1 Individual-based modelling of elephant population

2 dynamics using remote sensing to estimate food availability

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35 ## Abstract

36 Strategies for the conservation and management of many wild species requires an improved

37 understanding of how population dynamics respond to changes in environmental conditions,

38 including key drivers such as food availability. The development of mechanistic predictive models, in

39 which the underlying processes of a system are modelled, enables a robust understanding of these

40 demographic responses to dynamic environmental conditions. We present an individual-based

41 energy budget model for a mega-herbivore, the African elephant (*Loxodonta africana*), which relates

42 remotely measured changes in food availability to vital demographic rates of birth and mortality.

43 Elephants require large spaces over which to roam in search of seasonal food, and thus are vulnerable

44 to environmental changes which limit space use or alter food availability. The model is constructed

45 using principles of physiological ecology; uncertain parameter values are calibrated using approximate

46 Bayesian computation. The resulting model fits observed population dynamics data well. The model

47 has critical value in being able to project elephant population size under future environmental

48 conditions and is applicable to other mammalian herbivores with appropriate parameterisation.

49 ## Keywords

50 Approximate Bayesian computation; Elephants; Energy budget; Individual-based modelling;

51 Population dynamics; Remote sensing.

52 ## Highlights

53 - Energy-budget model of how individual elephants respond to changes in forage

54 - Population size and structure emerge from model outputs

55 - Predicts changes in population dynamics induced by climate and land-use change

56 - Can be adapted for other mammalian herbivores in grassland ecosystems

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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, 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 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-expending processes. These equations are broadly applicable to a wide variety of taxa, but parameters controlling these relationships vary interspecifically.

95 Occasionally, these parameters have been empirically determined for a species, but more often than

96 not this information is lacking. Empirical studies to estimate values are not always feasible due to

97 funding and time constraints, lack of appropriate methods and equipment, or ethical considerations.

98 Elephants, like many mega-herbivores, are a species for which empirical determination of some

99 physiological parameters is intrinsically difficult: elephant physiology does not lend itself to laboratory

100 studies nor can physiological parameters be readily determined in the field. Estimation of parameter

101 values is however possible using inverse modelling if, as here, data to hand include records of key

102 drivers (food availability) and resulting population dynamics.

103 Here we construct a model of individual energy budgets based on current understanding of

104 physiological ecology, with parameters specifying energy allocation between the vital life processes of

105 maintenance, growth and reproduction. Each individual in the IBM has its own energy budget and

106 lives in a population in an environment for which food availability is known from ground-truthed

107 remotely-sensed measurements. Emergent population dynamics are compared to observed rates of

108 reproduction and mortality, and parameter values are obtained through calibration using

109 approximate Bayesian computation (ABC; Van Der Vaart et al., 2015) – an example of inverse

110 modelling. Our aim is to develop a mechanistic model with good predictive qualities that can serve to

111 forecast future population dynamics in response to climate change and alternative management

112 scenarios.

113 ## 2. Materials and methods

114 ### 2.1. Study system

115 The Amboseli basin (bounding coordinates: -2.02N, -3.28S, 38.03E, 36.67W) covers an area of

116 approximately 8000km^2, straddling the southern border of Kenya and the northern border of

117 Tanzania. It comprises the central Amboseli National Park (ANP; 392km^2) and surrounding landscape

118 (Croze and Lindsay, 2011).The habitat consists of semi-arid savannah and bush, with permanent

119 swamp vegetation present within ANP (Fig. 1). Fluctuations in vegetation availability and quality are

120 driven by two wet seasons: the short-rains (November-December) and the long-rains (March through

121 May; Croze & Lindsay, 2011). The basin is home to over 1600 individually-known and monitored

122 elephants (Lee et al., 2013). The population has remained largely undisturbed by poaching, although

123 human population growth and a shift from nomadic pastoralism to sedentary farming poses a

124 significant threat to the future of Amboseli elephants (Western et al., 2009), as elephant habitats

125 become increasingly human-dominated and human responses to elephants become shaped by local

126 political and cultural dynamics (Okello, 2005).

127 ### 2.2. Elephant population dynamics

128 The Amboseli Elephant Research Project (AERP) has monitored more than 3,300 individually-known

129 elephants from over 60 family groups in the Amboseli basin since 1972. Elephants are identified by

130 means of a photo recognition file illustrating unique identifying features; calves are identified through

131 association with their known mothers (Moss et al., 2011). Censuses are attempted on a monthly basis

132 for all family groups noting individuals present and those missing. By tracking individuals in this

133 manner throughout their lives, birth and death dates are recorded.

