METHODOLOGICAL INSIGHTS

Predicting time-specific changes in demographic processes using remote-sensing data

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Summary

1. Models of wildlife population dynamics are crucial for sustainable utilization and management strategies. Fluctuating ecological conditions are often key factors influencing both carrying capacity, mortality and reproductive rates in ungulates. To be reliable, demographic models should preferably rely on easily obtainable variables that are directly linked to the ecological processes regulating a population.

2. We compared the explanatory power of rainfall, a commonly used proxy for variability in ecological conditions, with normalized differential vegetation index (NDVI), a remote-sensing index value that is a more direct measure of vegetation productivity, to predict time-specific conception rates of an elephant population in northern Kenya. Season-specific conception rates were correlated with both quality measures. However, generalized linear logistic models compared using Akaike's information criteria showed that a model based on the NDVI measure outperformed models based on rainfall measures.

3. A predictive model based on coarse demographic data and the maximum seasonal NDVI value was able to trace the large variation in observed season-specific conception rates (Range 0–0·4), with a low median deviation from observed values of 0·07.

4. By combining the model of season-specific conception rates with the average seasonal distribution of conception dates, the monthly number of conceptions (range 0–22) could be predicted within ±3 with 80% confidence.

5. *Synthesis and applications.* The strong predictive power of the normalized differential vegetation index on time-specific variation in a demographic variable is likely to be generally applicable to resource-limited ungulate species occurring in ecologically variable ecosystems, and could potentially be a powerful factor in demographic population modelling.

Key-words: demographic modelling, elephants, NDVI, rainfall, reproductive rates, ungulates

Introduction

Inter-annual fluctuations in ecological quality have been shown to influence reproduction and mortality in numerous taxa (elk, Garrott *et al.* 2003; wildebeest, Sinclair, Dublin & Borner 1985; Pascual & Hilborn 1995; red kangaroo, McCarthy 1996; locusts, Todd *et al.* 2002; weeds, Freckleton & Watkinson 1998), causing large temporal variation in population growth rates (Tuljapurkar 1990). Models that accurately predict such time-specific population dynamics are of great management and economic importance (Gordon, Hester & Festa-Bianchet 2004). Population viability analyses have classically incorporated the variance in reproductive rates as a stochastic parameter, thereby accounting for estimated variability in population survival curves and extinction probabilities, although error in these estimates renders the results of such analyses questionable (Beissinger & Westphal 1998). A similar approach is often used in management or harvesting models (Xie *et al.* 1999; Calvert & Gauthier 2005). If the variability in

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reproductive rates is not easily estimated, it is generally accounted for by choosing a conservative estimate of allowable off-take at which level the population is thought to be safe from the perils of overharvesting (Milner-Gulland & Lhagvasuren 1998). Currently models of demographic variation are commonly based on easy-to-measure proxy variables, such as rainfall (Pascual & Hilborn 1995; Madsen & Shine 1999; Georgiadis, Hack & Turpin 2003; Ogutu & Owen-Smith 2003; Owen-Smith, Mason & Ogutu 2005). However, to be more reliable, such models should rely on direct measures of underlying ecological processes regulating the focal population rather than proxy factors (Brashares & Arcese 2002). Such direct measures of time-specific ecological quality may be available from high-resolution remote-sensing data.

Species that inhabit ecosystems with known limiting factors are often modelled by basing population changes on these salient factors (reviewed by Gaillard *et al*. 2000). For example, in tropical and subtropical savanna areas with relatively low annual variation in temperatures and day length, precipitation is the main factor determining seasons (Huntely 1982). In these areas, rainfall has generally been used as an indirect measure of the seasonal changes in green biomass in an ecosystem (Sinclair, Mduma & Arcese 2000) and harvesting models of savanna ungulates have been based on rainfall as a predictor of time-specific carrying capacity and population growth rate (Pascual & Hilborn 1995; Georgiadis, Hack & Turpin 2003). However, apart from availability of drinking water, rainfall mainly affects ungulates indirectly via its effect on vegetation productivity. Records of precipitation, temperature or day length may not reflect changes in vegetation productivity if other factors have a compounding influence. For example, in savanna ecosystems variability in rainfall pattern, soil type and the degree of habitat degradation can have significant effects on the response of vegetation to rain (du Plessis 2001; Wessels *et al*. 2004). This indirect and often complex connection between the proxy variable and the actual factors influencing population dynamics may result in low explanatory power of the model. Such error may lead to repeated overharvesting or poorly conceived conservation programmes, pushing the size of a population to levels where recovery takes an extended period or is not possible.

