ORIGINAL ARTICLE

Drivers of megaherbivore demographic fluctuations: inference from elephants

M. J. Trimble, S. M. Ferreira & R. J. van Aarde

Conservation Ecology Research Unit, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

Abstract

Environmentally induced variation in survival and fecundity generates demographic fluctuations that affect population growth rate. However, a general pattern of the comparative influence of variation in fecundity and juvenile survival on elephant population dynamics has not been investigated at a broad scale. We evaluated the relative importance of conception, gestation, first year survival and subsequent survivorship for controlling demographic variation by exploring the relationship between past environmental conditions determined by integrated normalized difference vegetation index (INDVI) and the shape of age distributions at 17 sites across Africa. We showed that, generally, INDVI during gestation best explained anomalies in age structure. However, in areas with low mean annual rainfall, INDVI during the first year of life was critical. The results challenge Eberhardt's paradigm for population analysis that suggests that populations respond to limited resource availability through a sequential decrease in juvenile survival, reproductive rate and adult survival. Contrastingly, elephants appear to respond first through a reduction in reproductive rate. We conclude that this discrepancy is likely due to the evolutionary significance of extremely large body size – an adaptation that increases survival rate but decreases reproductive potential. Other megaherbivores may respond similarly to resource limitation due to similarities in population dynamics. Knowing how vital rates vary with changing environmental conditions will permit better forecasts of the trajectories of megaherbivore populations.

Introduction

Age-specific survival and birth rates determine the growth rate and age structure of closed populations. These variables change over time in response to changing environmental conditions, competitor abundance, density-dependence, predation intensity, disease incidence and human intervention (Sibly & Hone, 2002). In predator-free environments, resource availability, mediated by stochastic environmental variation and population density, strongly influences population dynamics (Sæther, 1997), possibly via sequential effects on juvenile mortality, fecundity and adult survival (Eberhardt, 2002). African elephants *Loxodonta africana* (Blumenbach, 1979) like most megaherbivores (adult body size $\geq 1000\,\text{kg}$), are not especially sensitive to predation (Owen-Smith, 1988), and large herbivores do not typically respond to density until they approach carrying capacity (Sibly & Hone, 2002). Therefore, environmentally induced variation in resource availability should drive elephant demographic fluctuation, that is variation in population size, growth rate and age structure.

Adult survival in large herbivores has a high elasticity, so changes in adult survival should have a disproportionately large effect on growth rate; however, variation in fecundity and juvenile survival may be greater and more frequent (Gaillard et al., 2000), prompting more temporal variation in population growth. Because elephant adult survival is relatively constant (Owen-Smith, 1988), variation in fecundity and juvenile survival likely drives population responses to changing environmental conditions.

However, studies of different elephant populations have highlighted the importance of different factors for influencing demographic fluctuations. Juvenile elephants are especially sensitive to drought-induced mortality (Moss, 2001; Loveridge et al., 2006). During dry periods, they may die from dehydration, inadequate nutrition, increased energy expenditure, intensified conflict with people (Moss, 2001) and lion predation, especially when juveniles can no longer keep up with the breeding herd's long movements between water sources and areas of adequate forage (Loveridge et al., 2006). Jachmann (1980) found a correlation between rainfall and the peaks and troughs of the age distribution of the Malawian
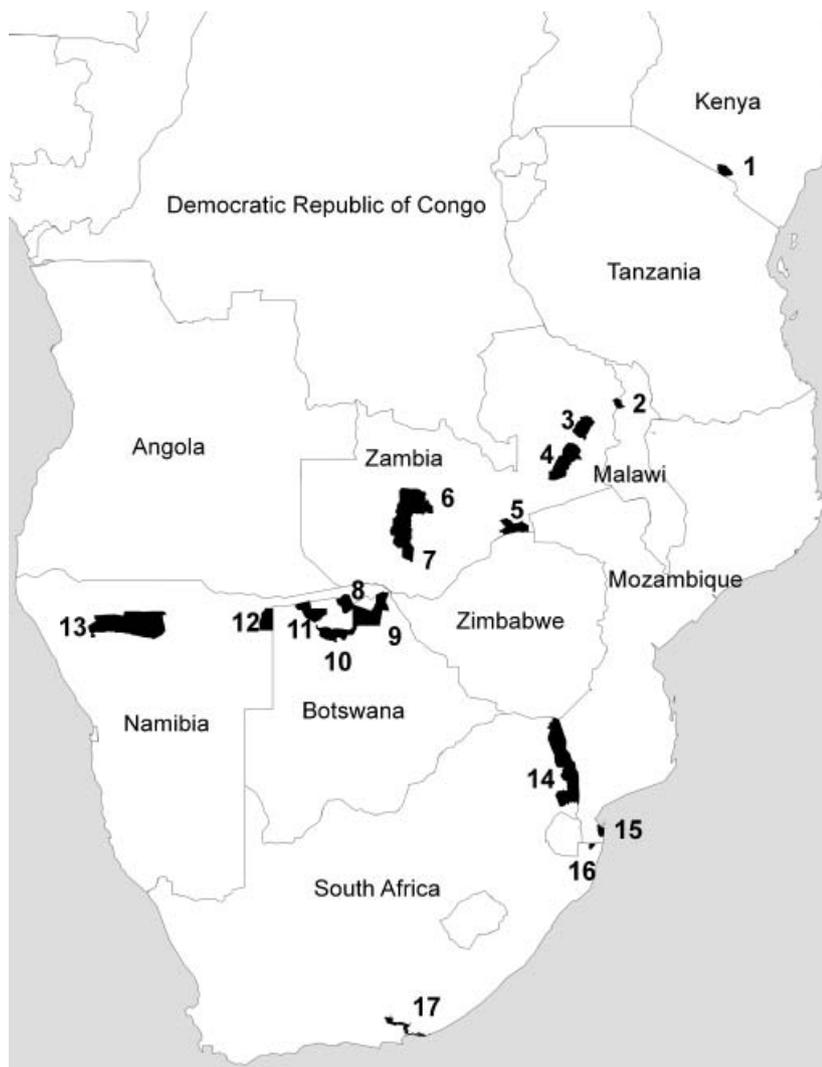
Figure 1 Locations of study sites. Rapid Elephant Population Assessments were carried out at 17 sites spanning seven African countries: (1) Amboseli National Park, (2) Vwaza Marsh Game Reserve, (3) North Luangwa National Park, (4) South Luangwa National Park, (5) Lower Zambezi National Park, (6) northern Kafue National Park, (7) southern Kafue National Park, (8) Linyanti Wildlife Reserve, (9) Chobe National Park, (10) Moremi Wildlife Reserve, (11) Ngamiland 11, (12) Khaudum Game Reserve, (13) Etosha National Park, (14) Kruger National Park, (15) Maputo Elephant Reserve, (16) Tembe Elephant Park and (17) Addo Elephant National Park.