134 *Births*: New-born and young calves are aged based on body size and proportions, skin colouration,

135 motor coordination, and behaviour of both mother and calf (Moss, 1988). Since 1978, when the last

136 family unit was identified, age estimates are mostly within 1 month (see Supplementary Materials:

137 TRACE 3.2). The age of individuals born prior to start of the study was estimated using techniques

138 including hind foot length (Lee and Moss, 1995, 1986; Western et al., 1983), tooth eruption and wear

139 (Laws, 1966), tusk length (Moss, 1996, 1988) and circumference at the lip (Pilgram and Western,

140 1986), and shoulder height and back length (Croze, 1972; Laws et al., 1975; Lee and Moss, 1995;

141 Moss, 1996; Shrader et al., 2006; Trimble et al., 2011). Age was backdated to give an estimate of birth

142 date for all individuals and has been validated by collection of lower jaws post-mortem whenever

143 possible (Lee et al., 2012).

144 *Deaths*: Determining date of death for individual elephants has proven more difficult. In family

145 groups, if an adult female was absent but her youngest calves present, the family was monitored

146 closely. If her absence was prolonged for more than a week, while the rest of the family were sighted

147 with her youngest offspring, she was assumed dead. For calves under three years old, absence whilst

148 their mother was present suggested the calf had died. If a juvenile female or an adult female with her

149 calves was missing, these individuals were assumed dead if not sighted for a month with their family.

150 Once it was concluded an individual had died, the death date was recorded as the midpoint between

151 when the individual was last seen alive and when they were first noted as missing. Rarely (<5% of

152 records), mortalities were more directly monitored due to illness or injury, or when carcasses were

153 found and identified. For the purposes of model analysis, we defined 'calf' mortality as deaths

154 occurring in individuals less than two years of age and 'adult and juvenile' mortality as deaths

155 occurring in individuals two years or older. This reflects the differing energetic thresholds controlling

156 mortality in these groups: calf mortality occurs when mothers' stores (fat) reaches zero; adult and

157 juvenile mortality occurs beyond this point, when all non-essential structural tissues (muscles) have

158 also been depleted.

159 For the purposes of model development and calibration, we modelled the population dynamics of

160 four family groups (IBs, LBs, VAs and WAs). These families were chosen due to regular monitoring

161 providing good confidence in birth and death dates, and good understanding of movement patterns

162 owing to GPS collars fitted to females in these families (Boult et al. in review). Individual demographic

163 records were used to initiate the model elephant population (n = 126 on 1st March 2000; see

164 Supplementary Materials: TRACE table 5) and provided annual records of elephant population

165 dynamics for model calibration (on 1st October 2000-2016; see 2.5.1).

166 2.3. Estimating food availability

167 We estimated food availability using 16-day composite values of the Normalised Difference

168 Vegetation Index (NDVI; MOD13Q1 product; Didan, 2015). NDVI is a general measure of the

169 greenness of the top layer of the Earth's surface and generally correlates well with ground-based

170 measures of vegetation biomass, primary productivity and leaf area index, and has been widely used

171 in models of animal performance and movement (reviewed in Pettorelli et al., 2011, 2005). We

172 obtained measures of NDVI from the NASA Terra-MODIS (Moderate Resolution Imaging

173 Spectroradiometer) mission accessed via the Oak Ridge National Laboratory web service (Vannan et

174 al., 2011). Terra-MODIS was used rather than Aqua-MODIS because of the longer NDVI time-series

175 available (Terra operational since 2000, Aqua since 2002). We chose not to combine the two MODIS

176 sensors given that cloud cover was not a particular issue for satellite observation of Amboseli. Data

177 were filtered using the MOD13Q1 QA flags so that only 'good' quality NDVI observations were

178 considered in our calculations. NDVI values were ground-truthed using on-the-ground measures of

179 herb-layer biomass, collected biannually in ANP since 1982 (Lindsay, 1982, 1994, 2011; see TRACE

180 3.1). A single median NDVI value was calculated for the combined home ranges of family groups (95%

181 kernel density estimates; Fig. 1; Shannon et al., 2006) for each 16-day composite and converted to

182 biomass (kg m^{-2}) in the model. The decision to use a single median NDVI value at each time step was

183 taken firstly, because of uncertainty as to where each family was in its range and secondly, to reduce

184 model run time.

185 2.4. Model description

186 The model relates spatiotemporal variation in food availability to changes in vital demographic rates

187 through individual energy budgets. Individuals forage on locally available food and the assimilated

188 energy is allocated to the energy-expending processes of life; from this population dynamics emerge

189 (Johnston et al., 2014; Railsback and Grimm, 2012; Sibly et al., 2013). In the future the model may be

190 applied as a tool for predicting the response of elephant populations to projected variation in food

191 availability resulting from climate change or land-use management strategies.

