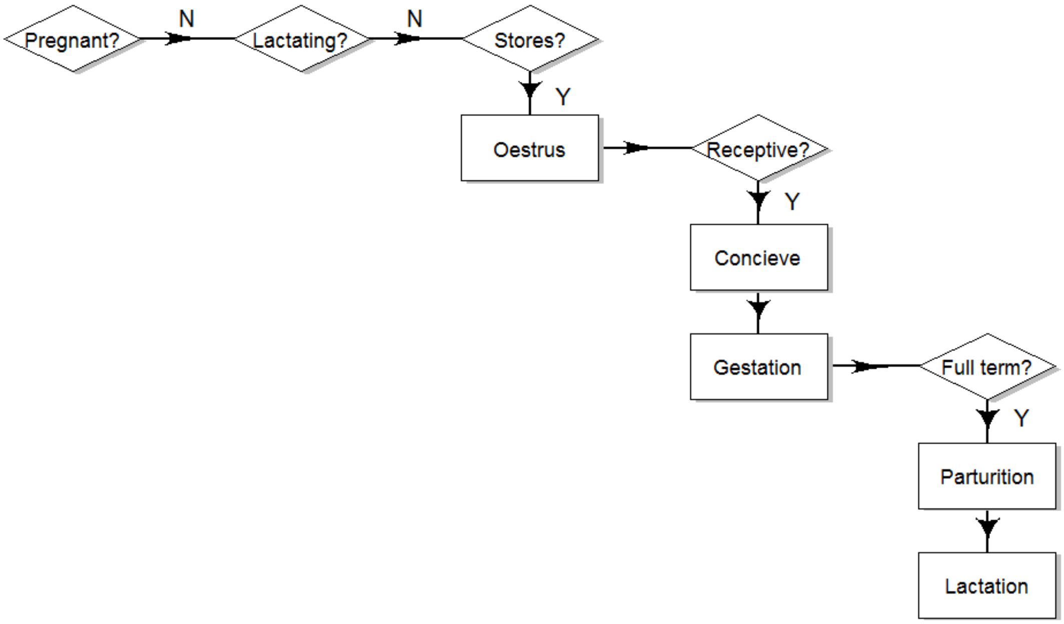


Figure B.4. Summary of female reproductive cycle (key: diamonds = conditions, rectangles = processes, Y = yes, N = no).

Gestation in elephants lasts 661 days (Poole *et al.*, 2011) during which time, a female must commit energy to the growth of the foetus. Foetal growth is described by Equation B.4a so that daily addition of foetal mass (fGR; kg day^{-1}) can be calculated using Equation B.4b.

Equation B.4a.

$$Fmass = (fg\ P_{count})^3$$

where $Fmass$ = mass of foetus at time t (kg)

fg = foetal growth constant (see B.3)

P_{count} = age of foetus (days since conception)

Equation B.4b.

$$fGR = 3fg^3 \times \left(\frac{Fmass^{\frac{1}{3}}}{fg}\right)^2$$

where fGR = foetal growth rate (kg day^{-1})

fg = foetal growth constant (see B.3)

$Fmass$ = mass of foetus (kg)

If energy reserves ($E_{assim} + E_{stor}$) are insufficient to cover the costs of maximal foetal growth, the mother miscarries and is no longer pregnant. If growth is sufficient and the full term of the pregnancy is reached, parturition occurs. Mother and calf are linked at this point to allow the energy budget of the mother to relate to that of her calf. The mother is no longer pregnant, but commences lactation.

The sex of the calf is determined at random with equal probability of becoming a female or male (Amboseli population as of May 2018: 1328 F: 1320 M). The initial parameters of the calf are set: age is set to zero; all energetic rates are calculated accordingly; in females all reproductive variables are set to false (oestrus, pregnant, lactating in females) and reproductive counts to zero; structural mass (M_{struct}; kg) is set as birth mass (M_0; kg) for males and females accordingly, whilst energetic reserves (E_{assim} + E_{stor}) are set to zero.

Lactation continues until the calf is weaned at four years old (1460 days), but the amount of energy required for lactation varies throughout this period (Oftedal 1985; Figure B.5). Before the calf reaches a year old, milk forms the sole energy intake and so the energy provided by lactation must fully cover the costs of maintenance and growth. If the mother dies in this phase, so does the calf. Lactation peaks (E_{PL}) when the calf is a year old. Between a year and two years of age, the calf remains milk-dependent, and dies if its mother does, but the amount of milk supplied by the mother decreases at a constant rate daily as the calf begins to supplement this diet with vegetation. From two to four years of age, the calf is no longer dependent on milk, and could survive without its mother, but will continue to suckle at a decreasing rate. As the mother supplies less milk, the calf begins to increase its intake of vegetation to cover the costs of energy expenditure.

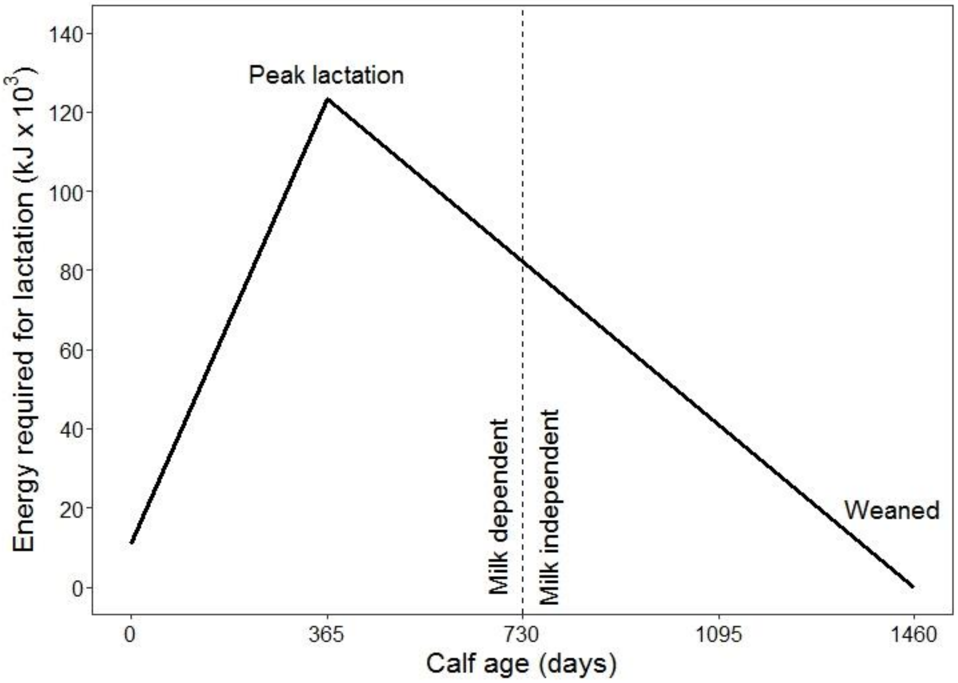


Figure B.5. The energetic costs of lactation for elephant mothers match the increasing needs of the growing calf until it reaches a year of age. Thereafter the amount of milk produced reduces until the calf is weaned at four years old. For the first two years of life, the calf is dependent on its mother's milk and thus dies if its mother dies.

If the mother has sufficient energy reserves (E_{assim} + E_{stor}) available, she produces the maximum amount of milk given the age of the calf. If not, the mother will provide as much milk as her reserves (E_{stor}) allow. Calves over a year of age may be able to make up for this deficit by consuming more vegetation. If a calf dies, the mother stops lactating.

Energy reserves: If assimilated energy (E_{assim}; KJ) remains following all energy expending processes (maintenance, growth and reproduction), this is converted and stored as fat (M_{stor}; kg) and thus added to energy stores (E_{stor}; KJ) up until a maximum is reached ($stor_{max}$; kg).

Mortality: Mortality in the model happens for several reasons. Firstly, if the energetic costs of maintenance cannot be met by energy reserves nor structural tissues, the individual has utilised all possible energy and starves to death. Second, if the mother of a milk-dependent calf dies, the calf too dies as it is unable to survive without its mother's milk. Third, background mortality is included to account for deaths arising from stochastic events such as poaching, predation, disease or injury. When energy stores remain, background mortality is set at a constant rate for all individuals (MR_{back}). However, this rate increases during starvation (when $E_{stor} = 0$) to account for the increased susceptibility of starving individuals to disease and risk-taking behaviour (Equation B.5; Figure B.6; Foley et al., 2001).

Equation B.5.

$$mort = MR_{back} - \frac{1}{MR} \times \ln \frac{M_{struct}}{M_{opt}}$$

where MR_{back} = background mortality rate (day^{-1}; see B.3)

MR = scaling coefficient (see B.3)

M_{struct} = structural mass (kg)

M_{opt} = optimum structural mass for age (kg; Equation B.3a)

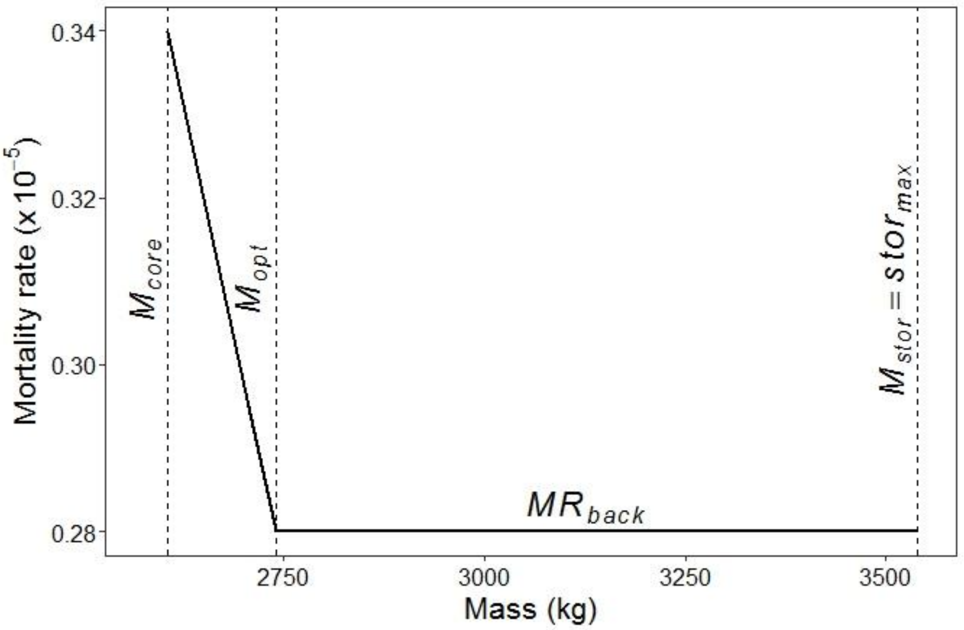


Figure B.6. Condition dependent stochastic mortality. When storage tissues remain (stores > 0), daily probability of mortality due to stochastic events occurs at a background rate (MR_{back}). When all storage tissues are depleted, and an individual enters starvation, mortality rate increases to simulate the increasing susceptibility to disease and more risky behaviours causing death.