Kasungu National Park population and posited that low rainfall in some years resulted in higher calf mortality.

Contrastingly, recent studies highlighted the role of fecundity in instigating demographic fluctuations. In South Africa's Addo Elephant National Park, elephant birth rates are positively correlated with rainfall during the year of conception (Gough & Kerley, 2006). Additionally, in Samburu National Reserve, Kenya, conception rate varies with vegetative productivity [measured with normalized difference vegetation index (NDVI)], whereas prenatal and juvenile survival do not (Wittemyer, Rasmussen & Douglas-Hamilton, 2007b). However, this model has not been confirmed for other populations.

We evaluate the relative influence of fecundity and juvenile survival on inter-annual demographic variation at 17 sites across Africa by exploring the relationship between a measure of environmental conditions, integrated normalized difference vegetation index (INDVI), and the shape of age distributions generated by Rapid Elephant Population Assessments (REPAs, Ferreira & van Aarde, 2008). We partition fecundity into conception rate and prenatal survi-

val and separate juvenile survival into first year survival and subsequent survivorship. These variables form the foundation of four biological hypotheses to explain demographic fluctuations. Namely, aberrations in observed age distributions should be primarily associated with (1) INDVI during the year before conception if conception rate is the principal driving variable; (2) INDVI during the 22-month gestation period if prenatal survival is most important; (3) INDVI within the year of birth if environmental factors primarily affect first year survival rates; (4) cumulative conditions after the first year of birth if survivorship is most influential. We assess the relative support for these four hypotheses with model selection procedures.

Methods

Demographic data

REPAs (Ferreira & van Aarde, 2008) were carried out at 17 sites spanning seven countries (Fig. 1). We surveyed each area once between 2003 and 2006 from mid-September to

Table 1 Results of model selection to explore the relationship between past environmental conditions determined by INDVI and the shape of age distributions at each of 17 study sites, 11 large undisturbed populations grouped and sites grouped based on mean annual rainfall – low ($<$522 mm), medium ($>$522 $<$786 mm) and high ($>$786)

