

Individual-based modelling of elephant population dynamics using remote sensing to estimate food availability

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Individual-based modelling of elephant population dynamics using remote sensing to estimate food availability

Victoria L. Boulton (*corresponding author*)^a

- ^a University of Reading, School of Biological Sciences, UK
- Victoria.Boulton@pgr.reading.ac.uk or vlboulton93@hotmail.com
- 105 Harborne Building, University of Reading, Whiteknights, Reading, Berkshire, RG6 6AS, United Kingdom
- Tel: +44(0)7772 654 616

Tristan Quaife^b

- ^b University of Reading, Department of Meteorology, UK
- t.l.quaife@reading.ac.uk

Vicki Fishlock^{c, d}

- ^c Amboseli Trust for Elephants, Kenya & ^d Psychology, Faculty of Natural Sciences, University of Stirling, UK
- vfishlock@elephanttrust.org

Cynthia J. Moss^c

- ^c Amboseli Trust for Elephants, Kenya
- cmoss@elephanttrust.org

Phyllis C. Lee^{d, c}

- ^d Psychology, Faculty of Natural Sciences, University of Stirling, UK & ^c Amboseli Trust for Elephants, Kenya
- phyllis.lee@stir.ac.uk

Richard M. Sibly^a

- ^a University of Reading, School of Biological Sciences, UK
- r.m.sibly@reading.ac.uk

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 fits 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.

Keywords

Approximate Bayesian computation; Elephants; Energy budget; Individual-based modelling; Population dynamics; Remote sensing.

Highlights

- Energy-budget model of how individual elephants respond to changes in forage
- Population size and structure emerge from model outputs
- Predicts changes in population dynamics induced by climate and land-use change
- Can be adapted for other mammalian herbivores in grassland ecosystems

1. Introduction

Elephants are simultaneously a species of conservation concern and problem for coexisting humans (Evans and Adams, 2018; Hoare, 2000). 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 (Browne-Nunez et al., 2013; Wittemyer, 2011). 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 et al., 2006; Wittemyer et al., 2007); when resources are limited, animals 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 exacerbate 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 et al., 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-expenditure 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 ground-truthed 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.

2. Materials and methods

2.1. Study system

The Amboseli basin (bounding coordinates: -2.02N, -3.28S, 38.03E, 36.67W) covers an area of approximately 8000km², straddling the southern border of Kenya and the northern border of Tanzania. It comprises the central Amboseli National Park (ANP; 392km²) and surrounding landscape (Croze and Lindsay, 2011). The habitat consists of semi-arid savannah and bush, with permanent swamp vegetation present within ANP (Fig. 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 over 1600 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 et al., 2009), as elephant habitats

become increasingly human-dominated and human responses to elephants become shaped by local political and cultural dynamics (Okello, 2005).