The normalized differential vegetation index (NDVI), obtained from the NOAA-AVHRR (National Oceanic & Atmospheric Administration-Advanced Very High Resolution Radiometer) and SPOT-Vegetation (Satellite Pour l'Observation de la Terre) programmes is an index value calculated as the ratio between remote-sensing red and near infra-red reflection. As such, it is a measure of an area's greenness and a direct measure of spatially explicit vegetation productivity (Goward & Prince 1995) as well as a quantitative measure of temporal variability in productivity (Scanlon *et al*. 2002). Hence, NDVI potentially provides a better, more direct, measure for predicting time-specific rates of reproduction and mortality in resource-limited ungulates, by

circumventing some of the problems of methods based on less direct measurements.

Season-specific variation in vegetation productivity, measured by NDVI, is strongly correlated with conception rates in non-pregnant females in a wild, African savanna elephant *Loxodonta africana* population, potentially driving characteristic demographic fluctuations in free-ranging elephant populations (G. Wittemyer, H. B. Rasmussen, I. Douglas-Hamilton, unpublished data). Furthermore, mortality rates have been linked to seasonal quality in the same population (Wittemyer *et al*. 2005), creating a strong combined effect of variability in vegetation productivity on population dynamics. These results were based on complete population knowledge of known pregnancies and number of non-pregnant females, and demonstrate the potential utility of NDVI as a core parameter in demographic population models.

The aims of this study were three-fold. First, we compared the ability of NDVI vs. rainfall to explain time-specific variation in demographic processes in a wild ungulate. We did this by investigating the explanatory power of the two ecological correlates on season-specific conception rates of the intensively monitored Samburu elephant population (Wittemyer 2001; Wittemyer *et al*. 2005). Secondly, we developed a predictive regression model of season-specific conception rates based on NDVI and coarse demographic data that are easily obtained from populations with little or no prior knowledge. Finally, we assessed the accuracy of our model for predicting the intraseason distribution of conceptions on a fine temporal scale. To our knowledge, this is the first time remote-sensing NDVI data have been used for modelling temporal changes in demographic processes.