Population	Population estimate	Sample size	Annual rainfall (mm)	r^2 of global model	AIC_c best model[a]	w_i of best model	Other plausible models	Relative variable importance			
								1	2	3	4
Small[c]											
Addo	459	162	401	0.352	1	0.355	3; 4	0.521[b]	0.219	0.237	0.269
Tembe	167	91	743	0.249	2	0.288	1; 3; 4	0.255	0.426[b]	0.271	0.271
Vwaza	270	109	788	0.218	2	0.272	1; 3; 4	0.278	0.403[b]	0.263	0.273
Maputo	200	107	785	0.281	4	0.262	1; 2; 3	0.323	0.242	0.277	0.391[b]
Disturbed[c]											
South Luangwa	4459	517	878	0.0856	4	0.238	1; 2; 3	0.283	0.284	0.284	0.342[b]
North Kafue	582[d]	424	956	0.160	2	0.213	1; 3; 4	0.299	0.317[b]	0.315	0.276
Other[c]											
Etosha	2057	249	406	0.421	3 (2)	0.218	1; 2; 4	0.270	0.340	0.349[b]	0.276
Moremi	31 191[e]	314	466	0.349	2	0.265	1; 3; 4	0.259	0.408[b]	0.305	0.268
Ngamiland 11	3579[f]	469	497	0.341	3	0.222	1; 2; 4	0.314	0.274	0.346[b]	0.293
Chobe	40 767	490	521	0.609	3 (1)	0.234	1; 2; 4	0.307	0.277	0.345[b]	0.279
Khaudum	3787	442	524	0.413	2	0.239	1; 3; 4	0.278	0.363[b]	0.285	0.295
Kruger	12 427	408	561	0.659	1	0.313	2	0.477[b]	0.365	0.232	0.254
Linyanti	8725[g]	357	562	0.329	2	0.307	1; 3; 4	0.253	0.443[b]	0.229	0.303
Amboseli	1417	314	668	0.643	1 (1,2)	0.223	1,2; 2; 3; 4	0.518[b]	0.516	0.189	0.190
Lower Zambezi	1477	300	769	0.520	1	0.504		0.623[b]	0.265	0.186	0.216
South Kafue	810[d]	279	847	0.856	2	0.454		0.238	0.802[b]	0.206	0.197
North Luangwa	3235	447	927	0.572	2	0.257	1,2; 1; 3; 4	0.406	0.514[b]	0.227	0.212
Grouped (11 sites)				0.201	1,2,3,	0.212	1,2,3,4; 1,2; 2,3; 2,4; 2	0.540	0.994[b]	0.532	0.322
Low rainfall (four sites)				0.131	3	0.192	2,3; 1; 2; 4	0.315	0.453	0.563[b]	0.308
Medium rainfall (five sites)				0.250	2	0.274	1,2; 2,3; 2,4	0.400	0.941[b]	0.291	0.321
High rainfall (two sites)				0.650	1,2	0.252	1,2,3; 2,3; 2	0.590	0.956[b]	0.389	0.231

Population estimates are from Blanc et al. (2007) unless otherwise noted. Model codes represent 1 – conditions before conception, 2 – conditions during gestation, 3 – first year conditions and 4 – cumulative conditions after the first year.

[a]Models in parentheses indicate selected best when using variables constructed with 'core period' conditions yielded different results.

[b]The top ranked variable for each site or group.

[c]See discussion for explanation of population classification.

[d]Guldemond et al. (2005).

[e]Estimate for Okavango Delta.

[f]Jackson et al. (2008).

[g]Estimate for Caprivi Region.

early November. We used digital photogrammetry (Shrader, Ferreira & van Aarde, 2006a) to estimate shoulder heights or back lengths of elephants in breeding herds; we followed a predetermined flight plan and surveyed each herd encountered (see Table 1 for sample sizes). We compared these estimates with sex-specific growth curves to estimate age using the method developed by Shrader et al. (2006b). Given the confidence intervals for the growth function (Shrader et al., 2006b), we incorporated uncertainty in age assignment by Monte Carlo simulation (Ferreira & van Aarde, 2008) and created proportional female age distributions for yearly age classes from 1 to 15, the limit of accurate female age assessment via photogrammetry (Shrader et al., 2006b).

To quantify deviations in each site's age distribution, the observed age structure data were smoothed into an age frequency function according to the log-polynomial regression (Caughley, 1977). This model represents the expectation that proportional age class frequencies should decline by a constant fraction with increasing age when age specific mortality is constant and the age distribution is stable. Thus, we considered deviations from the predicted model indicative of non-constant mortality or varying birth rates. We quantified these anomalies by calculating standardized residuals of the observed versus predicted proportional frequency for each age class.

Intra-annual reproductive patterns

To determine the periods over which environmental conditions should affect conception rate, prenatal survival, first year survival and survivorship at each site, we assessed the relationship between intra-annual reproductive patterns and environmental conditions using monthly conception and birth data collected from published sources (Table 2). We compared intra-annual reproductive patterns to monthly rainfall. When more than 1 year of data was available for a

Table 2 Monthly birth and conception data collected from published accounts

Data type	Population	Country	Years of data	Reference	Rainfall source
Births	Kasungu National Park (NP)	Malawi	1	Jachmann (1986)	Kasungu Admarc;
	Lake Manyara NP	Tanzania	5	Douglas-Hamilton (1972)	Kasungu Boma
	Amboseli NP	Kenya	20 + year mean	Moss (2001)	
Conceptions	Luangwa Valley	Zambia	6	Hanks (1972)	Chipata; Mpika
	Chirisa Safari Area	Zimbabwe	2	Craig (1984)	Lusulu
	Chizarira NP	Zimbabwe	1	Craig (1984)	Lusulu
	Hwange NP	Zimbabwe	2	Williamson (1976)	Hwange NPA
	Mana Pools NP	Zimbabwe	5	Kerr (1978)	Rucomiche
	west Gonarezhou NP	Zimbabwe	2	Sherry (1975)	Rutenga
	east Gonarezhou NP	Zimbabwe	2	Sherry (1975)	Rutenga
	Kruger NP	South Africa	6	Smuts (1975)	
	north Murchinson Falls NP	Uganda	3.5	Laws & Parker (1968), Laws et al. (1975)	Laws et al. (1975)
	south Murchinson Falls NP	Uganda	3.5	Laws & Parker (1968), Laws et al. (1975)	Laws et al. (1975)
	Tsavo East NP	Kenya	3.5	Laws & Parker (1968), Laws et al. (1975)	Laws et al. (1975)
	Mkomazi NP	Tanzania	1.5	Laws & Parker (1968), Laws et al. (1975)	Laws et al. (1975)

Rainfall source indicates the paper or rain station that provided rainfall data.
Station data were obtained from the African Data Dissemination Service (http://earlywarning.usgs.gov/adds/index.php, accessed October 2007).
To make the birth and conception datasets comparable, we backdated births by 22 months, the gestation period of elephants.

site, we pooled monthly conception and rainfall data so that each site contributed equally towards the analysis. Conception and rainfall data were then converted to proportions. We used one-way ANOVA to assess conception timing separately for eastern and southern African populations using the full complement of sites. We then used data from the populations for which we had rainfall information to assess the relationship between monthly rainfall and monthly conceptions.