192 In the Supplementary Material, we provide a TRACE document ("TRAnsparent and Comprehensive

193 model Evaludation"; Augusiak and Van den Brink, 2014; Grimm et al., 2014, 2010; Schmolke et al.,

194   2010) containing evidence that our model was thoughtfully designed, correctly implemented,

195   thoroughly tested, well understood, and appropriately used for its intended purpose. This includes a

196   complete model description in the standard Overview, Design concepts and Details format (ODD;

197   Grimm et al., 2010).

198   2.4.1.   State variables and scales

199   The modelled environment represents the combined home ranges of the four family groups as a

200   single patch (Fig. 1), characterised by the time-specific median NDVI, resulting biomass, and energy

201   content of its vegetation. The elephant population in the model comprises the individuals in four

202   family groups – adult females and their immature offspring of both sexes (males become independent

203   of their natal group at 12 years old). These four families comprised 126 individuals at the time of

204   model initiation (1st March 2000). Elephants are characterised by variables describing their physiology

205   in terms of age, sex, mass, energetic processes and reproductive states. Each individual experiences

206   life through its own energy budget, the details of which depend on its age and sex. The model runs in

207   daily time steps from the 1st March 2000 until the 20th November 2016 – the time period for which

208   Terra-MODIS NDVI data was available.

209   2.4.2.   Model schedule

210   Elephants in the model execute procedures to update their energy budget once a day. The energy

211   budget model follows that described by Sibly et al. (2013; Fig. 2). Each individual begins with the

212   intake of energy if food is available in the environment. The assimilated energy along with energy in

213   storage tissues (fat) make up the 'energy reserves', and are available for use in energy expending

214   processes: maintenance takes priority, after which come growth and/or reproduction depending on

215   age, sex and energy reserves. Following maintenance, if energy reserves remain, sexually immature

216   individuals (females <9 years old and males <19) grow. Growth in elephants is prolonged (Hollister-

217   Smith et al., 2007; Karkach, 2006; Shrader et al., 2006), and individuals continue to grow beyond

218   sexual maturity if energy is available after paying the costs of reproduction. Only females reproduce in

219   the model as males disperse prior to sexual maturity. If energy remains following maintenance,

220   sexually mature females proceed through the reproductive cycle. Assimilated energy is always

221   utilised first and energy from stores is used only if required. If maintenance costs cannot be met by

222   reserves, individuals enter starvation and metabolise non-essential structural tissues (muscles). If

223   these tissues are depleted, an individual dies. Background mortality accounts for stochastic mortality

224   events.

225   The energy budget of an individual therefore responds to the energy available from food in the

226   environment. When food is abundant, as in wet seasons, energy intake exceeds energy-expenditure,

227 and individuals may allocate energy maximally to all processes and accumulate stores. When food is

228 limited, as in dry seasons or dry years (droughts), energy expenditure may outweigh energy intake,

229 and individuals must utilise stores in order to maintain growth and reproduction. Thus, as food

230 availability cycles through abundance and limitation, an individual's energy balance fluctuates

231 between positive and negative, and body composition (see TRACE 4.2) responds accordingly (Fig. 3).

232 2.4.3. Sub-models

233 Full details of each procedure, including equations and parameter derivation, are described in the

234 TRACE document.

235 *Energy intake*: Ingestion rate (IR; kg day^{-1}) depends on body size (scales to the ¾ power; Brown *et al.*

236 2004), age, food density (biomass) and consumer (elephant) density. In terms of age, elephants less

237 than a year old obtain all energy through the ingestion of milk; individuals are milk-dependent until

238 two years of age but begin supplementing milk intake with vegetation after a year; between the ages

239 of one and four, decreasing milk ingestion is supplemented with increasing vegetation intake; at four

240 years old elephants are weaned and feed entirely on vegetation. Suckling individuals first ingest milk

241 from their mother then, if over a year old, will ingest vegetation. The maximum vegetation IR is

242 reduced by the rate of ingestion already achieved through suckling. Food density (kg m^{-2}) also

243 influences vegetation ingestion, following a Holling type II functional response (Holling 1959; Lindsay

244 1994). This is adjusted according to a Beddington-DeAngelis functional response to account for

245 consumer-density dependent ingestion rate (Beddington, 1975; DeAngelis et al., 1975). If no food is

246 available, IR is zero. IR is converted to energy given the energy content of food (KJ kg^{-1}). Only a

247 proportion of energy ingested in milk or vegetation is available for energy expending processes

248 following assimilation efficiencies.

249 *Maintenance*: Basal metabolic rate (BMR; KJ day^{-1}) scales allometrically to the ¾ power with total

250 body mass and accounts for the standard costs of maintenance essential for survival, so has first call

251 on energy reserves (Sibly et al., 2013). If insufficient reserves remain to cover BMR, an individual

252 enters starvation and non-essential structural tissues (muscles) may be metabolised to cover these

253 costs (Atkinson et al., 1996). If all non-essential structural tissue is depleted, an individual dies.

254 *Growth*: After birth male and female elephants follow von Bertalanffy growth curves (Lindeque and

255 van Jaarsveld, 1993) resulting in the sexual dimorphism in stature observed in elephants. Parameters

256 of the von Bertalanffy growth curve fitted to shoulder height in the Amboseli elephants were taken

257 from Lee and Moss (1995) and the equation adapted to describe growth in mass rather than length

258 (Sibly et al., 2013). Daily growth rates depend on current structural mass and energy available. The

259   energy required to fuel maximum growth fuels both the synthesis and the energy content of new

260   tissue (KJ day^{-1}). If insufficient energy is available to grow maximally, growth may continue more

261   slowly. Any growth achieved is added to structural mass (kg).