Ageing: The age of individuals in days and years is monitored and updated at the end of each time step.

B.3. Data evaluation

This TRACE element provides supporting information on: The quality and sources of numerical and qualitative data used to parameterize the model, both directly and inversely via calibration, and of the observed patterns that were used to design the overall model structure. This critical evaluation will allow model users to assess the scope and the uncertainty of the data and knowledge on which the model is based.

Summary:

Empirical data were utilised in design, implementation, calibration and validation of the EEB as follows:

- Remotely-sensed measures of vegetation and ground-based measures of biomass were used to estimate the temporal and spatial dynamics of food availability
- Longitudinal demographic data collected by the Amboseli Elephant Research Project provide a record of the initial model population and both calibration and validation population dynamics data
- Prior parameterisation was achieved via literature searches for model parameters

Estimating Food Availability

Elephants are generalist herbivores, meaning almost all standing plant biomass could be considered food (Lindsay, 2011). Mapping the food available to an elephant therefore requires quantification of all plant biomass over the spatial and temporal scales at which an elephant lives. Since a single elephant may range over hundreds of kilometres (Viljoen, 1989; Thouless, 1996; Leggett, 2006; Wall *et al.*, 2013) and live for 70 years (Moss, Croze and Lee, 2011a), this presents an infeasible task for traditional ecological methods (Kerr and Ostrovsky, 2003; Pfeifer *et al.*, 2012). Remote sensing presents a relatively hands-free-low-effort (Nilsen, Herfindal and Linnell, 2005) means of collecting such data whilst remaining powerful across space and time (Le Roux *et al.*, 1997; Kerr and Ostrovsky, 2003; Nilsen, Herfindal and Linnell, 2005; Willems, Barton and Hill, 2009).

We obtained remotely sensed measures of vegetation from the NASA Terra-MODIS (Moderate Resolution Imaging Spectroradiometer) mission. Specifically, we used 16-day composite values of the Normalised Difference Vegetation Index (NDVI; MOD13Q1 product; Didan, 2015) to infer time-specific values of vegetation quantity, accessed via the Oak Ridge National Laboratory web service (Vannan *et al.*, 2011). Data were filtered using the MOD13Q1 QA flags so that only 'good' quality NDVI observations were considered in our calculations.

NDVI values were calibrated using on-the-ground measures of herb-layer biomass, collected biannually in the Amboseli National Park since 1982 (Lindsay, 2011). All methods for measuring biomass were designed by W.K.Lindsay and are documented in detail in Lindsay 1982 and 1994. Herb-layer biomass alone was considered a suitable measure of food available to elephants as the Amboseli ecosystem has low tree cover and Amboseli elephants are predominantly grazers. Given the dates and location of on-the-ground biomass measures (kg m^{-2}), the corresponding NDVI value was determined and compared. Locations with high levels of canopy cover were removed from the analysis to ensure NDVI was responding to the herb-layer alone. The resulting relationship is described by Equation B.6 and Figure B.7.

Equation B.6.

$$Biomass = \frac{(2666 \times NDVI - 270)}{1000} \times p$$

where $NDVI$ = time and location specific NDVI value

p = total area represented by model (m^2)

Following the calibration of NDVI, we constructed a time-series of NDVI to infer spatiotemporally specific food availability from March 1st 2000 to November 20th 2016. For each 16-day composite NDVI image, we extracted all NDVI pixel values falling within the model environment (combined home ranges of four elephant family groups; see B.4) and calculated a single median NDVI value. Thus, time-specific NDVI values are loaded into the model every 16 ticks (using NetLogo's 'csv' extension; Wilensky 1999) and converted to biomass using equation B.6.

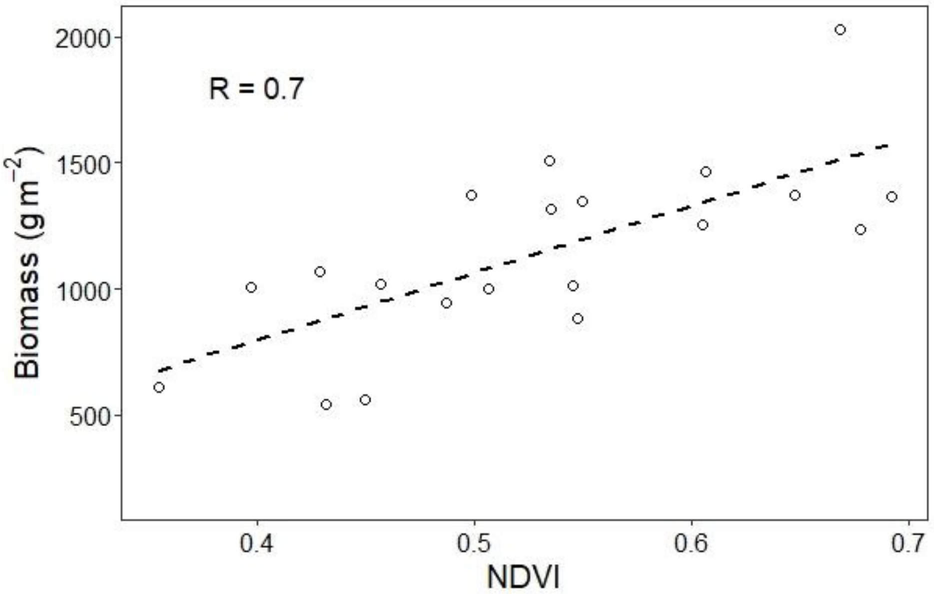


Figure B.7. Relationship between NDVI and on-the-ground measures of herb-layer-biomass in the Amboseli National Park, 2000-2016.

Elephant Population Data

The Amboseli Elephant Research Project (AERP) has monitored more than 3,300 individually-known elephants from over 60 family groups in the Amboseli ecosystem since 1972. Elephants are identified by means of a photo recognition file illustrating unique identifying features; calves are identified through association with their known mothers (Moss, Croze and Lee, 2011b). Censuses are attempted on a monthly basis for all family groups noting individuals present and those missing. By tracking individuals in this manner throughout their lives, birth and death dates are recorded.

Births: New-born and young calves are aged based on body size and proportions, skin colouration, motor coordination, and behaviour of both mother and calf (Moss, 1988). Since 1978, when the last family unit was identified, age estimates are within 1 month for 82.5% of births and within 6 months for 15.1% (n = 2601). The age of individuals born prior to start of the study was estimated using techniques including hind foot length (Western, Moss and Georgiadis, 1983; Lee and Moss, 1986, 1995), tooth eruption and wear (Laws, 1966), tusk length (Moss, 1988, 1996) and circumference at the lip (Pilgram and Western, 1986), and shoulder height and back length (Croze, 1972; Laws, Parker and Johnstone, 1975; Lee and Moss, 1995; Moss, 1996; Shrader *et al.*, 2006; Trimble *et al.*, 2011). Age was backdated to give an estimate of birth date for all individuals and has been validated by collection of lower jaws post-mortem whenever possible (Lee *et al.*, 2012).

Deaths: Determining date of death for individual elephants has proven more difficult. In family groups, if an adult female was absent but her youngest calves present, the family was monitored closely. If her absence was prolonged for more than a week, while the rest of the family were sighted with her youngest offspring, she was assumed dead. For calves under three years old, absence whilst their mother was present suggested the calf had died. If a juvenile female or an adult female with her calves was missing, these individuals were assumed dead if not sighted for a month with their family. Once it was concluded an individual had died, the death date was recorded as the midpoint between when the individual was last seen alive and when they were first noted as missing. Rarely (<5% of records), mortalities were more directly monitored due to illness or injury, or when carcasses were found and identified. For the purposes of model analysis, we defined 'calf' mortality as deaths occurring in individuals less than two years of age and 'adult and juvenile' mortality as deaths occurring in individuals two years or older. This reflects the differing energetic thresholds controlling mortality in these groups: calf mortality occurs when mothers' stores (fat) reaches zero; adult and juvenile mortality occurs beyond this point, when all non-essential structural tissues (muscles) have also been depleted.

For the purposes of model development and calibration, we modelled the population dynamics of four family groups (IBs, LBs, VAs and WAs). These families were chosen due to regular monitoring providing good confidence in birth and death dates, and good understanding of movement patterns owing to GPS collars fitted to females in these families (Boult, Sibly, *et al.*, 2018).

Individuals alive on March 1st 2000 were included in model initiation (n = 126; Table B.3). Age and sex were assigned, along with reproductive status of females. Reproductive status was determined given birth dates of previous and subsequent calves for each female, a gestation period of 661 days (Poole *et al.*, 2011) and a lactation period of four years.

Table B.3. The initial population on 1st March 2000 was derived from longitudinal demographic data collected by the AERP. The population consists of members of the IB, LB, VA and WA families.