This analysis suggested that a peak in monthly conceptions should occur 1 month after peak rainfall (see 'Results'). Additionally, conception peak has been shown to follow peak seasonal NDVI by c. 1 month (Wittemyer et al., 2007b). Thus, for each site in our analysis, we calculated mean monthly rainfall [extracted from Worldclim 5 arc-minute precipitation maps representative of 1950–2000 (http://www.worldclim.org, accessed October 2007)] and mean monthly maximum NDVI. When the month with highest mean rainfall and highest mean maximum NDVI were the same for a site, we assumed the conception peak occurred in the subsequent month. When peak rainfall and peak NDVI differed by 1 month, we used the rainfall data to determine conception peak, and when they differed by 2 months, we assumed the conception peak would occur after the middle month. We based our estimate of conception peak for Amboseli on published data (Moss, 2001).

Given these site-specific estimates of conception peak, we determined the periods over which we expected environmental conditions to affect conception rate, prenatal survival, first year survival and survivorship for each age class at each site. Thus, we could expect conception rate to be affected by the conditions in the year before conception, prenatal survival during the gestation period 22 months before birth, first year survival in the year after birth and survivorship over the subsequent life of the age class. Additionally, our analysis suggested that most conceptions occur during a 4-month period in southern Africa (see

'Results'). To assess the robustness of our approximation of a birth peak population, we also determined the core periods that would affect the four variables by eliminating from the analysis 4-month periods surrounding conception, birth and end of the first year of life.

NDVI variability

Vegetation productivity was assessed with NDVI (see Pettorelli et al., 2005). For the period from 1984 to 2003, we used 15-day composites [National Oceanographic and Atmospheric Association's Advanced Very High Resolution Radiometer (AVHRR) processed by the Global Inventory Monitoring and Modeling Studies group and downloaded from the Global Land Cover Facility: http://glcf.umiacs.umd.edu/data/gimms, accessed September 2007]. For 2002 to 2006, we used 10-day composites [The Centre National d'Etudes Spatiales's Satellite Pour l'Observation de la Terre, Vegetation (SPOT-VGT) processed and distributed by VITO: http://free.vgt.vito.be/, accessed October 2007].

Both datasets were converted to the −1 to + 1 NDVI scale (Pettorelli et al., 2005). Monthly composites were created by selecting the highest value for each pixel from two 15-day composites for the AVHRR dataset and three 10-day composites for the SPOT-VGT dataset; this method reduces noise caused by cloud cover, water and shadow (Pettorelli et al., 2005). We further reduced noise by ignoring negatively valued pixels in subsequent analysis. We calculated the mean NDVI for each month over the spatial extent of each of the 17 study areas. Mean NDVI values closely correlated with maximum and minimum pixel values for each site indicating adequate representation of variability. We combined and calibrated the two datasets using a 2-year overlap.

Next, we generated NDVI indices to represent the conditions expected to affect conception rate, prenatal survival, first year survival and survivorship for each age class at each site. We summed the monthly average NDVI values for each

site over each period to generate INDVI, a proxy for total vegetative production (Pettorelli *et al.*, 2005). To standardize this value among sites, we divided the INDVI for each period by its site-specific mean over the study period. For conception rate, prenatal survival and first year survival variables, we used standardized INDVIs. However, for survivorship, we used the number of below average years experienced by each age class.

Model selection

The hypotheses that deviations in age distributions were caused by environmentally induced variation in conception rate, prenatal survival, first year survival, subsequent juvenile survivorship or a combination thereof were expressed as 15 candidate models (Table 3). These models were assessed with

Table 3 Set of candidate models

Model	Parameters
$y = \alpha_0 + \alpha_1 x_1 + \alpha_2 x_2 + \alpha_3 x_3 + \alpha_4 x_4$	6
$y = \alpha_0 + \alpha_1 x_1 + \alpha_2 x_2 + \alpha_3 x_3$	5
$y = \alpha_0 + \alpha_1 x_1 + \alpha_2 x_2 + \alpha_4 x_4$	5
$y = \alpha_0 + \alpha_1 x_1 + \alpha_3 x_3 + \alpha_4 x_4$	5
$y = \alpha_0 + \alpha_2 x_2 + \alpha_3 x_3 + \alpha_4 x_4$	5
$y = \alpha_0 + \alpha_1 x_1 + \alpha_2 x_2$	4
$y = \alpha_0 + \alpha_1 x_1 + \alpha_3 x_3$	4
$y = \alpha_0 + \alpha_1 x_1 + \alpha_4 x_4$	4
$y = \alpha_0 + \alpha_2 x_2 + \alpha_3 x_3$	4
$y = \alpha_0 + \alpha_2 x_2 + \alpha_4 x_4$	4
$y = \alpha_0 + \alpha_3 x_3 + \alpha_4 x_4$	4
$y = \alpha_0 + \alpha_1 x_1$	3
$y = \alpha_0 + \alpha_2 x_2$	3
$y = \alpha_0 + \alpha_3 x_3$	3
$y = \alpha_0 + \alpha_4 x_4$	3

The global model contains all four variables: x_1 = conditions before conception, x_2 = conditions during gestation, x_3 = conditions during the first year of life and x_4 = cumulative conditions thereafter. Model parameters are represented by α's.