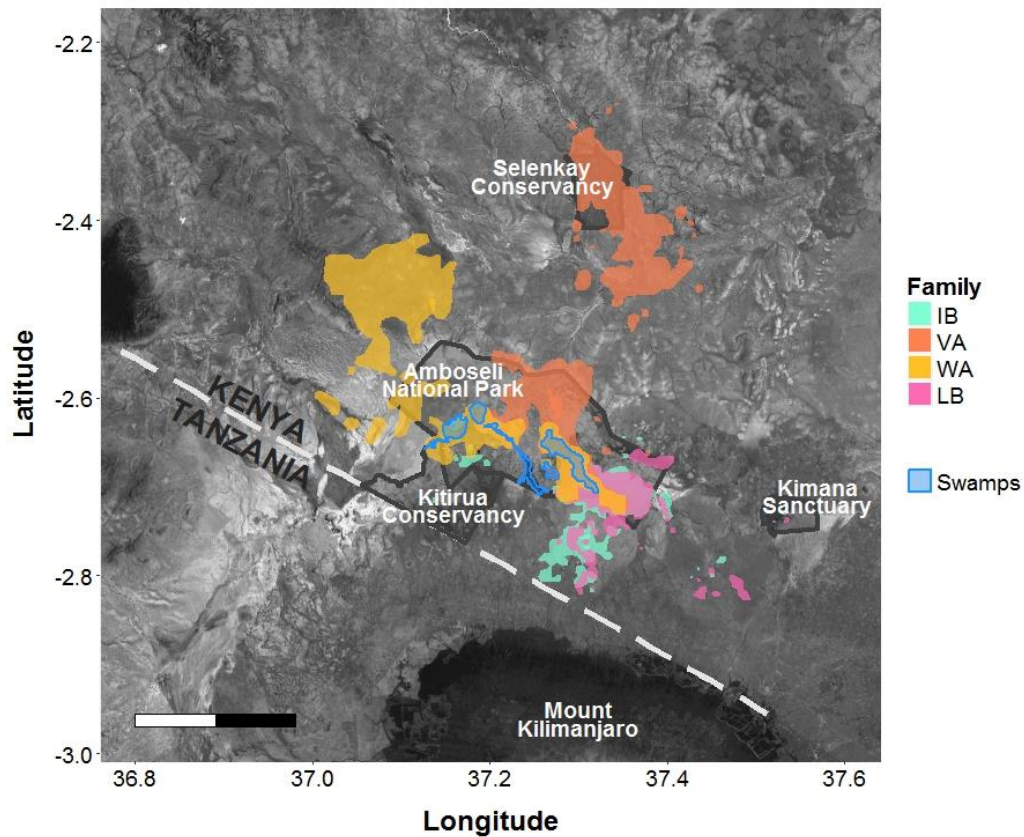


Figure 1. The home ranges (coloured polygons) of elephant family groups (IB, LB, VA and WA) included in the model. This represents the spatial extent of NDVI used to calculate time-specific food availability. Protected areas are indicated by dark grey boundaries, the international border between Kenya and Tanzania by the dashed white line, and the central Amboseli swamps in blue. Scale bar represents 10km (divisions of 5km).

2.2. 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 basin 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 et al., 2011). 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 Supplementary Materials: TRACE 3.2). The age of individuals born prior to start of the study was estimated using techniques including hind foot length (Lee and Moss, 1995, 1986; Western et al., 1983), tooth eruption and wear (Laws, 1966), tusk length (Moss, 1996, 1988) and circumference at the lip (Pilgram and Western, 1986), and shoulder height and back length (Croze, 1972; Laws et al., 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 et al. in review). Individual demographic records were used to initiate the model elephant population ($n = 126$ on 1st March 2000; see Supplementary Materials: TRACE table 5) and provided annual records of elephant population dynamics for model calibration (on 1st October 2000-2016; see 2.5.1).

2.3. 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 Pettoirelli 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 ground-truthed using on-the-ground measures of herb-layer biomass, collected biannually in ANP since 1982 (Lindsay, 1982, 1994, 2011; see TRACE 3.1). A single median NDVI value was calculated for the combined home ranges of family groups (95% kernel density estimates; Fig. 1; Shannon et al., 2006) 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.

2.4. 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 (Johnston et al., 2014; Railsback and Grimm, 2012; Sibly et al., 2013). 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 the Supplementary Material, 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).

2.4.1. State variables and scales

The modelled environment represents the combined home ranges of the four family groups as a single patch (Fig. 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 was available.

2.4.2. 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; Fig. 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 (Hollister-Smith et al., 2007; Karkach, 2006; Shrader et al., 2006), 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.

