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

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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.

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

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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 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 8000 km^2, straddling the southern border of Kenya and the northern border of Tanzania. It comprises the central Amboseli National Park (ANP; 392 km^2) 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 and 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).

2.2. Elephant population dynamics

The Amboseli Elephant Research Project (AERP) has monitored more than 3300 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.

2.2.1. 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).

2.2.2. 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) reach 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. 2018). 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 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