Akaike's information criterion (AIC) for each site individually, for grouped data and for sites classified by mean annual rainfall. We used least squares regression to parameterize the models and calculated AIC_c, a form of AIC corrected for small sample size (Burnham & Anderson, 2002).

To assess the support for alternate models, we calculated AIC_c differences (Δ_i) where the estimated best model has $\Delta_i = 0$. Values from 0–2 indicate substantial support; 4–7, considerably less support and > 10, essentially no support (Burnham & Anderson, 2002). We also calculated Akaike weights (w_i), the normalized relative likelihood of the model given the data, and relative variable importance, the sum of w_i's of all the models in the set containing a particular variable (Burnham & Anderson, 2002).

Results

Intra-annual reproductive patterns

Our analysis of published records indicated that in both southern and eastern Africa, monthly conception rate was correlated with monthly rainfall (Fig. 2). Linear regression worked best, and the relationship was strongest for rainfall with a 1-month lag (square root transformations normalized southern Africa's rainfall and conception data, $y = 0.70x + 0.08$, $r^2 = 0.57$, $F_{1,94} = 125.60$, $P < 0.01$; for eastern Africa, $y = 0.98x + 0.0003$, $r^2 = 0.40$, $F_{1,62} = 41.04$, $P < 0.01$). Conception rate in southern Africa clearly peaked during the wet season ($F_{11,107} = 20.43$, $P < 0.01$) with 40% of conceptions occurring in January and February and 67% from December to March (Fig. 2). Our site-specific assessment of conception timing mirrored this finding – an estimated peak conception month between January and March was indicated for all 17 sites. Conceptions were more evenly distributed in East Africa. Here, the two faint peaks in December and May (Fig. 2) might be associated with the two wet seasons, but these differences were not significant ($F_{11,59} = 0.70$, $P = 0.73$), possibly because of the smaller
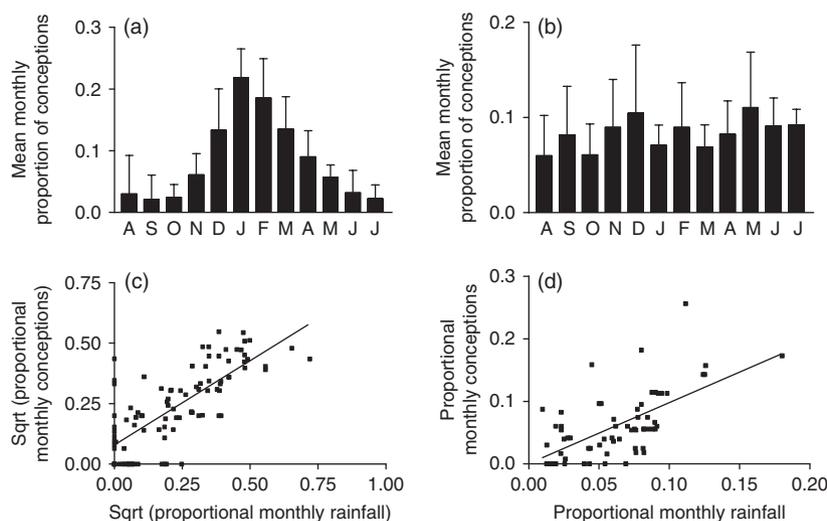

Figure 2 Intra-annual patterns of conception in African elephants *Loxodonta africana*. We illustrate the monthly mean proportional frequency of conceptions and standard deviations for (a) southern African populations ($n = 9$) and (b) eastern African populations ($n = 5$). We show the association between proportional monthly rainfall lagged by 1 month and proportional monthly conceptions in (c) southern Africa and (d) eastern Africa.

sample size or because wet season timing is more spatially variable in East Africa.

Effects of environmental conditions on inter-annual survival and reproductive rates

Standardized residuals of the age distributions were not generally related to age, although residual magnitude decreased significantly with age for three populations ($\alpha = 0.05$). Age-specific mean magnitudes of standardized residuals ranged from 0.13 for the 13-year class to 0.33 for the 15-year class, and were not evenly distributed among ages although there was no apparent pattern to deviations. Because deviations were highest for the oldest age class, possibly due to error in age assignment, we removed the 15-year class from further analysis.