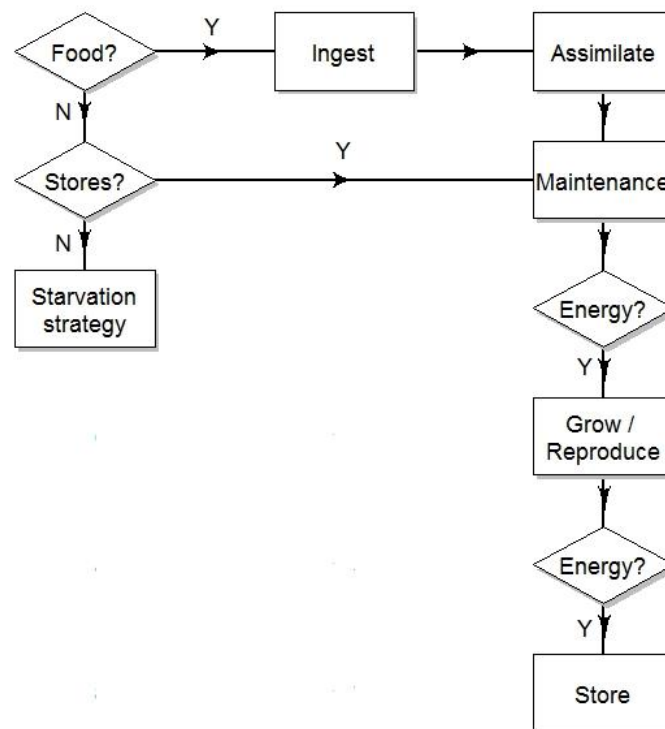


Figure 2. Overview of the daily updating of each individual's energy budget. If energy is available through reserves, an individual will utilise this energy in maintenance, growth and reproduction. If insufficient energy remains to cover costs of maintenance, individuals enter starvation. These energy 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 TRACE 4.2) responds accordingly (Fig. 3).