Name	*Family*	*Mother*	*Age (years)*	*Age (days)*	*Sex*	*Pregnant*	*p_count*	*Lactating*	*l_count*
ION	IB	?	30	60	Female	FALSE	0	TRUE	121
ILK	IB	INE	21	0	Female	FALSE	0	TRUE	1065
ISO	IB	ISI	20	120	Female	FALSE	0	TRUE	335
IDA	IB	ING	16	330	Female	FALSE	0	TRUE	121
ILE	IB	IVY	15	30	Female	TRUE	274	FALSE	0
ISB	IB	ISI	10	60	Female	FALSE	0	FALSE	0
IPI	IB	ILK	7	0	Female	FALSE	0	FALSE	0
IVA	IB	ISI	5	90	Female	FALSE	0	FALSE	0
IDO	IB	IVY	5	60	Female	FALSE	0	FALSE	0
IDG	IB	ING	4	0	Female	FALSE	0	FALSE	0
IDY	IB	ING	0	60	Female	FALSE	0	FALSE	0
ILD	IB	ION	0	90	Female	FALSE	0	FALSE	0
INE	IB	?	51	60	Female	FALSE	0	TRUE	609
ISO99	IB	ISO	0	330	Female	FALSE	0	FALSE	0
INE8	IB	INE	1	240	Female	FALSE	0	FALSE	0

ISL9	IB	ISL	1	0	Female	FALSE	0	FALSE	0
IDA9	IB	IDA	0	90	Female	FALSE	0	FALSE	0
ISI	IB	?	64	60	Female	FALSE	0	TRUE	91
ING	IB	?	37	60	Female	FALSE	0	TRUE	91
IOL	IB	?	32	60	Female	FALSE	0	TRUE	91
IDH	IB	ILK	2	330	Female	FALSE	0	FALSE	0
ISL	IB	ING	13	0	Female	TRUE	182	TRUE	366
IVY	IB	?	28	60	Female	FALSE	0	TRUE	366
IVY99	IB	IVY	1	0	Female	FALSE	0	FALSE	0
494	IB	ION	10	60	Male	NA	NA	NA	NA
492	IB	IVY	10	0	Male	NA	NA	NA	NA
514	IB	ING	8	90	Male	NA	NA	NA	NA
556	IB	INE	5	90	Male	NA	NA	NA	NA
557	IB	IOL	5	90	Male	NA	NA	NA	NA
676	IB	IOL	0	60	Male	NA	NA	NA	NA
675	IB	ISI	0	60	Male	NA	NA	NA	NA
493	IB	INE	9	90	Male	NA	NA	NA	NA
591	IB	ION	5	0	Male	NA	NA	NA	NA
544	IB	ISO	6	120	Male	NA	NA	NA	NA
590	IB	IDA	4	180	Male	NA	NA	NA	NA
LAM	LB	LUC	13	0	Female	FALSE	0	TRUE	0
LET	LB	?	60	60	Female	FALSE	0	FALSE	0
LEL	LB	LAN	15	30	Female	FALSE	0	TRUE	121
LATA	LB	LAN	9	120	Female	FALSE	0	FALSE	0
LTP	LB	LAN	0	30	Female	FALSE	0	FALSE	0
LUC	LB	?	37	60	Female	FALSE	0	TRUE	366
LEA	LB	?	35	60	Female	FALSE	0	TRUE	274
LOI	LB	LEA	20	150	Female	FALSE	0	TRUE	121
LEH	LB	LEA	16	300	Female	TRUE	609	TRUE	1308
LIT	LB	LEA	5	90	Female	FALSE	0	FALSE	0
LAN	LB	LET	31	60	Female	FALSE	0	TRUE	60
LTH	LB	LOB	0	0	Female	FALSE	0	FALSE	0
LTA	LB	LOI	8	120	Female	FALSE	0	FALSE	0
LEN	LB	LOI	4	0	Female	FALSE	0	FALSE	0
LAC	LB	LOI	0	90	Female	FALSE	0	FALSE	0
LOT	LB	LEA	13	60	Female	FALSE	0	FALSE	0
LOB	LB	LUC	20	30	Female	FALSE	0	TRUE	0
LOR	LB	LET	19	60	Female	TRUE	335	FALSE	0
LLY	LB	LUC	9	30	Female	TRUE	60	FALSE	0
LAM0	LB	LAM	0	0	Male	NA	NA	NA	NA
597	LB	LAN	5	0	Male	NA	NA	NA	NA
497	LB	LEA	9	90	Male	NA	NA	NA	NA
681	LB	LEA	0	270	Male	NA	NA	NA	NA
616	LB	LEH	3	210	Male	NA	NA	NA	NA
679	LB	LEL	0	90	Male	NA	NA	NA	NA

596	LB	LET	5	60	Male	NA	NA	NA	NA
545	LB	LOB	6	240	Male	NA	NA	NA	NA
634	LB	LOB	2	330	Male	NA	NA	NA	NA
615	LB	LOR	4	60	Male	NA	NA	NA	NA
560	LB	LUC	5	90	Male	NA	NA	NA	NA
680	LB	LUC	1	0	Male	NA	NA	NA	NA
496	LB	LET	10	0	Male	NA	NA	NA	NA
VEG	VA	VEE	32	60	Female	TRUE	182	TRUE	1186
MAT	VA	VEA	31	60	Female	FALSE	0	TRUE	91
VEL	VA	VER	28	60	Female	FALSE	0	TRUE	1186
VES	VA	VEE	27	60	Female	TRUE	639	TRUE	1216
VAR	VA	VAN	26	60	Female	FALSE	0	TRUE	1065
VEN	VA	VEE	21	90	Female	TRUE	213	TRUE	547
VIV	VA	VIO	20	270	Female	TRUE	213	TRUE	1216
VEV	VA	VEE	15	120	Female	TRUE	335	TRUE	1186
VLK	VA	VER	15	30	Female	FALSE	0	TRUE	121
VSK	VA	VAR	15	30	Female	FALSE	0	TRUE	821
VLR	VA	VES	14	30	Female	FALSE	0	FALSE	0
VNN	VA	MAT	13	150	Female	FALSE	0	TRUE	121
VUR	VA	VIO	13	0	Female	TRUE	425	FALSE	0
VNA	VA	VEL	9	300	Female	FALSE	0	FALSE	0
VIG	VA	VEN	9	60	Female	FALSE	0	FALSE	0
VIN	VA	VAR	8	60	Female	FALSE	0	FALSE	0
VLA	VA	VIO	5	0	Female	FALSE	0	FALSE	0
VRV	VA	VEE	4	0	Female	FALSE	0	FALSE	0
VDL	VA	VER	4	0	Female	FALSE	0	FALSE	0
VTT	VA	VAR	2	330	Female	FALSE	0	FALSE	0
VGS	VA	VEG	3	60	Female	FALSE	0	FALSE	0
VTG	VA	VEV	3	60	Female	FALSE	0	FALSE	0
VVH	VA	VIV	3	90	Female	FALSE	0	FALSE	0
VXN	VA	VEL	3	60	Female	FALSE	0	FALSE	0
VIM	VA	VEN	1	150	Female	FALSE	0	FALSE	0
VGO	VA	VSK	2	60	Female	FALSE	0	FALSE	0
VID	VA	VIR	59	60	Female	FALSE	0	TRUE	0
VER	VA	?	45	60	Female	TRUE	213	FALSE	0
VEE	VA	VIC	53	60	Female	FALSE	0	FALSE	0
VIO	VA	VIC	36	60	Female	FALSE	0	TRUE	121
471	VA	VEE	11	330	Male	NA	NA	NA	NA
481	VA	VER	11	0	Male	NA	NA	NA	NA
522	VA	VIO	9	30	Male	NA	NA	NA	NA
537	VA	VEE	8	60	Male	NA	NA	NA	NA
536	VA	VEG	7	300	Male	NA	NA	NA	NA
538	VA	VER	7	300	Male	NA	NA	NA	NA
535	VA	VES	8	60	Male	NA	NA	NA	NA
551	VA	VID	6	330	Male	NA	NA	NA	NA

573	VA	MAT	6	0	Male	NA	NA	NA	NA
574	VA	VEN	5	90	Male	NA	NA	NA	NA
625	VA	VES	3	90	Male	NA	NA	NA	NA
VLK9	VA	VLK	0	90	Male	NA	NA	NA	NA
VNN9	VA	VNN	0	90	Male	NA	NA	NA	NA
700	VA	MAT	0	60	Male	NA	NA	NA	NA
735	VA	VID	0	0	Male	NA	NA	NA	NA
699	VA	VIO	0	90	Male	NA	NA	NA	NA
WIL	WA	WEN	42	60	Female	FALSE	0	TRUE	578
WIN	WA	WEN	30	60	Female	FALSE	0	TRUE	91
WND	WA	WEN	25	270	Female	FALSE	0	TRUE	0
WNN	WA	WIL	13	90	Female	TRUE	639	FALSE	0
WLW	WA	WIN	8	150	Female	FALSE	0	FALSE	0
WIG	WA	WIN	0	60	Female	FALSE	0	FALSE	0
WOU	WA	WND	7	120	Female	FALSE	0	FALSE	0
WDA	WA	WND	2	60	Female	FALSE	0	FALSE	0
503	WA	WIL	9	330	Male	NA	NA	NA	NA
575	WA	WIL	6	0	Male	NA	NA	NA	NA
655	WA	WIL	1	210	Male	NA	NA	NA	NA
626	WA	WIN	4	0	Male	NA	NA	NA	NA
736	WA	WND	0	0	Male	NA	NA	NA	NA

Annual population dynamic data were also used in model calibration (on 1st October 2000-2017; see B.6). Records of the number of births, calf (milk-dependent calves less than two years old) and adult / juvenile (two years or older) deaths, and population size were calculated at the end of each Amboseli year. Amboseli years run from 1st October to 30th September each year and correspond to the annual cycle of rain (Croze and Lindsay, 2011). Adult / juvenile and calf mortality were considered separately because controls on mortality are different for milk-dependent calves than for those that can survive on vegetation alone: milk-dependent calves die when mothers enter starvation (mothers stop producing milk at this point), but adults and juveniles may survive starvation through depletion of some structural tissues (see B.4). The model parameters were therefore calibrated against 68 data points: 17 population sizes, 17 adult and juvenile mortality rates, 17 annual birth rates and 17 annual calf mortality rates (Figure B.8).