262   *Reproduction*: Only female reproductive processes are represented in the model as males disperse

263   prior to sexual maturity. If energy remains following maintenance, sexually mature females proceed

264   through the reproductive cycle: oestrus, conception, gestation, parturition and lactation. Sexually

265   mature females experience oestrus and conceive if not already pregnant or lactating a milk-

266   dependent calf (<2 years), provided they have sufficient storage tissue (Bronson and Manning, 1991;

267   Wittemyer et al., 2007). Gestation typically lasts ~660 days (Poole et al., 2011) during which time a

268   female commits energy to foetal growth. If insufficient reserves remain to cover the energetic costs of

269   foetal growth (the synthesis and energy content of new tissue) the mother miscarries. Parturition

270   occurs at the end of gestation. Mother and calf are linked to relate the energy budget of a calf to that

271   of its mother. The sex of the calf is determined at random with equal probability of becoming a

272   female or male. The new-born calf has age zero and no energetic reserves. The mother lactates until

273   the calf is weaned at four years old, but the energy required for lactation varies throughout this

274   period (Oftedal 1985). Before the calf is a year old, milk forms the sole energetic intake so fully covers

275   the costs of maintenance and growth. Lactation peaks when the calf is a year old. For the first two

276   years of life, the calf is milk-dependent and so dies if its mother does, but after peak lactation, the

277   amount of milk supplied by the mother decreases at a constant daily rate as the calf increasingly

278   supplements this diet with vegetation. From two to four years of age the calf suckles at a decreasing

279   rate and is no longer dependent on milk, and can survive without its mother. The mother lactates

280   maximally if her energy reserves allow, but otherwise provides as much milk as her reserves allow.

281   Calves over a year of age may make up for this deficit by consuming more vegetation. If a mother dies

282   or enters starvation, lactation stops and the fate of the calf depends on its age and food availability. If

283   a calf dies, the mother stops lactating.

284   *Energy reserves*: If assimilated energy remains following all expenditure it is stored as fat until a

285   maximum is reached.

286   *Mortality*: In addition to mortality events described above, background mortality is included to

287   account for deaths arising from stochastic events such as poaching, predation, disease or injury.

288   When storage tissues remain, background mortality occurs at a constant rate for all individuals. This

289   rate increases during starvation to account for the increased susceptibility of starving individuals to

290   disease and risk-taking behaviour (Foley et al., 2001).

291   2.5. Analysis

292   2.5.1.   Calibration

293   Eleven parameters were deemed uncertain and thus required calibration to accurately predict

294   population dynamics (see TRACE 6). We calibrated these parameters using rejection approximate

295   Bayesian computation (ABC; Van Der Vaart *et al.* 2015): parameter values were sampled randomly

296   from uniform prior distributions ranging from roughly half to double the reference values; the model

297   was simulated 100,000 times; the 30 simulations which best fit the data (annual population size, birth

298   and mortality rates on 1st October 2000-2017) were accepted. We chose to accept the 30 best fitting

299   runs as a compromise between including only well-fitting runs and the need to produce posterior

300   distributions (van der Vaart et al., 2015). Simulations were run in parallel through R 3.3.1 using the R

301   package *RNetLogo* (Thiele, 2014; Thiele et al., 2012).

302   2.5.2.   Local sensitivity analysis

303   Local sensitivity analysis identified relative sensitivities of population size, birth rates, adult and

304   juvenile mortality, and calf mortality rates to changes in calibrated parameter values. Changes in

305   outputs were averaged over a 10% increase and decrease in each parameter, and over ten repeated

306   simulations to account for stochasticity in the model. While one parameter was tested all others were

307   kept at their calibrated values.

308   2.5.3.   Validation

309   To validate the model we compared model outputs to independent data from families not used in

310   model calibration for the time period 2000 - 2016. We used the 30 parameter sets accepted in the

311   ABC to simulate the population dynamics of six intensively recorded Amboseli elephant family groups

312   (AAs, FBs, GBs, JAs, KB2s and OBs; n = 105 initially on 1st March 2000). These families spend more time

313   in Amboseli National Park and thus use a different area to that used in model calibration (Remelgado

314   et al., 2017). However, the ranging patterns of these families have only been recorded within ANP.

315   Therefore, median NDVI was extracted from the 95% density kernels of known ranging within ANP and

316   the model was used to estimate the total area used by these families (see TRACE 4.1). The model was

317   initialised for these individuals (population on 1st March 2000; see TRACE table 6) and run with the

318   adjusted NDVI input data.

319   2.6. Hypothetical range loss scenario

320   To demonstrate the potential of the model to estimate elephant population size under environmental

321   change scenarios, we implemented two hypothetical range loss scenarios representing a 10% and 50%

322   reduction in home ranges. We assumed that the median NDVI was unaffected by range loss.

323   Increasing human populations in the Amboseli basin could result in elephant range loss through the

324   conversion of elephant habitats to cropland, over-grazing by livestock, the installation of fences or
325   transport links which may prevent movement across the ecosystem, or increasing HEI and resulting
326   avoidance of these areas by elephants. We ran each scenario with the 30 parameter sets accepted in
327   the ABC.