Methods

STUDY AREA AND POPULATION

Long-term demographic data were obtained from a free-ranging elephant population using the Samburu and Buffalo Springs national reserves in northern Kenya, approximately 60 km north of the equator at a longitude of 37°E. The study area consists of semi-arid savanna bushland dominated by *Acacia tortilis* and *Commiphora* woody plant species and a large diversity of grasses and forbs*,* with patches of riparian woodland dominated by *Acacia elatior* and *Hyphaena coriacea* along the semi-permanent Ewaso Ngiro River and its tributaries (Barkham & Rainy 1976). The annual rainfall pattern in this ecosystem is bimodal but highly variable, with the majority of the annual, average precipitation of 380 mm (range 143–847, years 1960–2002) occurring during November–January and April–May (Fig. 1). The study population inhabiting the national reserves and surrounding areas consists of approximately 900 individuals (males, females and juveniles), which have been individually identified using distinct features such as ear markings (Douglas-Hamilton 1972; Moss 1988, 1996) and continuously monitored since 1997 by the
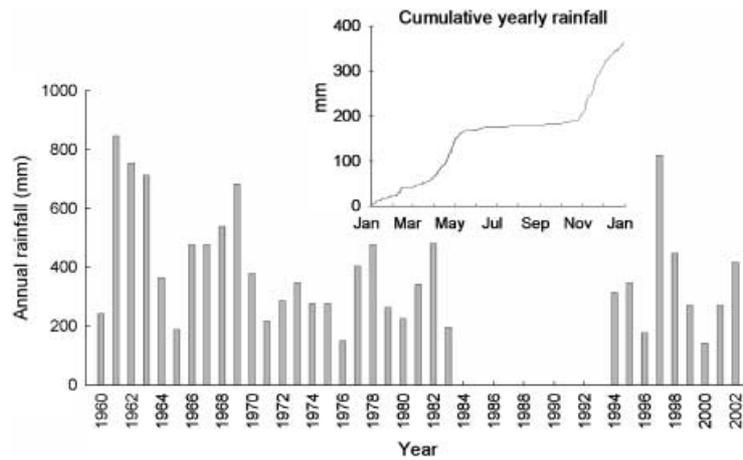
Fig. 1. Yearly rainfall recorded in Archer's Post between 1960 and 2002; data between 1984 and 1993 are not available. Insert: average yearly cumulative rainfall (data from 1996 to 2002).
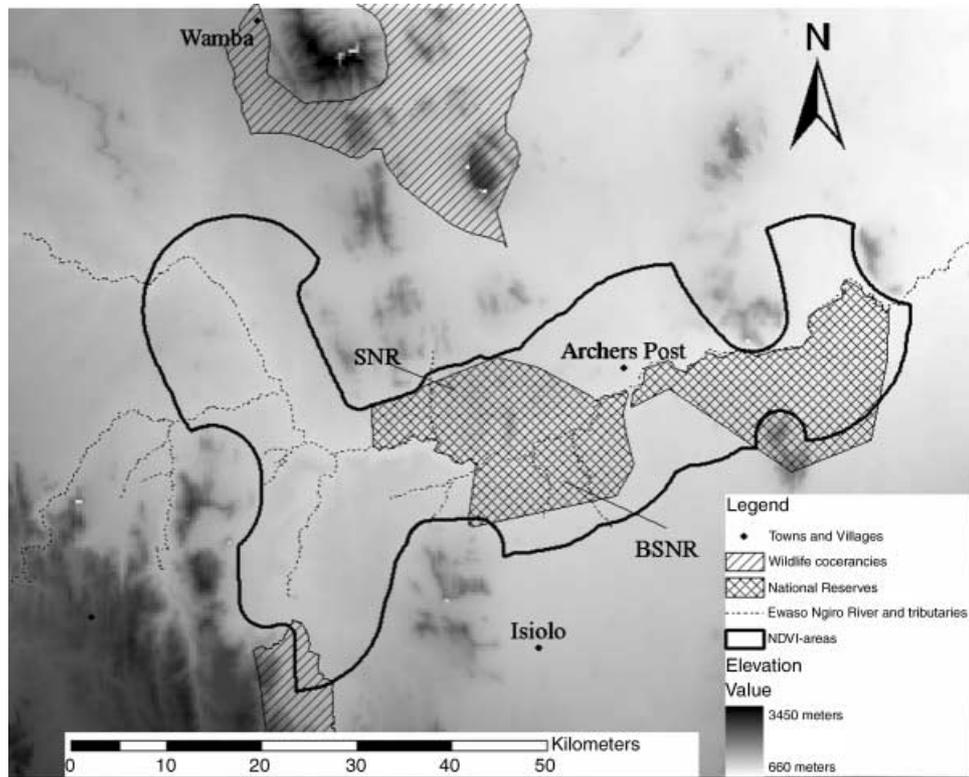

Fig. 2. Core study area of Samburu (SNR) and Buffalo Springs (BSNR) national reserves and area used for NDVI extraction.

Save the Elephants Samburu Project (Wittemyer 2001; Wittemyer *et al*. 2005). Out of the approximately 220 known adult females (defined as females that have reproduced at least once), this study used demographic data collected on a total of 170 that were observed within the two national reserves (Fig. 2) more than 3 months year^{-1} during the 7-year study period. These females and their offspring were consistently found in stable family groups, which have been quantitatively defined (Wittemyer, Douglas-Hamilton & Getz 2005), facilitating identification of mortality and birth. The birth dates of calves can be accurately estimated (± 1 week) up to 1 month after birth (Moss 1988, 1996, 2001). Of the 265 calves born between 1998 and 2004,

95% were observed within 1 month of their estimated date of birth and the remaining were observed within the season of birth. The date of conception was obtained by subtracting the average gestation period of 656 days (Moss 1983) from the date of birth, giving corresponding dates of conceptions for these calves between mid-1996 and mid-2002. These highly accurate data, including pregnant and non-pregnant periods for individual females, were used to investigate the effect of rainfall and NDVI on demographic processes in the study population over a period of 7 years (13 wet seasons).