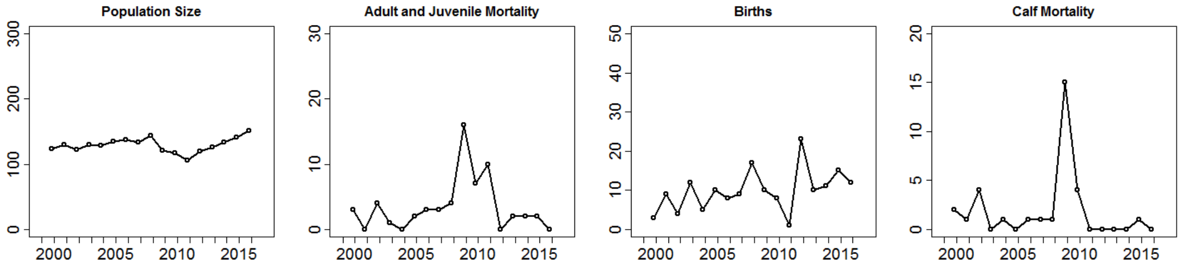


Figure B.8. Population dynamic data used in calibration of model parameters: population size, birth rate, adult and calf mortality rates of four elephant families (IBs, LBs, VAs, WAs).

To validate the model we compared model outputs to independent data from families not used in model calibration. We used the 30 parameter sets accepted in the ABC to simulate the population dynamics of six intensively recorded Amboseli elephant family groups (AAs, FBs, GBs, JAs, KB2s and OBs). These families are resident in Amboseli National Park and thus use a different area to that used in model calibration (see B.4). The model was thus adapted to incorporate the different starting population on 1st March 2000 (Table B.4), spatial extent and NDVI input data. All model structure and parameters remained the same (Figure B.9).

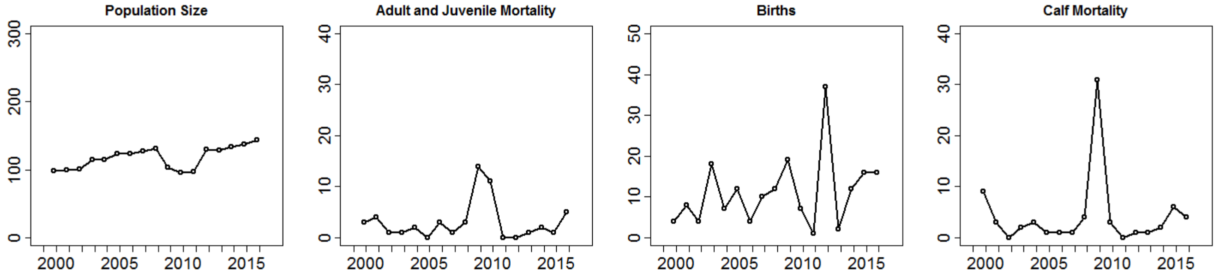


Fig B.9. Population dynamics data used to validate the model: population size, birth rate, adult and calf mortality rates of resident elephant families (AAs, FBs, GBs, JAs, KB2s and OBs).

Table B.4. Initial population on 1st March 2000 used to initiate the validation of the model. Data derived from Amboseli Elephant Research Project individual-based longitudinal demographic data.

Name	*Family*	*Mother*	*Age (years)*	*Age (days)*	*Sex*	*Pregnant*	*p_count*	*Lactating*	*l_count*
AAN	AA	AST	2	210	Female	FALSE	0	FALSE	0
ABR	AA	AUD	5	150	Female	FALSE	0	FALSE	0
AGA	AA	ANB	32	60	Female	FALSE	0	TRUE	1035
ALC	AA	AST	7	0	Female	FALSE	0	FALSE	0
ALI	AA	ANB	38	60	Female	FALSE	0	TRUE	759
ALT	AA	AGA	18	0	Female	FALSE	0	TRUE	60
ALX	AA	AGA	6	330	Female	FALSE	0	FALSE	0
AMB	AA	AMY	18	270	Female	FALSE	0	TRUE	121
AME	AA	ALY	32	60	Female	FALSE	0	TRUE	91
AMY	AA	?	48	60	Female	FALSE	0	TRUE	305
AMY9	AA	AMY	0	300	Female	FALSE	0	FALSE	0
ANG	AA	AMY	15	60	Female	FALSE	0	FALSE	0
ANH	AA	AME	18	90	Female	FALSE	0	TRUE	152
ANH99	AA	ANH	0	120	Female	FALSE	0	FALSE	0
ANN	AA	AME	9	300	Female	FALSE	0	FALSE	0
ART	AA	ALI	2	0	Female	FALSE	0	FALSE	0
AST	AA	ALI	21	60	Female	FALSE	0	TRUE	943
AUD	AA	AMY	27	330	Female	TRUE	630	FALSE	0
AVA	AA	AME	0	60	Female	FALSE	0	FALSE	0
FAD	FB	FEL	1	270	Female	FALSE	0	FALSE	0
FAN	FB	FRE	31	60	Female	TRUE	416	TRUE	974
FAN7	FB	FAN	2	240	Female	FALSE	0	FALSE	0
FAR	FB	FAN	12	240	Female	TRUE	324	FALSE	0
FAW	FB	FAY	20	30	Female	FALSE	0	TRUE	60
FAY	FB	FRE	35	60	Female	FALSE	0	TRUE	486
FCA	FB	FAW	0	30	Female	FALSE	0	FALSE	0
FEL	FB	?	36	60	Female	FALSE	0	TRUE	639
FLM	FB	FLO	9	0	Female	FALSE	0	FALSE	0
FLS	FB	FLO	16	270	Female	FALSE	0	TRUE	366
FOR	FB	FAN	6	210	Female	FALSE	0	FALSE	0
FRE	FB	?	65	60	Female	FALSE	0	FALSE	0
FRT	FB	FAY	8	90	Female	FALSE	0	FALSE	0
GAIL	GB	GRA	16	330	Female	FALSE	0	TRUE	305
GAM	GB	GWE	8	0	Female	FALSE	0	FALSE	0
GCA	GB	GEO	3	0	Female	FALSE	0	FALSE	0
GEE	GB	GLO	9	240	Female	FALSE	0	FALSE	0
GEN	GB	GLE	4	0	Female	FALSE	0	FALSE	0
GEO	GB	GLA	20	300	Female	FALSE	0	TRUE	1124
GER	GB	?	52	60	Female	TRUE	600	FALSE	0
GGB	GB	GLA	0	0	Female	FALSE	0	FALSE	0

GGR	GB	GOL	3	90	Female	FALSE	0	FALSE	0
GHT	GB	?	3	30	Female	FALSE	0	FALSE	0
GIG	GB	GLA	12	0	Female	TRUE	82	FALSE	0
GLA	GB	?	37	60	Female	FALSE	0	TRUE	29
GLO	GB	?	56	60	Female	FALSE	0	FALSE	0
GMB	GB	GEO	8	0	Female	FALSE	0	FALSE	0
GMM	GB	GWE	3	0	Female	FALSE	0	FALSE	0
GNA	GB	GRA	7	120	Female	FALSE	0	FALSE	0
GOL	GB	GLO	25	330	Female	FALSE	0	TRUE	0
GOL0	GB	GOL	0	0	Female	FALSE	0	FALSE	0
GOO	GB	GLO	20	60	Female	TRUE	204	FALSE	0
GRA	GB	?	50	60	Female	TRUE	265	TRUE	1065
GRB	GB	GER	12	300	Female	FALSE	0	TRUE	29
GSA	GB	GRA	13	30	Female	TRUE	630	FALSE	0
GTU	GB	GAIL	0	300	Female	FALSE	0	FALSE	0
GWE	GB	GRA	20	270	Female	TRUE	355	TRUE	1096
JAM	JA	JOY	9	330	Female	FALSE	0	FALSE	0
JAN	JA	JES	17	30	Female	FALSE	0	FALSE	0
JEAN	JA	JOL	1	240	Female	FALSE	0	FALSE	0
JOD	JA	JOA	20	120	Female	FALSE	0	TRUE	91
JOL	JA	JEZ	23	90	Female	FALSE	0	TRUE	609
JOY	JA	?	59	60	Female	TRUE	477	FALSE	0
JTT	JA	JOD	0	60	Female	FALSE	0	FALSE	0
KATE	KB2	KAM	15	120	Female	TRUE	82	FALSE	0
KDD	KB2	KYR	0	300	Female	FALSE	0	FALSE	0
KDZ	KB2	KAM	10	0	Female	FALSE	0	FALSE	0
KIE	KB2	KLE	0	300	Female	FALSE	0	FALSE	0
KYR	KB2	KLE	15	60	Female	FALSE	0	TRUE	305
ODI	OB	?	34	60	Female	FALSE	0	TRUE	29
OKI	OB	ODI	9	0	Female	FALSE	0	FALSE	0
OLA	OB	OME	11	120	Female	TRUE	112	FALSE	0
OLV	OB	OTT	0	300	Female	FALSE	0	FALSE	0
OME	OB	?	47	60	Female	FALSE	0	TRUE	91
OME9	OB	OME	0	60	Female	FALSE	0	FALSE	0
OPR	OB	OPH	15	90	Female	FALSE	0	TRUE	0
OPR0	OB	OPR	0	0	Female	FALSE	0	FALSE	0
OPR6	OB	OPR	4	0	Female	FALSE	0	FALSE	0
ORG	OB	OMO	8	60	Female	FALSE	0	FALSE	0
ORN	OB	ODI	5	60	Female	FALSE	0	FALSE	0
OTT	OB	ODI	17	120	Female	FALSE	0	TRUE	305
OZO	OB	OME	15	150	Female	FALSE	0	TRUE	29
OZO0	OB	OZO	0	0	Female	FALSE	0	FALSE	0
483	AA	AMY	10	0	Male	NA	NA	NA	NA
505	AA	ALI	8	150	Male	NA	NA	NA	NA
511	GB	GLE	8	270	Male	NA	NA	NA	NA

512	GB	GLA	8	90	Male	NA	NA	NA	NA
532	GB	GOL	8	0	Male	NA	NA	NA	NA
543	FB	FEL	7	0	Male	NA	NA	NA	NA
548	OB	OME	6	90	Male	NA	NA	NA	NA
559	KB2	KLE	6	60	Male	NA	NA	NA	NA
577	AA	AMB	5	0	Male	NA	NA	NA	NA
578	AA	ALT	5	60	Male	NA	NA	NA	NA
579	AA	AME	5	60	Male	NA	NA	NA	NA
588	FB	FLO	5	60	Male	NA	NA	NA	NA
592	JA	JOY	5	0	Male	NA	NA	NA	NA
593	JA	JOD	5	0	Male	NA	NA	NA	NA
614	GB	GER	4	0	Male	NA	NA	NA	NA
629	AA	AGA	2	300	Male	NA	NA	NA	NA
633	GB	GRA	2	330	Male	NA	NA	NA	NA
670	FB	FLS	1	0	Male	NA	NA	NA	NA
718	GB	GRB	0	0	Male	NA	NA	NA	NA
ALT0	AA	ALT	0	30	Male	NA	NA	NA	NA
AMB9	AA	AMB	0	90	Male	NA	NA	NA	NA
FAY8	FB	FAY	1	90	Male	NA	NA	NA	NA
ODI0	OB	ODI	0	0	Male	NA	NA	NA	NA

Prior Parameterisation

Parameters marked * were deemed uncertain and subjected to inverse parameterisation ($stor_{scaling}$, $maxIR_{scaling}$, hsc, DD, AE_{veg}, AE_{milk}, B_0, E_0, E_{PL}, MR_{back} and $MR_{scaling}$; see B.6).