3.   Results

328   3.1. Calibration

330   We determined goodness of model fit to data using R^2 coefficient of determination. Model fits to the
331   population dynamic data are shown in Fig. 4. Adult and juvenile mortality rates were well predicted by
332   the model, which accurately replicated low levels of background mortality and captured the high
333   mortality rate associated with a drought in 2009. Modelled calf mortality also matched observations
334   well, again capturing background and drought-related rates, although the prediction for 2005 was too
335   high. Birth rates were well replicated throughout the simulation period, including low birth rates
336   following the 2009 drought and the subsequent 'baby-boom' in 2012, with the exception of under-
337   prediction in 2014 and 2015. As a result of model fit to birth and death rates, overall predictions of
338   population size were good, with slight under-prediction from 2014 onwards owing to the lower than
339   observed birth rates.

340   3.2. Sensitivity analysis

341   Sensitivities of key variables to model parameters are shown in Table 1 as the % change in the variable
342   relative to 10% changes in parameter values. Adult and juvenile mortality was the least and calf
343   mortality the most sensitive variable. Calf mortality was especially sensitive to parameters controlling
344   energy intake from milk (AE_{milk} and E_0) as expected given that milk provides the primary source of
345   energy for calves, and to B_0 which controls metabolic rate, the main source of energetic expenditure
346   for elephant calves. All population variables were relatively sensitive to parameters controlling energy
347   intake (hsc, $maxIR_{scaling}$ and AE_{veg}).

348   3.3. Validation

349   The model with its calibrated parameter values was validated by comparing its predictions with
350   independent data from a different family groups utilising a different area (Fig. 5). Model predictions
351   match these data well though the peak in birth rates was predicted a year late following the 2009
352   drought.

353   3.4. Hypothetical range loss scenarios

354   To demonstrate the model's potential application, we modelled the population size of the four family
355   groups (IBs, LBs, VAs, and WAs) given hypothetical reductions of 10% and 50% of their home ranges

[Type here]

356 (Fig. 6). Over the time period for which the model was calibrated, a 10% reduction in range had little

357 impact on the population size predictions throughout, whilst a 50% range loss predicts the end

358 population size was generally below 100 individuals, compared to 151 in reality.

359 ## 4. Discussion

360 Following calibration, the model generally fits the data well and in particular predicts the critical

361 events induced by the 2009 drought. The Amboseli elephant population as a whole declined by 25%

362 during the drought; in our modelled families, 16 adults and 15 calves died. Starving adult females

363 struggled to meet the demands of reproduction, resulting in the deaths of young calves and failure of

364 pregnancies. Despite the drought breaking at the end of 2009, the 22-month gestation period of

365 elephants meant there was a two-year lag in births with low numbers of births occurring in 2010 and

366 2011, but since drought acts to synchronise female reproduction there was a 'baby-boom' in 2012.

367 Such drought-induced population dynamics are critical in the natural regulation of population size and

368 are captured by the model, as indicated by the high R^2 values.

369 Elevated calf mortality predicted by the model in 2005 was the result of low median NDVI during this

370 period. In contrast to the 2009 drought, we believe elephants were able to buffer this period of low

371 productivity in 2005 by being more selective in their foraging locations and retreating to the fairly

372 constant source of food in the ANP swamps, hence mortality rates are low. This was not possible

373 during the 2009 drought, which began with a prolonged period of low rainfall in 2008, meaning 'fall-

374 back' resources such as the swamps were already depleted by the time the official drought occurred

375 in 2009. This resulted in the high mortality rates of both adults and calves in 2009. The under-

376 prediction of birth rates in 2014-2015 in both the calibration and validation of the model is possibly

377 because densities of other grazers are not considered in the model. The number of grazers in the

378 Amboseli basin remained in low for a prolonged period following the drought, limiting competition for

379 food for elephants. Incorporation of interspecific competitor density would be expected to improve

380 model fit to birth rates post-2009, as elephants access more food and reproduce more readily. The

381 under-prediction of population size from 2014 onwards results from under-prediction of birth rates in

382 this period.

383 The sensitivity analysis provided further support that the model was working accurately. The

384 robustness of adult and juvenile mortality to changes in parameter values reflects generally low

385 mortality rates in adult elephants whose large body size and substantial energy reserves allow them to

386 buffer fluctuations in energy intake and expenditure. Calf mortality on the other hand is extremely

387 sensitive, indicative of the vulnerability of young elephants to environmental changes (Foley et al.,

388 2008; Wato et al., 2016; Woolley, 2008). The overall sensitivity of all model outputs to parameters

389   controlling energy intake confirms that food availability is the key driver of elephant population

390   dynamics. This endorses the use of mechanistic approaches in modelling the bottom-up processes

391   controlling population dynamics.