The ability of the global model including all four variables to explain variability in age structures differed for the 17 sites (r^2 ranged from 0.09 for the worst fit to 0.86 for the best) (Table 1). For small populations and populations that have a history of heavy poaching, r^2 was low. For relatively large, undisturbed populations, the global model generally performed well and r^2 was higher. A single variable model was selected best for each of the 17 sites. A model including only gestation was selected as the best model in eight cases and a conception model was selected best in a further four cases. Thus, for 12 out of 17 sites, conditions during conception and gestation best explained anomalies in age distributions. At the remaining five sites, first year survival was selected three times and subsequent survivorship twice. However, for 15 sites, multiple models were plausible given the data, and the Akaike weights were relatively low.

For each site, we calculated the relative variable importance by summing the Akaike weights of all the models containing a given variable. In the three instances where conception period was selected the most important variable, on average it scored 1.65 times higher than the second most important, gestation in three cases and cumulative survivorship in one. In the eight cases where gestation was selected best, it averaged 1.58 times more important than the second most important, conception in three cases, first year survival in three and survivorship in two. When the first year of life was selected, it averaged only 1.08 times more important than the next variable, conception in two out of three cases, gestation in one. Finally, when survivorship was selected, it scored 1.21 times higher than the second choice variable, gestation in one case and first year survival in the other. Thus, variables reflecting the reproductive component out-performed survival variables. Additionally, while reproductive variables were selected most important in 12 out of 17 cases, in 10 cases they were selected second most important.

We repeated the model selection procedure on grouped data from the 11 relatively large, undisturbed populations (Table 1). The model containing conception period, gestation period and first year of life was selected best with gestation clearly the most influential variable. However, the global model for the grouped data had a relatively low explanatory power ($r^2 = 0.20$). Thus, it seems that responses

to changing environmental conditions are site specific. We noted that the selected site-specific models tended to associate with mean annual rainfall. For three of four drier savanna systems (annual rainfall < 522 mm), a first year survival model was selected. The intermediate savannas (annual rainfall > 522 and < 786 mm) tended towards a mix of conception and gestation models, and a gestation model was selected best for the two wetter savannas (annual rainfall > 786 mm).

In an attempt to control for this site specificity, we grouped sites based on rainfall. For high rainfall sites, r^2 increased markedly and a model incorporating conception and gestation was selected. However, for intermediate rainfall, the increase was modest and a gestation model was selected. For low rainfall areas, r^2 decreased and first year survival was the selected model.

We confirmed that the analysis is robust to potential effects of the spread of conceptions around the predicted conception peak by repeating model selection using variables generated from core periods not including months during the conception, birth and end of first year transitions. The selected model only changed for three populations (Table 1). Amboseli changed from a conception model to one incorporating conception and gestation, not surprising given that the two variables were very close in importance. Chobe and Etosha changed from first year survival models to conception and gestation, respectively, highlighting the importance of the first few months of life for juvenile survival.

Discussion

Our intra-annual analysis of elephant reproductive patterns demonstrates a clear relationship between conception timing and rainfall, and conception rate in elephants also relates to NDVI (Wittemyer et al., 2007b). Additionally, environmental conditions influence elephant survival (Moss, 2001; Loveridge et al., 2006). However, in our study, the environmental conditions affecting reproduction rather than post-parturition survival better explained deviations in age distributions at sites with medium and high rainfall, in agreement with patterns found by Wittemyer et al. (2007b). However, in dry savannas, first year survival appears to drive demographic fluctuations with one exception – Moremi, part of the Okavango Delta swamp, may be functionally similar to wetter savannas.

Breeding herds are water dependent and drink every few days (Leggett, 2006). Therefore, they must frequently travel between water and suitable forage. Water sources (natural or artificial) are available year round at all 17 sites. However, most low rainfall savannas have low primary productivity and less natural surface water than wetter savannas; therefore, the distance elephants must travel between food resources and water may be greatest in dry savannas (e.g. de Beer & van Aarde, 2008; Harris et al., 2008). Juvenile elephants may not be able to keep up with the herd on long treks, succumbing to dehydration, starvation or predation. Conversely, in wetter savannas with more widely distributed surface water, distances between water and areas with suitable forage may be substantially less (e.g. Grainger, van

Aarde & Whyte, 2005; Harris *et al.*, 2008) and drought induced juvenile mortality atypical.

Environmental conditions during gestation appear to be particularly influential for inducing anomalies in age distributions as conditions during gestation tended to be the most important variable in our analysis. This could be due to increased prenatal survival under good conditions and increased prenatal mortality when conditions are poor. Wittemyer, Ganswindt & Hodges (2007*a*) found that endocrine activity might link environmental conditions and gestation success. It is possible that variation in prenatal survival produces variable birth rates while conception rates remain relatively constant. However, Wittemyer *et al.* (2007*b*) estimated that prenatal morality affects only 7% of conceptions in Samburu.

An alternative explanation is that prenatal mortality is indeed rare, but conditions during gestation strongly affect the body condition of the newborn and its probability of survival post-parturition. However, if this were the case, we would expect the conditions during the first year of life to be an important explanatory variable – unlikely given that first year survival was generally only the third most important variable after conception and gestation. Nonetheless, the phenomenon of birth weight affecting subsequent survival has been reported for several ungulates (see Gaillard *et al.*, 1997).