Half saturation coefficient (hsc): Ingestion rates were estimated through observations of elephants at various food densities in Amboseli National Park to produce a functional response curve (Lindsay, 1994). The half saturation coefficient is the food density at which half the maximum ingestion rate is achieved (Mulder and Hendriks, 2013). Reading from Lindsay's functional response curves, maximum ingestion rates were 159 and 96g min^{-1} for male and female elephants, respectively, and the food density at which half of this was achieved was 0.26 and 0.16 kg m^{-2}. For simplicity, a mean value of both sex's half saturation coefficients was used in the model (0.21 kg m^{-2})*.

Maximum ingestion rate scaling coefficient ($maxIR_{scaling}$): Maximum ingestion rates estimated by Lindsay (1994) were converted to kg day^{-1} assuming elephants feed for 16 hours a day (Lindsay, 2011). Given the average asymptotic mass of 4690 and 2740kg for males and females, respectively (Lee and Moss, 1995), the allometric equation describing maximum ingestion rate (Equation B.1a) can be rearranged, giving an estimate of the scaling coefficient at 0.27 for males and 0.24 for females. A single mean value of 0.255 is used in the model*.

Assimilation efficiency of vegetation (AE_{veg}): The assimilation efficiency has been estimated for elephants by both Rees (1982) and Wiegert & Evans (1967) as 22.4% and 32.5%, respectively. The mean of these two estimates was used in the model*.

Taxon-specific normalization constant (B_0): Lindsay (2011) presented estimates of elephant daily basal metabolic rate (BMR) from various sources. Peters (1983) estimated basal metabolism using equation B.2 and found BMR (MJ) to scale with mass to the quarter power using a taxon-specific normalisation constant of 0.293. B_0 was therefore taken as 293 in the model to calculate BMR in KJ*.

Growth constants (GR_m / GR_f): Lindeque & van Jaarsveld (1993) compared logistic, Gompertz and von Bertalanffy growth curves to the post-natal growth of elephants in the Etosha National Park, concluding that the von Bertalanffy provided the best fit. Using this information, Lee & Moss (1995) calculated the von Bertalanffy growth constant for shoulder height for known aged African elephants in the Amboseli elephant population as 0.07134 for males and 0.12763 for females. The von Bertalanffy equation was adapted to describe growth in mass rather than height (Sibly *et al.*, 2013). The resulting growth curves are presented in Figure B.10.

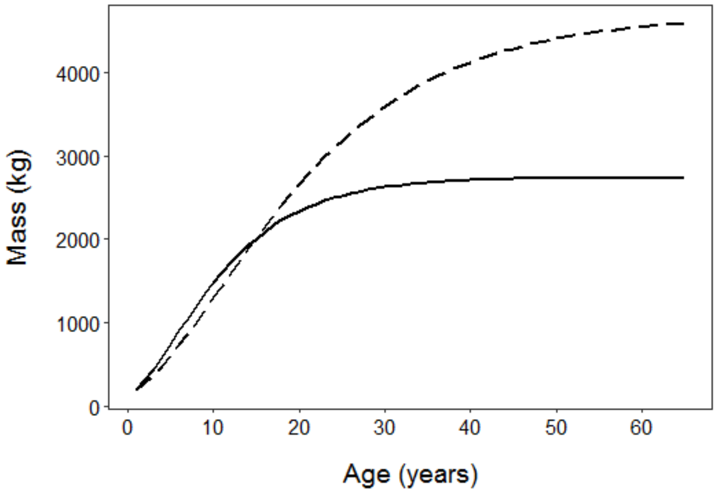


Figure B.10. Growth curves of male (dashed) and female (solid) elephants follow the von Bertalanffy growth equation if sufficient forage is available.

Body fat threshold required for oestrus cycling($oest_{on}$): Temporal variation in conceptions of elephants suggests that they experience condition-dependent oestrus; few conceptions occurred in years when the maximum NDVI value (used as a proxy for vegetation abundance) was low which is suggestive of a physiological threshold under which elephants do not enter oestrus and conceive (Wittemyer, Rasmussen and Douglas-Hamilton, 2007). Estimates of this physiological threshold are not available for elephants but have received some attention in humans, and Bronson & Manning (1991) suggest that 20% body fat is required for oestrus cycling. The proportion of body fat (M_{stor}; kg) in relation to total mass (M_{tot}; kg) required for oestrus cycling was therefore taken as 0.2.

Foetal growth constant (fg): Non-linear equations were compared to data points of foetal mass provided by Lee (pers. comm.). A power equation provided the best fit to the data with a foetal growth constant of 0.0069 (Figure B.11).

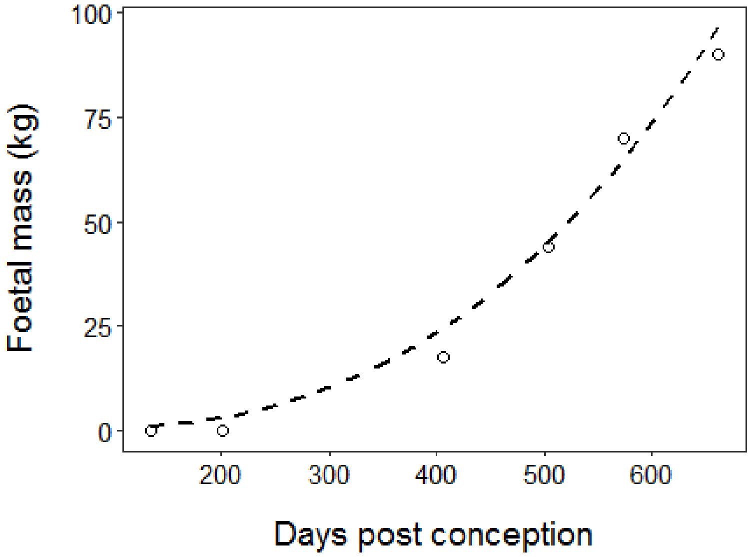


Figure B.11. Foetal growth curve (dashed line) fitted using unpublished data (points) collected by Lee (pers.comm.)

Maximum storage tissue scaling ($stor_{max}$): Pitts & Bullard (1968) described the fat content of the body of mammals using Equation B.7, where $stor_{scaling}$ is 0.06*.

Equation B.7. $$Stor_{max} = stor_{\ scaling}\ M_{tot}{}^{0.2}$$

where $Stor_{max}$ = maximum amount of storage tissue (kg)

$stor_{\ scaling}$ = coefficient for scaling maximum stores with total mass

M_{tot}= total mass (kg)

Core proportion of structural tissues (core_prop): Despite several body condition indices developed for elephants, quantification of the proportion of structural tissues which can or cannot be metabolised are not available. Like elephants, polar bears undergo regular periods of fasting, where energy balance is negative (see Figure B.3), when sea-ice melts and they are limited in their ability to catch their usual prey of seals. Atkinson *et al.* (1996) observed a 10% decline in lean body mass (or structural tissues) of polar bears during this period, suggesting the core proportion of structural tissues in polar bear in less than 0.9. Given the lack of an elephant-specific reference value, we utilised 0.9 as a starting point for *core_prop*. After model testing, we found that a value of 0.951 provided best model fit. This was not subjected to further calibration.

Energy demands of lactation (E_0 / E_{PL}): Lactation curves are not available for elephants and there are too few data points with which to fit such a curve. However elephants are considered to follow a type I curve (Wood, 1967): the energetic demands of lactation increase until peak lactation at which point the mother can no longer meet the growing demands of the calf and begins the weaning process. Oftedal (1985) described the allometric equation scaling energy demands of peak lactation with a mother's mass (Equation B.8). Energetic demand of peak lactation (E_{PL}) was therefore calculated as 112,170KJ day^{-1}*. The energy invested in lactation on the first day of the calf's life (E_0) has not been measured in elephants. We assume that the mother's milk production covers the energetic demands of metabolism and growth in the calf following conversion efficiencies. The conversion efficiency of the mother's energy reserves to energy available in milk is 0.84 in cows* (AE_{milk}; Agricultural Research Council 1980). E_0 was therefore calculated for new-born male and female calves as 12236KJ day^{-1} and 11537KJ day^{-1}, respectively. A single mean value of 11886KJ day^{-1} is used in the model*.

Equation B.8.

$$E_{PL} = 44\ {M_{struct}}^{0.7}$$

where E_{PL} = energetic demand of peak lactation (KJ day^{-1})

M_{struct}= structural mass (kg)

Mortality (MR_{back} / $MR_{scaling}$): Background mortality accounts for deaths occurring as a result of stochastic events such as poaching, predation, human-elephant conflict, disease or injury. A baseline background daily mortality rate (MR_{back}) was calculated as 2.74 x 10^{-5}* from life history tables presented in Lee *et al.* (2011). Given that the chances of some causes of stochastic mortality increase when elephant body condition is poor, daily mortality rate increased during starvation ($MR_{scaling}$; Equation B.5; Figure B.6). We estimated $MR_{scaling}$ assuming that mortality rate was equal to MR_{back} when maximum structural tissues remained (M_{struct}) and increased as structural tissues were metabolised to cover the costs of maintenance during starvation.

B.4. Conceptual model evaluation

This TRACE element provides supporting information on: The simplifying assumptions underlying a model's design, both with regard to empirical knowledge and general, basic principles. This critical evaluation allows model users to understand that model design was not ad hoc but based on carefully scrutinized considerations.