392   Given the success of the model in predicting observed elephant population dynamics, we

393   demonstrated how this model may be applied to predict the response of elephant population size to

394   changes in their range. A range reduction of 50% caused the population size of modelled families to

395   decline, indicating that less absolute space would support fewer elephants. Whilst these scenarios

396   were hypothetical, the model may be easily adapted to simulate range reduction resulting from

397   specific land-management strategies such as the installation of fences or conversion of elephant

398   habitats into human-dominated landscapes, both of which are possible scenarios for the elephants of

399   Amboseli and elsewhere in Africa. The food availability input data may also be altered to simulate

400   changes in median NDVI resulting from, for example, climate change, provided the relationship

401   between NDVI and climatic variables is known. The use of NDVI here to represent herb-layer biomass

402   could be replicated in other open, grass-dominated ecosystems following ground-truthing. Ground-

403   truthing is crucial in order to exclude unintended land-cover types and identify any features which

404   may influence satellite-derived observations. By these means the model may also be readily applied to

405   other elephant populations whose ranging patterns are known, or to other mammalian herbivores

406   inhabiting grass-dominated ecosystems following re-parameterisation of the model. When considering

407   application to species with finer-scale movements, it may be necessary to utilise a remote sensing

408   product with higher spatial resolution, such as Landsat or Sentinel. Improvements in the estimation of

409   biomass or food availability may perhaps be possible using alternative sensors, such as LiDAR, or

410   alternative variables, such as the enhanced vegetation index (EVI) or net primary productivity (NPP).

411   With the increasing demand for predictive modelling of population responses to environmental

412   change (Wood et al., 2018), we believe mechanistic models which relate key drivers to population

413   dynamics are appropriate for improving understanding of the processes underlying demographics and

414   for providing robust predictions under novel environmental conditions. We have presented a model

415   which relates elephant population dynamics to food availability and may be applied to understanding

416   how elephants will cope given projected climate change scenarios, land-use change and management

417   strategies. We hope that this will be used as a tool to aid the conservation and management of

418   elephant populations and the ecosystems they inhabit, and may be applied to other species of interest

419   to wildlife managers.