It was essential for the analysis presented here to identify the seasonal-specific number of reproductively available females in the study population. At any one

Fig. 3. The proportion of females that conceived vs. the time elapsed since they gave birth to their previous calf. This analysis is based on 89 intercalving periods where two consecutive births were known. The points with calf ages at 0·5 and 2·5 years are indicated with vertical lines and used to parameterize the model.

time, females may be pregnant or potentially unreceptive because of a recovery period after birth. Disregarding six females that lost their calves immediately following birth and conceived within the following 6 months, no females conceived before 6 months after her last parturition date (Fig. 3). Thus, females were defined as reproductively available females from 6 months after their parturition date to the conception date of their next calf. The number of adult females in our study varied across seasons between 101 and 163, because of mortality and maturation of juvenile females. After giving birth for the first time, primiparous females from the study family groups were incorporated into the pool of adult females and considered reproductively available females at the beginning of the season in which they first conceived.
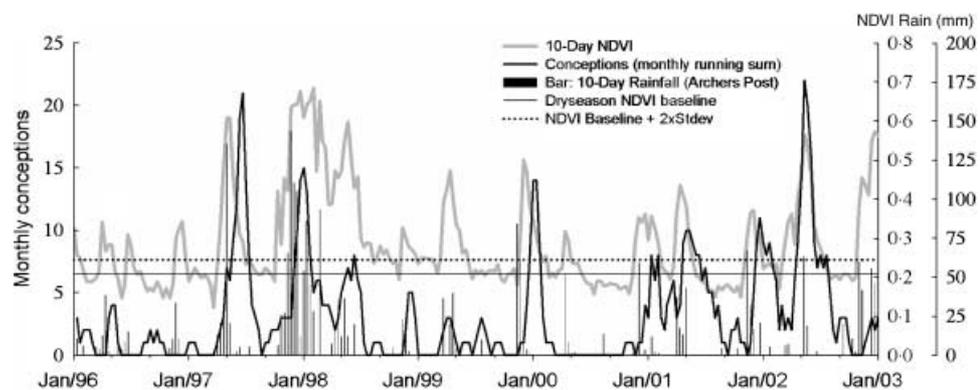
MEASURES OF ECOLOGICAL QUALITY

Daily rainfall measures were obtained from Archer's Post, the only long-term weather station in the area, situated adjacent to the core study area (Fig. 2). Wet seasons were defined as beginning during the first 10-day period with 10 mm or greater rainfall (the approximate amount of precipitation required to get a vegetative response) and ending during the last 10-day period with rain followed by 30 days of 0 mm rainfall. Single-day

showers between 2-week periods of 0 mm rainfall were not considered to illicit a seasonal change.

Remote-sensing 10-day composite recordings NDVI values (S10 products) were obtained from the SPOT (1998, 1999, 2000, 2001, 2002) and AVHRR (1996, 1997, 1998, 1999, 2000) programs (data currently available free at http://free.vgt.vito.be and ftp://disc1.gsfc.nasa.gov/data/avhrr/, accessed February 2006). To cover the entire study period (1996–2002), data from the AVHRR and SPOT programs were combined. The 2-year overlap between AVHRR AND SPOT data (1998–2000) revealed a shifted baseline for the two data sets and the AVHRR data were subsequently calibrated to SPOT level by adding 0·06 to all values. The mean 10-day NDVI values were extracted from an area defined by a 10-km buffer around permanent rivers in a 40-km radius from the centre of the core study area, in which hills and mountains were excluded (1771 km^2) (Fig. 2). This area was chosen because the study population seldom ventures further than 10 km away from permanent water or on to steep slopes (Save the Elephants unpublished radio-tracking data). The NDVI data were extracted using ArcView3·2© (ESRI, 380 New York Street, Redlands, CA, USA) and WinDisp 5·12 (http://www.fao.org/giews/english/windisp/windisp.htm, accessed February 2006). Using NDVI data, wet seasons were defined as occurring when values exceeded two standard deviations above the dry season baseline, except during the 1998 El Niño event when the two seasons were delineated by the lowest NDVI value recorded during the 8-month period of elevated NDVI values. NDVI values and rainfall records for the study period are shown in Fig. 4 together with the monthly number of conceptions. A breeding season was defined as a combined wet–dry cycle starting with the onset of a wet season and lasting until the subsequent wet season. The defined breeding seasons using either rainfall or NDVI were similar.