Summary:

The model relies on several underlying assumptions and conceptual theories:

- The spatial extent of the model has been guided by our previous work in modelling movement decisions of these elephant family groups
- The conceptual models of body composition, energy reserves and energy allocation are based on current understanding of physiological ecology

Environment

The Amboseli ecosystem (bounding coordinates:-2.02N,-3.28S, 38.03E, 36.67W) covers an area of approximately 8000km^2, straddling the southern border of Kenya and the northern border of Tanzania. It comprises the central Amboseli National Park (ANP; 392km^2) and surrounding landscape (Croze and Lindsay, 2011). The habitat consists of semi-arid savannah, with fluctuations in vegetation driven by two wet seasons: the short-rains (November-December) and the long-rains (March through May; Croze & Lindsay, 2011).

The home range of each elephant family was identified as the 95% kernel density estimates (Shannon *et al.* 2006; Figure B.1) using location data collected by GPS collars fitted to adult females Ida, Lobelia, Vicky and Willow from June 2011 for 12 months (Boult, Sibly, *et al.*, 2018). The total area of the combined home ranges covered 637,142,163 m^2 (p) and provided the spatial extent across which NDVI values were retrieved (see B.3).

The environment was adapted during model validation to represent the home ranges of the resident elephant families. Sightings data, in which the family group and the location based on a grid system within the Amboseli National Park, have been recorded since 1972. We used records of the six resident family groups from 2000 to 2016 to estimate their home ranges within the park (95% kernel density estimates). However, given that this only represents their ranging within ANP, the area of the estimated home ranges is too small to provide sufficient forage. We therefore used the model to estimate the size of the area which was roughly equal to that of ANP (p = 392,000,000 m^2).

Body Composition

All body tissue can be characterised as either structural or storage (Kooijman, 2000); total mass is the sum of these two tissues. In mammals, storage tissues consist mainly of fat in adipose tissue (Sibly *et al.*, 2013) which may be accumulated during times of positive energy balance and drawn from in times of food shortages (Figure B.3). The maximum amount of storage tissues an individual can sustain is a trade-off between the benefits of having reserves to get through tough times and the additional costs of mobility (Sibly *et al.*, 2013), and scales allometrically with structural mass so that larger individuals can sustain greater energy stores (Pitts & Bullard 1968; Equation B.7). An individual is considered in peak body condition when storage tissues reach maximum. Structural mass is determined by the growth curves described in Lee & Moss (1995; Figure B.10), and therefore varies with age, sex and an individual's previous ability to meet the energetic demands of growth. Structural tissues (e.g. skeleton, muscles and organs) can be further divided into those essential for survival and those that are not. Individuals have the ability to metabolise a non-essential structural tissues (muscle mass) to cover the costs of BMR during starvation (Atkinson and Ramsay, 1995).

Energy Reserves

Energy is available to an individual in the form of energy reserves. Reserves comprise assimilated energy, storage tissues and non-essential structural tissues (Atkinson, Nelson and Ramsay, 1996). Assimilated energy is that which is immediately available through the ingestion of food and forms the first port of call for all energy expending processes (maintenance, growth and reproduction). If assimilated energy proves insufficient to cover the costs of these processes, storage tissues may be depleted. If storage tissues are exhausted, the individual is deemed to be in starvation, at which point growth and reproduction stop. The individual may metabolise a small portion of structural tissues (Atkinson & Ramsay 1995) with the sole purpose of covering maintenance. This reflects the strategy of sacrificing current productivity (growth and reproduction) to improve the chances of future production. Should this small proportion of usable structural tissue also be depleted, the individual dies.

Depletion of storage tissue is more efficient than that of structural tissues; storage tissue has a higher energy content (39,300 KJ kg^{-1} compared to 7,000 KJ kg^{-1} of structural tissue; Peters 1983; Schmidt-Nielsen 1997; Sibly *et al.* 2013) and is more easily metabolised (depletion of structural tissue costs an additional 7000 KJ kg^{-1}).

Energy Budget Model

Food availability is a key driver of population dynamics, and the interaction between the two is modelled via an energy budget. There is little consensus regarding how energy budgets should be modelled in IBMs and the options vary in their assumptions (Sibly *et al.*, 2013). We have chosen to use the energy budget model proposed by Sibly *et al.* (2013), the key features of which are described hereafter (for details see B.2).

The principles of physiological ecology are grounded in evolutionary theory: organisms aim to optimise processes of survival, growth and reproduction to achieve maximum Darwinian fitness. It is generally accepted that energetic resources are allocated separately to maintenance, growth, reproduction and storage (Peters, 1983; Sibly and Calow, 1986a). Energetic resources are limited by the availability of food and how much an animal can intake. Thus, if more resources are allocated to one process, less will be available for others: as dictated by conservation of energy and matter (Sibly *et al.*, 2013). When food is abundant, resources may be allocated maximally to all energy-expending processes. However, when resources are limited, allocation of energy must be prioritised. The first priority is maintenance, since energy allocated to maintenance fuels the basic processes of life essential for survival. Following maintenance, for individuals not yet sexually mature, energy is then allocated to growth, and any remaining to stores. In determinate growers (those which reach maximal mass at sexual maturity), once sexually mature, energy is allocated to reproduction following maintenance, and then to stores. In indeterminate growers (those that continue to grow following first reproduction; this includes elephants), reproduction has priority over growth since reproduction is generally strongly favoured by natural selection (Sibly and Calow, 1986b), and only after reproduction and growth can energy be allocated to stores.

B.5. Implementation verification

This TRACE element provides supporting information on: (1) whether the computer code implementing the model has been thoroughly tested for programming errors, (2) whether the implemented model performs as indicated by the model description, and (3) how the software has been designed and documented to provide necessary usability tools (interfaces, automation of experiments, etc.) and to facilitate future installation, modification, and maintenance.

Summary:

To the best of our ability, we have ensured the model operates as described in this TRACE document, having employed various strategies of model checking. The model as described, along with associated files, are available to interested parties. For those wanting to use the model, guidelines are provided.

Model verification

The model was tested thoroughly to ensure the model performed as described. We made particular use of the in-built functionality provided by NetLogo 6.0.2: turtle and patch monitors were utilised to confirm energetic equations were calculated correctly; print statements showed the passage of individuals through the energy budget processes; the profiler extension ensured ordering proceeded as expected; plots monitored allometric scaling, followed individual energy budgets and body composition. We also implemented each sub-model individually in unique NetLogo instances. Finally, the model was checked by members of the IBM@Reading research group (http://ibmreading.wordpress.com).

How to install and use the model

The model is implemented in NetLogo 6.0.2, a programmable environment particularly suited to modelling complex, individual-based systems evolving over time (Wilensky, 1999). NetLogo is free to download and runs on all major operating systems. Version 6.0.2 can be downloaded here: https://ccl.northwestern.edu/netlogo/6.0.2/. The model and associated files are available in a supplementary zip file (available: https://github.com/vlboult93/EEB_Model.git). For those wishing to utilise the model, please begin by reading the enclosed 'READ_ME' file.

B.6. Model output verification

This TRACE element provides supporting information on: (1) how well model output matches observations and (2) how much calibration and effects of environmental drivers were involved in obtaining good fits of model output and data.

Summary:

Uncertain parameters in the model were calibrated using rejection approximate Bayesian computation. This resulted in good model fits to elephant population dynamic data, most notably, fitting the 'drought year' shows the importance of food availability as a driver of elephant population dynamics.

We deemed 11 parameters uncertain and thus requiring calibration ($stor_{scaling}$, $maxIR_{scaling}$, *hsc*, AE_{veg}, AE_{milk}, B_0, E_0, E_{PL}, MR_{back}, $MR_{scaling}$ *and DD)*. We calibrated these parameters using rejection approximate Bayesian computation (ABC; Van Der Vaart *et al.* 2015): parameter values were sampled randomly from uniform prior distributions ranging from roughly half to double their reference values (Table B.2 and see B.3); the model was simulated 100,000 times; the 30 simulations which best fit the empirical data (population size, birth and mortality rates) were accepted; posterior distributions were derived from the accepted runs (Figure B.12). Parameters B_0, E_0 and E_{PL} experienced the greatest degree of narrowing along with *hsc*. Given that *hsc* is responsible for controlling the relationship between food density and ingestion rate, and thus energy intake, it is sensible that this parameter was important in determining the model outputs. B_0, E_0 and E_{PL} on the other hand, control the rates of the two most energetically expensive processes, maintenance and lactation, hence the narrowing.

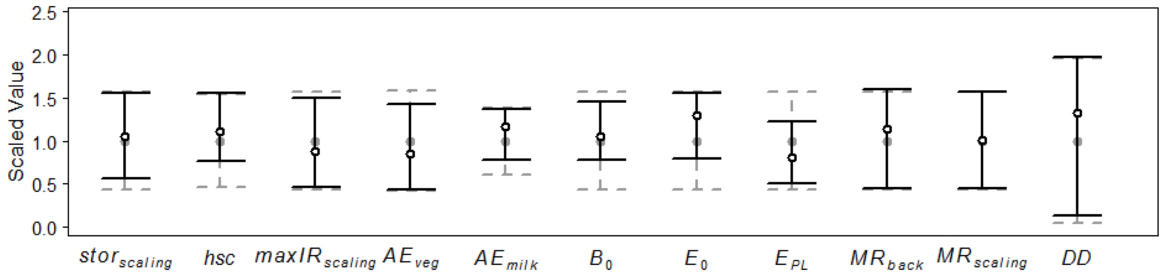


Figure B.12. Prior and posterior distributions of parameter values. Grey dashed lines show the priors; black lines the posteriors. Circles represent medians, whiskers 95% credible intervals. All parameter values were scaled by dividing by the corresponding literature values, so that a value of 1 corresponds to the value shown in Table B.2.