420

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429

Data Accessibility Statement

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

Competing Interests Statement

434 Declarations of interest: none

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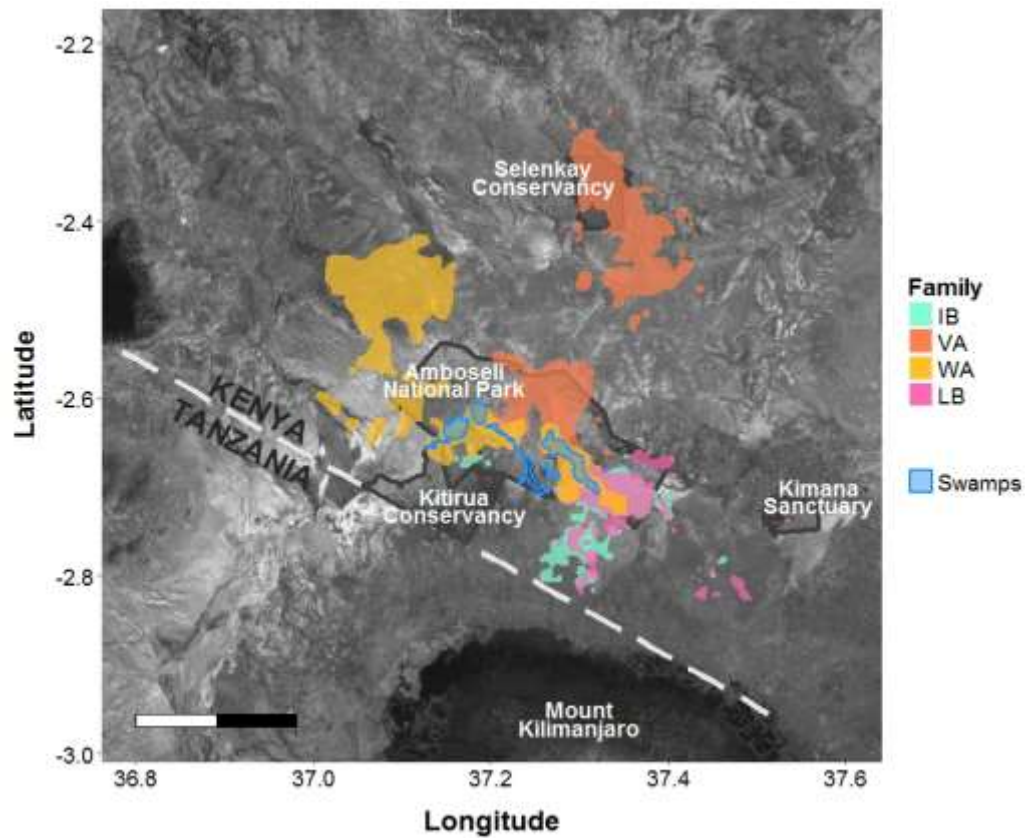
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Figure 1. The home ranges (coloured polygons) of elephant family groups (IB, LB, VA and WA) included in the model. This represents the spatial extent of NDVI used to calculate time-specific food availability. Protected areas are indicated by dark grey 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).
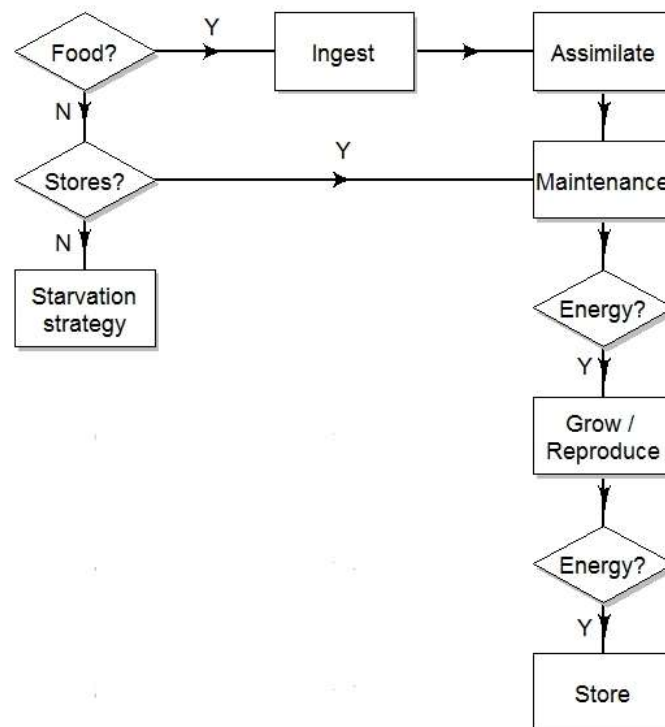
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Figure 2. Overview of the daily updating of each individual's energy budget. If energy is available through reserves, an individual will utilise this energy in maintenance, growth and reproduction. If insufficient energy remains to cover costs of maintenance, individuals enter starvation. These energy budgets cause births and deaths from which over time the population dynamics emerge.
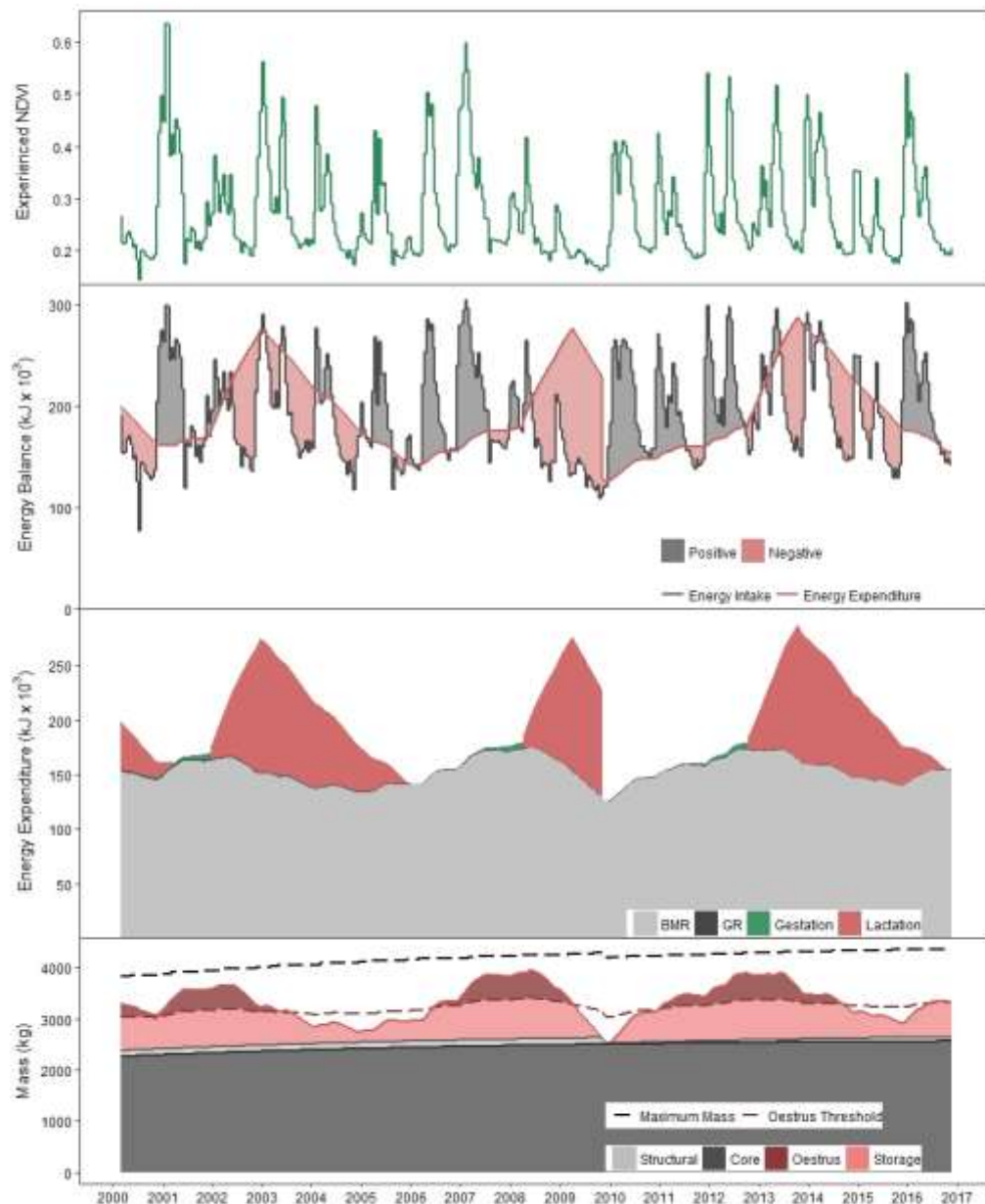
Figure 3. Energy balance and resulting body composition of adult female elephant, Ilka, throughout the model period 2000-2016. The top plot shows the NDVI experienced by Ilka. NDVI is used here as a proxy for food availability, peaking during the biannual wet seasons and declining as the dry seasons 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.