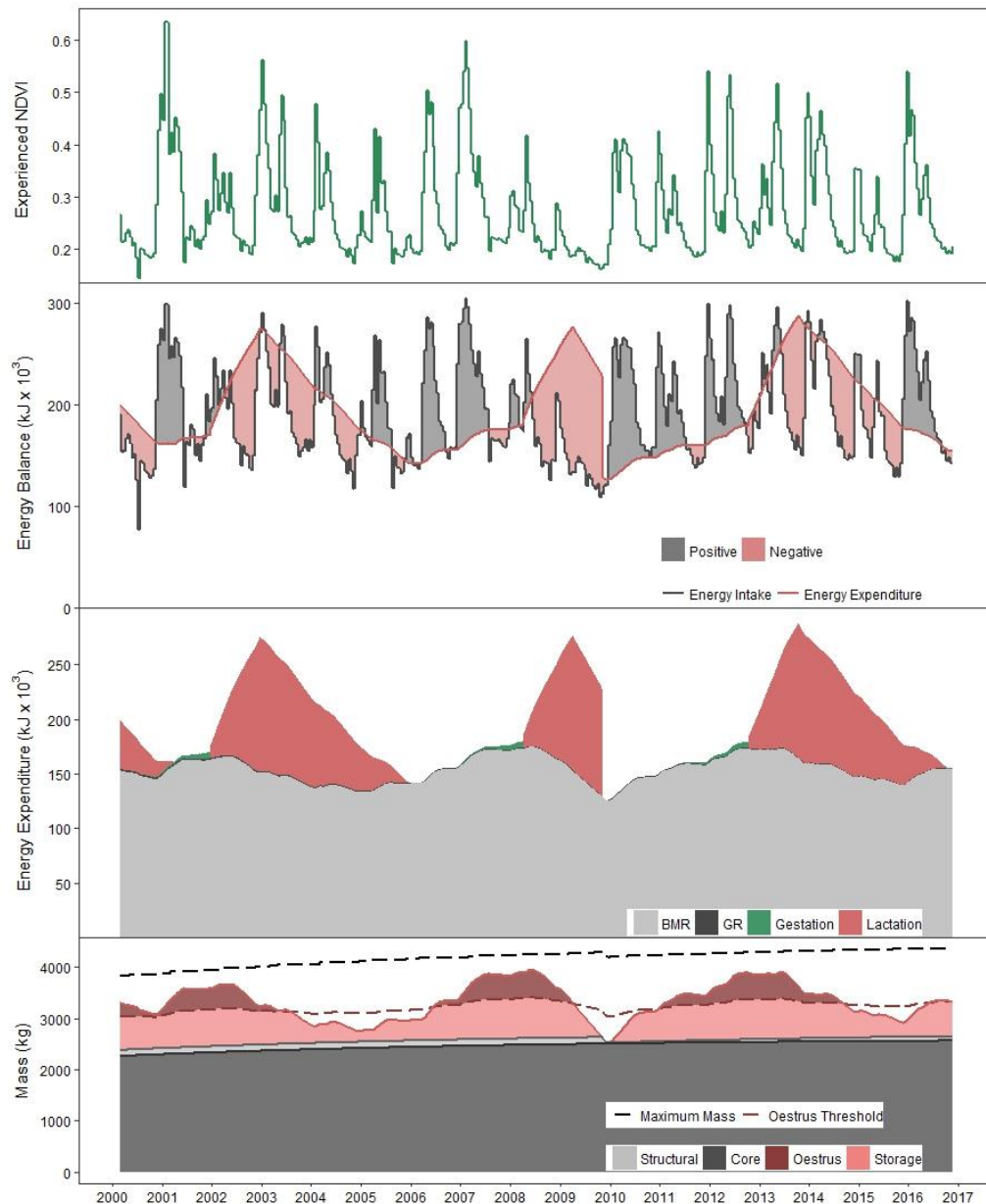


Figure 3. Energy balance and resulting body composition of adult female elephant, Ilka, throughout the model period 2000-2016. The top plot shows the NDVI experienced by Ilka. NDVI is used here as a proxy for food availability, peaking during the biannual wet seasons and declining as the dry seasons 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.

2.4.3. 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 $\frac{3}{4}$ 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 *et al.*, 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 $\frac{3}{4}$ 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 *et al.*, 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 *et al.*, 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 et al., 2001).

2.5. Analysis

2.5.1. Calibration

Eleven parameters were deemed uncertain and thus required calibration to accurately predict population dynamics (see TRACE 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 fit 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, 2014; Thiele et al., 2012).

2.5.2. 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.

2.5.3. 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 TRACE 4.1). The model was initialised for these individuals (population on 1st March 2000; see TRACE table 6) and run with the adjusted NDVI input data.

2.6. Hypothetical range loss scenario

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 basin 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.

3. Results

3.1. 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 Fig. 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.

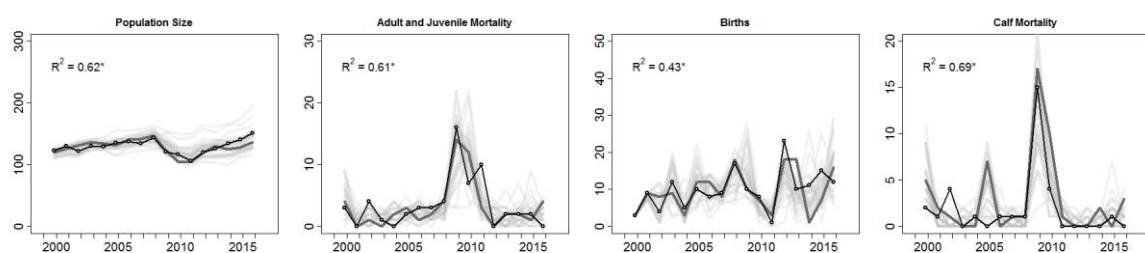


Fig 4. Population size, births and deaths for modelled families in Amboseli years 2000 – 2016. Black lines and open points show the data, the thick grey line is the best fitting simulation. Light grey lines show the 30 best fitting simulations indicating the uncertainty in model outputs that result from uncertainty in the values of parameters. Amboseli years run October to September. R^2 of best fitting simulation presented on plot. * indicates significance with $p < 0.05$.