Fits of the model to the data are shown in Figure B.13. Following calibration, we were satisfied that the model replicated the data well. Of particular importance to model fit was the demographic impacts of a drought in 2009. During this period, the Amboseli elephant population as a whole declined by 25%; in our modelled families, 16 adults and 15 calves died. Due to starvation in surviving elephants, females struggled to meet the demands of reproduction, resulting in the deaths of young calves and failure of pregnancies. Despite the drought breaking at the end of 2009, the 22-month gestation period of elephants meant there was a two-year lag in births with low numbers of births occurring in 2010 and 2011, but since drought acts to synchronise female reproduction by eliminating oestrus, there was a ‘baby-boom’ in 2012. These drought-induced population dynamics are critical in naturally regulating elephant population size and it is therefore crucial that models capture these dynamics if they are to accurately predict elephant population size. The high R^2 values indicate that model outputs capture drought-dynamics and correspond well with observed elephant population dynamics.

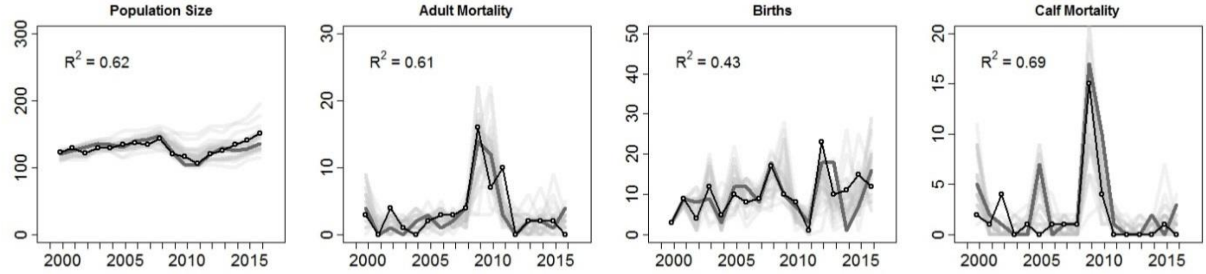


Figure B.13. Population size, births and deaths from Amboseli years 2000 – 2016. Black lines and open points show the data, the thick grey line is the best fitting simulation. Light grey lines show the 30 best fitting simulations indicating the uncertainty in model outputs that result from uncertainty in the values of parameters. Amboseli years run October to September. R^2 of best fitting simulation presented on plot.

Elevated calf mortality predicted by the model in 2005 was the result of low median NDVI during this period. In contrast to the 2009 drought, we believe elephants were able to buffer this period of low productivity in 2005 by being more selective in their foraging locations and retreating to the fairly constant source of food in the ANP swamps, hence mortality rates are low. This was not possible during the 2009 drought, which began with a prolonged period of low rainfall in 2008, meaning 'fall-back' resources such as the swamps were already depleted by the time the official drought occurred in 2009. This resulted in the high mortality rates of both adults and calves in 2009. The under-prediction of birth rates following the 2009 drought is possibly because densities of other grazers are not considered in the model. The number of grazers in the Amboseli ecosystem remained in low for a prolonged period following the drought, limiting competition for food for elephants. Incorporation of interspecific competitor density would be expected to improve model fit to birth rates post-2009, as elephants access more food and reproduce more readily.

B.7. Model analysis

This TRACE element provides supporting information on: (1) how sensitive model output is to changes in model parameters (sensitivity analysis), and (2) how well the emergence of model output has been understood.

Summary:

A local sensitivity analysis identified sensitive model outputs and confirmed influential model parameters.

Local sensitivity analysis identified relative sensitivities of population size, birth rates and adult and calf mortality rates to changes in calibrated parameter values. Changes in outputs were averaged over a 10% increase and decrease in each parameter, and over ten repeated simulations to account for stochasticity in the model. While one parameter was tested all others were kept at their calibrated values. Sensitivities are presented in Table B.5 as the % change in the variable relative to 10% changes in parameter values.

Adult and juvenile mortality was the least sensitive variable and calf mortality the most sensitive. The robustness of adult and juvenile mortality to changes in parameter values reflects generally low mortality rates in adult elephants whose large body size and substantial energy reserves allow them to buffer fluctuations in energy intake and expenditure. Calf mortality on the other hand is extremely sensitive, indicative of the vulnerability of young elephants to environmental changes (Foley, Pettorelli and Foley, 2008; Woolley, 2008; Wato *et al.*, 2016). In particular, calf mortality is highly sensitive to parameters controlling energy intake from milk (AE_{milk} and E_0), as expected given that milk provides the primary source of energy for calves, and B_0 given that this controls metabolic rate, the main source of energetic expenditure for elephant calves. All model outputs were somewhat sensitive to parameters controlling energy intake (*hsc*, $maxIR_{scaling}$ and AE_{veg}), which endorses the use of mechanistic approaches in modelling the bottom-up processes controlling population dynamics.

Table B.5. Sensitivities of population size, total number of births and mortalities, presented as % change in output relative to a 10% change in parameter (mean and standard error over ten repeated simulations and for changes above and below parameter value).

Parameter	Pop. size	Births	Adult Mort.	Calf Mort.
$stor_{scaling}$	-0.07 ± 3.02	0.02 ± 2.14	-0.14 ± 9.83	-0.31 ± 2.26
hsc	-2.3 ± 3.19	-1.3 ± 2.81	0.7 ± 12.39	0.94 ± 1.66
$maxIR_{scaling}$	4.76 ± 4.09	2.69 ± 3.26	-0.63 ± 15.91	-3.98 ± 1.68
AE_{veg}	4.34 ± 4.87	2.38 ± 3.38	-0.38 ± 15.88	-4.28 ± 2.16
AE_{milk}	-0.42 ± 2.82	-3.39 ± 4.57	0.7 ± 13.33	-14.93 ± 3.9
B_0	-3.71 ± 3.59	0.63 ± 3.9	0.18 ± 17.13	15.95 ± 2.83
E_0	-0.52 ± 3.37	-3.48 ± 5.71	0.74 ± 11.5	-15 ± 4.32
E_{PL}	-1.82 ± 2.59	-0.89 ± 2.64	0.86 ± 12.34	0.88 ± 2.14
MR_{back}	-0.15 ± 2.65	-0.14 ± 2.16	-0.05 ± 11.06	0.02 ± 1.09
$MR_{scaling}$	0.08 ± 1.95	0.05 ± 1.97	0.09 ± 10.38	-0.12 ± 2.36
DD	-1.19 ± 3.07	-0.67 ± 3.21	0.32 ± 10.88	0.65± 1.92

B.8. Model output corroboration

This TRACE element provides supporting information on: How model predictions compare to independent data and patterns that were not used, and preferably not even known, while the model was developed, parameterized, and verified. By documenting model output corroboration, model users learn about evidence which, in addition to model output verification, indicates that the model is structurally realistic so that its predictions can be trusted to some degree.

Summary:

The calibrated model was validated with independent population dynamic data for six other elephant family groups inhabiting the Amboseli ecosystem.

To validate the model we compared model outputs to independent data from families not used in model calibration. We used the 30 parameter sets accepted in the ABC to simulate the population dynamics of six intensively recorded Amboseli elephant family groups (AAs, FBs, GBs, JAs, KB2s and OBs). These families are resident in Amboseli National Park and thus use a different area to that used in model calibration (see B.3 and B.4). Resulting model fit for validation families is displayed in Figure B.14.

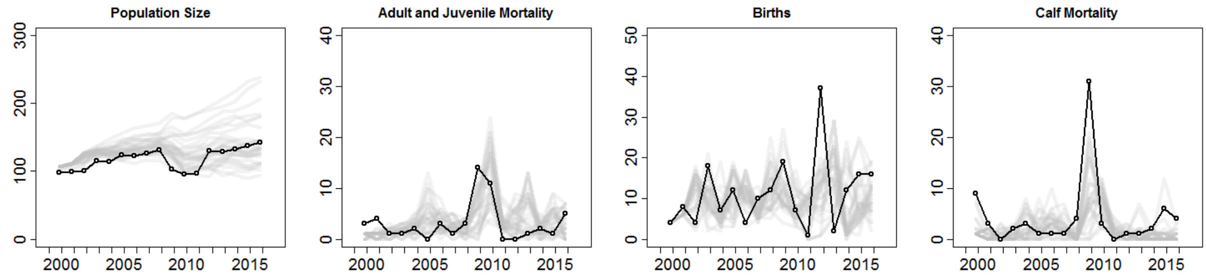


Figure B.14. Validation of model fit. Population size, births and deaths for resident families not used in model calibration. Black lines and open points show the data, light grey lines show the 30 simulations indicating the uncertainty in model outputs that results from uncertainty in the values of parameters.

The model and calibrated parameter values gave good predictions for the population dynamics of resident family groups, but could not match birth rates following the 2009 drought. The under-prediction of birth rates following the 2009 drought in both the calibration and validation of the model is possibly because densities of other grazers are not considered in the model. The number of grazers in the Amboseli ecosystem remained in low for a prolonged period following the drought, limiting competition for food for elephants. Incorporation of interspecific competitor density would be expected to improve model fit to birth rates post-2009, as elephants access more food and reproduce more readily.

C. Supplementary material for chapter 5

Figure C.1. Re-calibration of the IBM. The IBM presented in Boult, Quaife, et al. (2018) was developed and calibrated with just four family groups whereas here the IBM is applied to the whole population: the IBM re-calibrated accordingly. Black lines and open points show the data, the thick grey line is the best fitting simulation. Light grey lines show the 30 best fitting simulations indicating the uncertainty in model outputs that result from uncertainty in the values of parameters. Amboseli years run October to September.

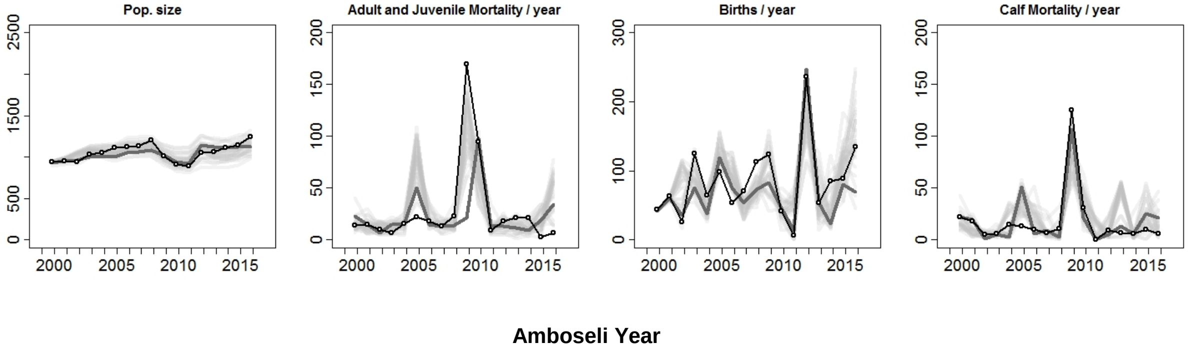


Table C.1. Stakeholder names, positions and organisations providing feedback on habitat loss scenarios. Stakeholders were asked to rank administrative units based on how likely elephants would have continued access to each area in 5-10 years' time. Feedback was compiled and used to construct habitat loss scenario D (see Figure 5.1d).