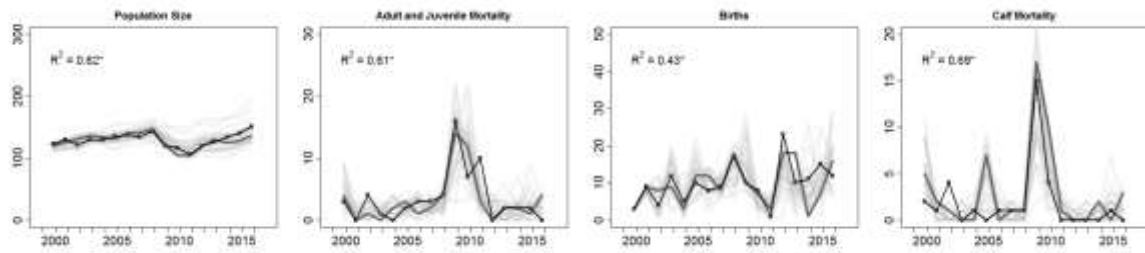
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Fig 4. Population size, births and deaths for modelled families in Amboseli years 2000 – 2016. Black lines and open points show the data, the thick grey line is the best fitting simulation. Light grey lines show the 30 best fitting simulations indicating 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 $p < 0.05$.
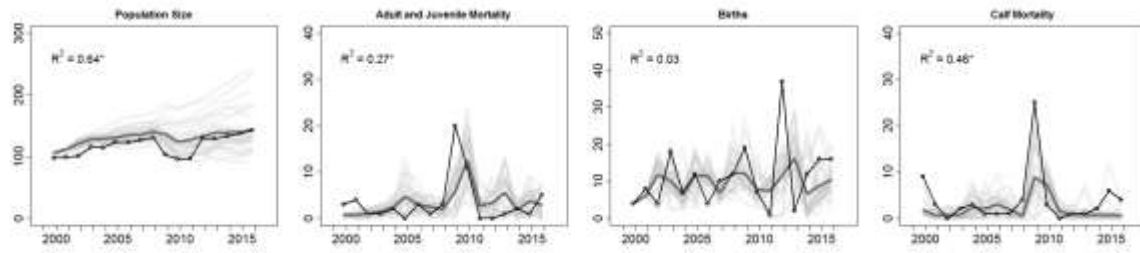
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Figure 5. Validation of model fit. Population size, births and deaths for families not used in model calibration. Black lines and open points show the data, light grey lines show the 30 simulations indicating the uncertainty in model outputs that results from uncertainty in the values of parameters. R^2 of mean simulation presented on plot. * indicates significance with $p < 0.05$.
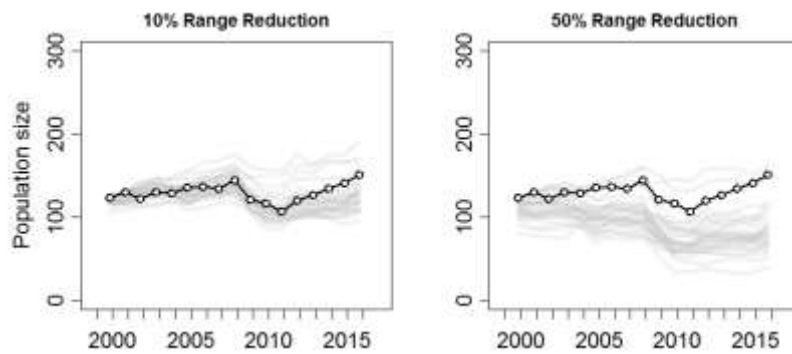
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Figure 6. Population size for modelled families in Amboseli years 2000 – 2016 given hypothetical scenarios of 10% and 50% range loss. Black lines and open points show the observed population size data, light grey lines show the 30 simulations indicating the uncertainty in model outputs that result from uncertainty in the values of parameters.

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 ± 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

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