Though the global model performed well for most sites, it did not perform well for small populations (Table 1). Environmental conditions may fail to explain anomalies in these age distributions because demographic stochasticity has a larger effect in small populations (Akçakaya, 2002), and reproductive synchronization (Moss, 2001; Wittemyer *et al.*, 2007*b*) may be common. Thus, individual reproductive history may dictate age distribution shape. However, most elephants in Africa live in populations with over 1000 individuals – 72 populations including an estimated 552 000 elephants (Blanc *et al.*, 2007).

The global model also performed poorly for South Luangwa and North Kafue. These populations have been heavily disturbed through poaching (Jachmann & Billiouw, 1997; Guldemond *et al.*, 2005), probably more so than neighboring North Luangwa (Borner, 2003) and South Kafue (see Guldemond *et al.*, 2005). Poaching induces variation in adult survival and fecundity (Barnes & Kapela, 1991) that might markedly affect the shape of age distributions and create aberrations independent from environmental conditions.

The fitted models were site specific – the selected best model and model coefficients varied between sites. Thus, the global model explained little variation in the grouped data from the 11 relatively large, undisturbed populations. This is unsurprising – populations living in different environments probably react disparately to variation in conditions. As we have shown, fecundity components appear more important in areas with medium and high rainfall while survival components are more influential in dry areas. Even after accounting for rainfall, site-specific effects remained, and a number of factors probably contribute (e.g. distribution of food and water, predation intensity, population density,

competition, disease incidence and human influence). Though these differences preclude constructing a predictive model based solely on environmental conditions, it might be possible to integrate these factors into models that explain additional demographic variation.

Our results have wider implications for other megaherbivore populations due to similarities in population dynamics induced by very large body size (Owen-Smith, 1988). The vital rates most susceptible to environmental stochasticity should also be the most sensitive to density dependence (Gaillard *et al.*, 2000). Therefore, identifying these vital rates should facilitate recognition of populations approaching density dependence, a salient issue in conservation management. For long-lived vertebrate populations approaching maximal levels, Eberhardt (2002) predicted a sequential response of decreased juvenile survival, reproductive rates and adult survival. Yet, our results indicate that population limitation in much of the elephant distributional range occurs initially through decreased reproductive rates. These findings mirror Owen-Smith's (1988) suggestion that the major regulatory response of megaherbivores to nutritional limitation occurs through changes in birth intervals and age at sexual maturity.

Natural selection favors adaptations that increase survival and reproductive rates (Brown & Sibly, 2006). Longevity scales with body size, so larger mammals have higher survival rates (Blueweiss *et al.*, 1978), and megaherbivores' large bodies reduce susceptibility to predation. However, size constrains birth rates (Blueweiss *et al.*, 1978), so megaherbivores have lower rates of mass specific reproduction than smaller mammals. Large body size should only be favored when it increases survival or overall reproductive success sufficiently to overcome production constraints (Brown & Sibly, 2006). Therefore, overall reproductive output of megaherbivores is probably highest when entering the long reproductive bout is delayed until success is likely (Wittemyer *et al.*, 2007*b*). Thus, the sequence of vital rate response to resource limitation in megaherbivores may differ fundamentally from that of smaller, shorter-lived species.

Variation in conception rate, prenatal survival, first year survival and cumulative juvenile survivorship probably all contribute to demographic fluctuations in elephant populations. However, our results highlight the importance of reproductive responses, especially during gestation. Juvenile survival appears to be important only in dry savannas. By understanding the mechanisms that drive megaherbivore population responses to changing resource availability, ecologists will be better equipped to recognize density dependence and account for cyclical climatic events and global warming when forecasting population trajectories.

Acknowledgments

References

Akçakaya, H.R. (2002). Estimating the variance of survival and fecundities. *Anim. Conserv*. **6**, 333–336.

Barnes, R.F.W. & Kapela, E.B. (1991). Changes in the Ruaha elephant population caused by poaching. *Afr. J. Ecol*. **29**, 289–294.

Blanc, J.J., Barnes, R.F.W., Craig, G.C., Dublin, H.T., Thouless, C.R., Douglas-Hamilton, I. & Hart, J.A. (2007). *African Elephant Status Report 2007: an update from the African Elephant Database. Occasional Paper Series of the IUCN Species Survival Commission, No. 33.*. Gland, Switzerland: IUCN/SSC African Elephant Specialist Group. IUCN.

Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R. & Sams, S. (1978). Relationships between body size and some life history parameters. *Oecologia* **37**, 257–272.

Borner, M. (2003). Annual Report Africa. *Frankfurt Zool. Soc. Annu. Rep. 2003* **1**, 10–18.

Brown, J.H. & Sibly, R.M. (2006). Life-history evolution under a production constraint. *Proc. Natl. Acad. Sci. USA* **103**, 17595–17599.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. New York: Springer-Verlag.

Caughley, G. (1977). *Analysis of vertebrate populations*. Chichester: John Wiley & Sons.

Craig, G.C. (1984). Foetal mass and date of conception in African elephants: a revised formula. *S. Afr. J. Sci*. **80**, 512–516.

De Beer, Y. & van Aarde, R.J. (2008). Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas? *J. Arid Environ*. **72**, 2017–2025.

Douglas-Hamilton, I. (1972). *On the ecology and behavior of the African elephants: the elephants of Lake Manyara*. PhD thesis, Oxford University.