Name	Position	Organisation
Jeremy Goss	Conservation Scientist	Big Life Foundation, Kenya
Jackson Mwato	Executive Director	Amboseli Ecosystem Trust, Kenya
Vicki Fishlock	Resident Scientist	Amboseli Elephant Research Project, Kenya

Table C.2. Habitat loss scenarios by numbers. The area available to elephants in each scenario and the percent area lost (compared to scenario A representing the total current extent of elephant ranging) is shown alongside the median elephant population size at the end of the projected period (2099) and the percent population decline (median compared to 2017 population size of 1247). This demonstrates that the number of elephants supported by the ecosystem is not directly proportional to the area available: it is also affected by the heterogeneity of vegetation.

Scenario	Area (km^2)	% area loss	Median pop.	% pop. loss
A – Full area	7232	-	1237.5	0.8
B – Human population growth	6330	12.5	1003.5	19.5
C – HEI	5990	17.2	1101.5	11.7
D – Stakeholder opinion	4893	32.3	712.5	42.9
E – Existing and proposed CAs	1833	74.7	469.0	62.4
F – Existing CAs only	1234	82.9	271.5	78.2

Figure C.2. Projected SPI. SPI was calculated for each Amboseli year (October-September) for the simulation period (2007-2099) using projected precipitation from the ISI-MIP 2b simulation round for four climate models and two RCPs. Shading shows SPI classification: dark blue = very wet, light blue = wet, white = normal, orange = dry and red = drought. Annual SPI classifications were used to project NDVI and food available to elephants in the model.

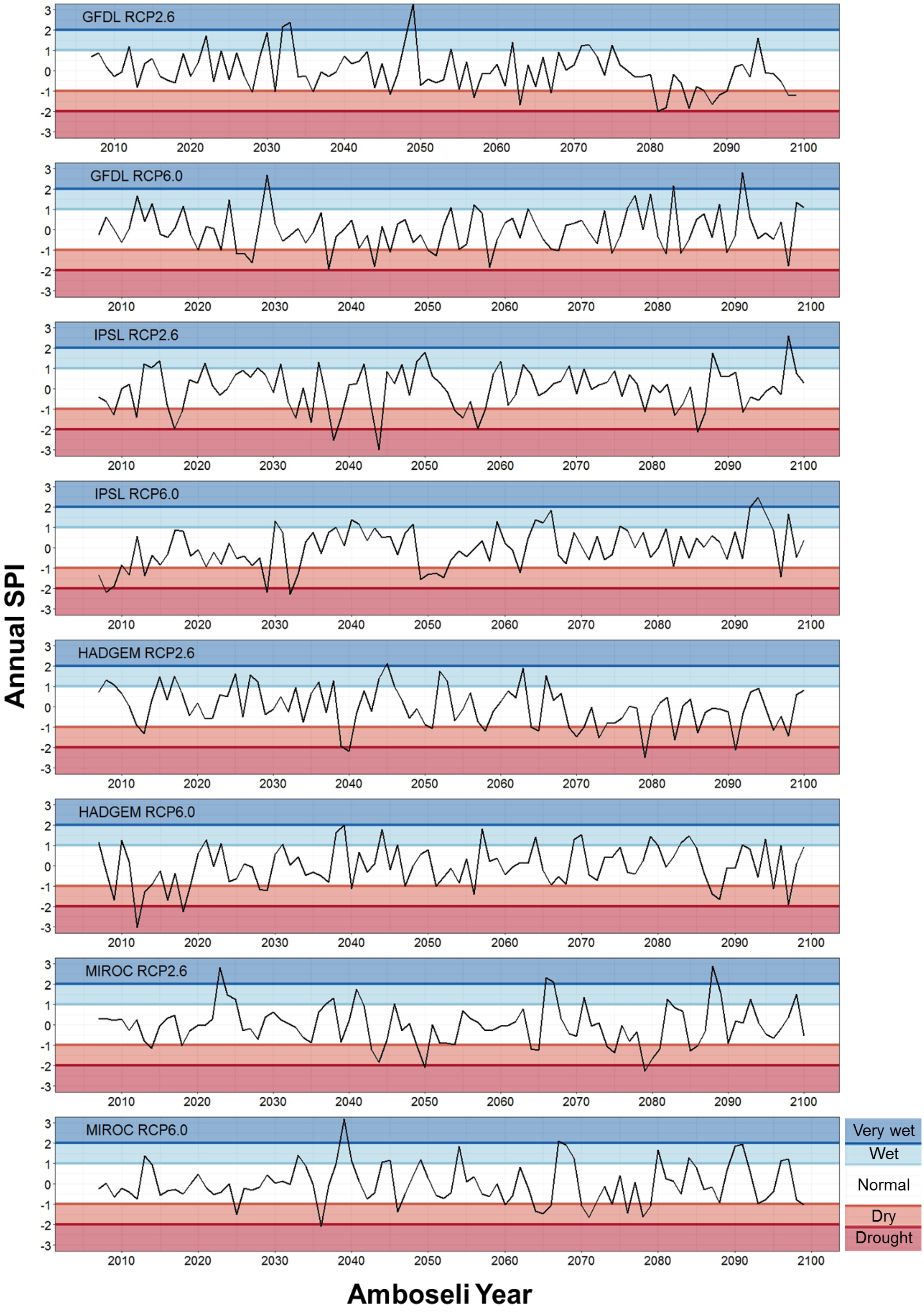
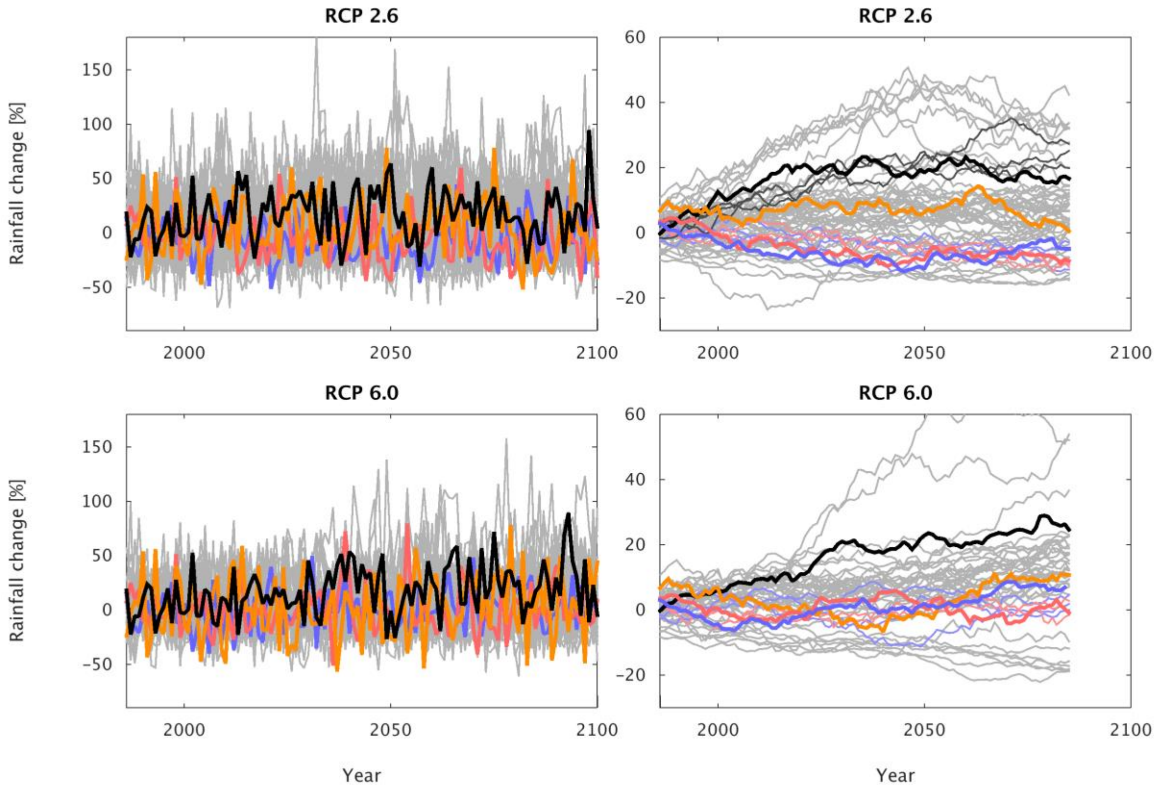


Figure C.3. ISI-MIP GCMs in comparison to other CMIP5 GCMs. We advise caution when interpreting our results because the four GCMs included in the ISI-MIP 2b experiments are not representative of the full range of CMIP5 GCM projections. Here thick coloured lines show GCMs included in the ISI-MIP 2b experiment, whilst thin coloured lines show additional ensemble members of these GCMs. Grey lines show all CMIP5 GCMs. Hence, if we had chosen to use alternative GCMs in our simulations, variation in projected rainfall between GCMs may have resulted in different elephant population projections.



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Publications

The following papers have been published and resulted from research conducted for this thesis:

Boult, V. L., Sibly, R. M., Quaife, T., Fishlock, V., Moss, C. J., & Lee, P. C. (2018). Modelling large herbivore movement decisions: beyond food availability as a predictor of ranging patterns. African Journal of Ecology, 57(1), 10–19.

Boult, V. L., Quaife, T., Fishlock, V., Moss, C. J., Lee, P. C., & Sibly, R. M. (2018). Individual-based modelling of elephant population dynamics using remote sensing to estimate food availability. Ecological Modelling, 387, 187–195.