3.2. Sensitivity analysis

Sensitivities of key variables to model parameters are shown in Table 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 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 \pm 3.02	0.02 \pm 2.14	-0.14 \pm 9.83	-0.31 \pm 2.26
Hsc	-2.30 \pm 3.19	-1.30 \pm 2.81	0.70 \pm 12.39	0.94 \pm 1.66
$maxIR_{scaling}$	4.76 \pm 4.09	2.69 \pm 3.26	-0.63 \pm 15.91	-3.98 \pm 1.68
AE_{veg}	4.34 \pm 4.87	2.38 \pm 3.38	-0.38 \pm 15.88	-4.28 \pm 2.16
AE_{milk}	-0.42 \pm 2.82	-3.39 \pm 4.57	0.70 \pm 13.33	-14.93 \pm 3.9
B_0	-3.71 \pm 3.59	0.63 \pm 3.9	0.18 \pm 17.13	15.95 \pm 2.83
E_0	-0.52 \pm 3.37	-3.48 \pm 5.71	0.74 \pm 11.5	-15.00 \pm 4.32
E_{PL}	-1.82 \pm 2.59	-0.89 \pm 2.64	0.86 \pm 12.34	0.88 \pm 2.14
MR_{back}	-0.15 \pm 2.65	-0.14 \pm 2.16	-0.05 \pm 11.06	0.02 \pm 1.09
$MR_{scaling}$	0.08 \pm 1.95	0.05 \pm 1.97	0.09 \pm 10.38	-0.12 \pm 2.36
DD	-1.19 \pm 3.07	-0.67 \pm 3.21	0.32 \pm 10.88	0.65 \pm 1.92

3.3. 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 (Fig. 5). Model predictions match these data well though the peak in birth rates was predicted a year late following the 2009 drought.

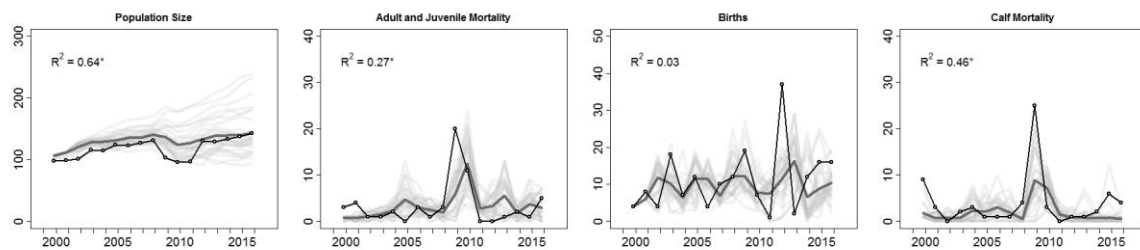


Figure 5. Validation of model fit. Population size, births and deaths for families not used in model calibration. Black lines and open points show the data, light grey lines show the 30 simulations indicating the uncertainty in model outputs that results from uncertainty in the values of parameters. R^2 of mean simulation presented on plot. * indicates significance with $p < 0.05$.

3.4. 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 (Fig. 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.

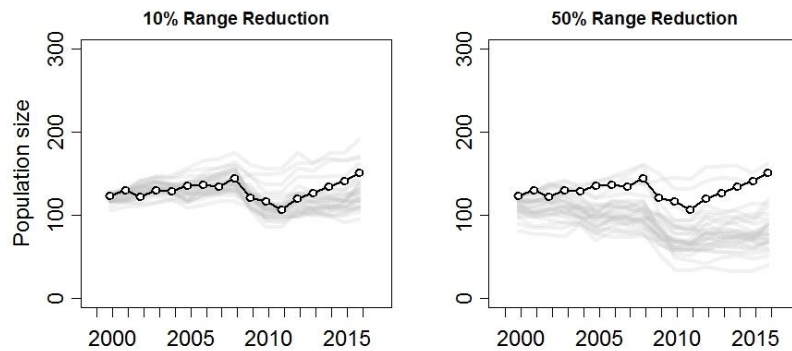


Figure 6. Population size for modelled families in Amboseli years 2000 – 2016 given hypothetical scenarios of 10% and 50% range loss. Black lines and open points show the observed population size data, light grey lines show the 30 simulations indicating the uncertainty in model outputs that result from uncertainty in the values of parameters.

4. Discussion

Following calibration, the model generally fits 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 basin 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. 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 et al., 2008; Wato et al., 2016; Woolley, 2008). 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 ground-truthing. Ground-truthing 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 et al., 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.

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Data Accessibility Statement

All data and files required to run the model and replicate the analyses are available in an online repository (https://github.com/vlboult93/EEB_Model.git).

Competing Interests Statement

Declarations of interest: none

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