Eberhardt, L.L. (2002). A paradigm for population analysis of long-lived vertebrates. *Ecology* **83**, 2841–2854.

Ferreira, S.M. & van Aarde, R.J. (2008). A rapid method to estimate some of the population variables for African elephants. *J. Wildl. Mgmt*. **72**, 822–829.

Gaillard, J.M., Boutin, J.M., Delorme, D., Laere, G.V., Duncan, P. & Lereton, J.D. (1997). Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia* **112**, 502–513.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Eco. Syst*. **31**, 367–393.

Gough, K.F. & Kerley, G.I.H. (2006). Demography and population dynamics in the elephants *Loxodonta africana* of Addo Elephant National Park, South Africa: is there evidence of density dependent regulation? *Oryx* **40**, 434–441.

Grainger, M., van Aarde, R. & Whyte, I. (2005). Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa. *Afr. J. Ecol*. **43**, 369–375.

Guldemond, R.A.R., Lehman, E.R., Ferreira, S.M. & van Aarde, R.J. (2005). Elephant numbers in Kafue National Park, Zambia. *Pachyderm* **39**, 50–56.

Hanks, J. (1972). Reproduction of elephant, *Loxodonta africana*, in the Luangwa Valley, Zambia. *J. Reprod. Fertil*. **30**, 13–26.

Harris, G.M., Russell, G.J., van Aarde, R.J. & Pimm, S.L. (2008). Rules of habitat use by elephants *Loxodonta africana* in southern Africa: insights for regional management. *Oryx* **42**, 66–75.

Jachmann, H. (1980). Population dynamics of the elephants in the Kasungu National Park, Malawi. *Neth. J. Zool*. **30**, 622–634.

Jachmann, H. (1986). Notes on the population dynamics of the Kasungu elephants. *Afr. J. Ecol*. **24**, 215–226.

Jachmann, H. & Billiouw, M. (1997). Elephant poaching and law enforcement in the central Luangwa Valley, Zambia. *J. Appl. Ecol*. **34**, 233–244.

Jackson, T.P., Mosojane, S., Ferreira, S.M. & van Aarde, R.J. (2008). Solutions for elephant *Loxodonta africana* crop raiding in northern Botswana: moving away from symptomatic approaches. *Oryx* **42**, 1–9.

Kerr, M. (1978). Reproduction of elephant in the Mana Pools National Park, Rhodesia. *Arnoldia* **8**, 1–11.

Laws, R.M. & Parker, I.S.C. (1968). Recent studies on elephant populations in East Africa. *Symp. Zool. Soc. (Lond.)* **21**, 319–359.

Laws, R.M., Parker, I.S.C. & Johnstone, R.C.B. (1975). *Elephants and their habitats: the ecology of elephants in North Bunyoro, Uganda*. Oxford: Clarendon Press.

Leggett, K. (2006). Effect of artificial water points on the movement and behavior of desert-dwelling elephants of north-western Namibia. *Pachyderm* **40**, 40–51.

Loveridge, A.J., Hunt, J.E., Murindagomo, F. & Macdonald, D.W. (2006). Influence of drought on predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded savannah. *J. Zool. (Lond.)* **270**, 523–530.

Moss, C. (2001). The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *J. Zool. (Lond.)* **255**, 145–156.

Owen-Smith, R.N. (1988). *Megaherbivores: the influence of very large body size on ecology*. Cambridge: University Press.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J. & Stenseth, N.C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol. Evol*. **22**, 503–510.

Sæther, B.E. (1997). Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends Ecol. Evol.* **12**, 143–149.

Sherry, B.Y. (1975). Reproduction of elephant in Gonarezhou south-eastern Rhodesia. *Arnoldia* **7**, 1–13.

Shrader, A.M., Ferreira, S.M. & van Aarde, R.J. (2006*a*). Digital photogrammetry and laser rangefinder techniques to measure African elephants. *S. Afr. J. Wildl. Res.* **36**, 1–7.

Shrader, A.M., Ferreira, S.M., McElveen, M.E., Lee, P.C., Moss, C.J. & van Aarde, R.J. (2006*b*). Growth and age determination of African savanna elephants. *J. Zool. (Lond.)* **270**, 40–48.

Sibly, R.M. & Hone, J. (2002). Population growth rate and its determinants: an overview. *Philos. Trans. Roy. Soc. B* **357**, 1153–1170.

Smuts, G.L. (1975). Reproduction and population characteristics of elephants in the Kruger National Park. *J. S. Afr. Wildl. Mgmt. Ass.* **5**, 1–10.

Williamson, B.R. (1976). Reproduction in female African elephant in the Wankie National Park, Rhodesia. *S. Afr. J. Wildl. Res.* **6**, 89–93.

Wittemyer, G., Ganswindt, A. & Hodges, K. (2007*a*). The impact of ecological variability on the reproductive endocrinology of wild female African elephants. *Horm. Behav.* **51**, 346–354.

Wittemyer, G., Rasmussen, H.B. & Douglas-Hamilton, I. (2007*b*). Breeding phenology in relation to NDVI variability in free-ranging African elephant. *Ecography* **30**, 42–50.