EFFECT OF ECOLOGICAL QUALITY MEASURES ON CONCEPTION RATES

The numbers of reproductively available females (N_{avail}) (range 22–96) that conceived ($N_{conceiv}$: range 0–50) or

Fig. 4. The 10-day rainfall totals recorded in Archer's Post (columns), median NDVI values from the extracted study area (grey line) and monthly numbers of conceptions (black line). The dry season NDVI baseline (solid line) and 2 SD from baseline (dotted line) are indicated.

did not conceive ($N_{non-conceiv}$: range 8–79) were obtained for each season and the proportion of available females conceiving (R_{avail}) was calculated as:

$$R_{avail} = N_{conceiv}/N_{avail} \qquad \text{eqn 1}$$

Initially different indices for each of the two measures of ecological quality were investigated. For rainfall, the three indices investigated were the: (i) duration of the rainfall-defined wet seasons ($Rain_{dur}$); (ii) total amount of rainfall per season ($Rain_{tot}$); and (iii) greatest 10-day amount of rainfall per season ($Rain_{max}$). For NDVI, the indices were the: (i) duration of the NDVI-defined wet seasons ($NDVI_{dur}$); (ii) sum of NDVI values above the baseline level per wet season ($NDVI_{tot}$); and (iii) maximum recorded NDVI value during a season ($NDVI_{max}$). The relationships between each of these indices and the number of conceiving/non-conceiving available females (binomially distributed) were assessed using logistic regression followed by inspection of the observed proportion conceiving (R_{avail}) vs. predicted. Based on these results, $Rain_{tot}$ and $NDVI_{max}$ were inverse-transformed and $Rain_{max}$ and $NDVI_{tot}$ were natural log-transformed to obtain linearity.

A degree of correlation (colinearity) existed between indices of the same quality measure. For rainfall the correlations were moderate, ranging between 0·26 and 0·58 ($Rain_{dur}$ vs. ln-$Rain_{max}$ $R^2 = 0·26$; $Rain_{tot}^{-1}$ vs. ln-$Rain_{max}$ $R^2 = 0·58$; $Rain_{dur}$ vs. $R^2 = 0·43$). However, for NDVI the correlations between the indices were very high, ranging between 0·84 and 0·93 ($NDVI_{max}^{-1}$ vs. $NDVI_{dur}$ $R^2 = 0·84$; $NDVI_{max}^{-1}$ vs. ln-$NDVI_{tot}$ $R^2 = 0·94$; ln-$NDVI_{tot}$ vs. $NDVI_{dur}$ $R^2 = 0·90$). Colinearity does not prevent a combined analysis; however, highly correlated factors require a large data set to separate potential effects and the correlated variables may interfere during analysis by 'sharing' their explanatory power, reducing the effects assigned to each (Zar 1999). Therefore only one of the NDVI indices, $NDVI_{max}$, was retained.

The quality indices were entered into combined multiple logistic regression models using conceiving/non-conceiving as the dependent variable. To assess which combination of indices had the highest explanatory power, the Akaike's information criteria corrected for small sample sizes (AICc) was used to compare alternative models (Burnham & Andersen 1998). Additionally the deviation between the observed proportion of females conceiving (R_{avail}) and the proportion predicted by the models was compared.

MODEL

Demographic data for models

Highly accurate demographic data are available only for closely studied populations in which demographic changes are often explicitly known (Gaillard *et al.* 2000). Thus, useful predictive models must be based on coarser data that can be easily obtained from populations with little to no prior information. The proportion of females known to be pregnant (giving birth less than 22 month later) and thus unable to conceive varied between 0·18 and 0·77 season⁻¹ in our study, demonstrating that the total number of females is a poor estimate of the number of reproductively available females for elephants. We therefore investigated whether the age of a female's youngest calf could serve to predict the reproductive state of its mother. Elephants have an average intercalving period of 4·5 years, conceiving when the average age of their youngest calf is just over 2 years (Moss 2001). A large fraction of females with calves older than 2 years are thus likely to be pregnant. Additionally, females with calves less than 6 months old did not conceive in the study population regardless of ecological conditions (Fig. 3). This is probably because of the high energetic costs associated with lactation (Oftedal 1984). Thus, the age class of a female's youngest calf may serve as a useful indicator for whether a female is available for reproduction. Assessment of the approximate ages of calves, particularly those between the ages of 0 and 3·5 years, are obtainable from field observations. Tusk eruption in calves occurs at approximately the age of 2 years for males and 2·5 years for females; calves under the age of 1 year can be accurately aged to within a month and those under the age of 10 years to within 1 year (Moss 1988, 1996, 2001). To assess which group of females with calves older the 0·5 years represented the best estimate of N_{avail}, the correlations between the known N_{avail} per season and females with calves aged 0·5–2, 2·5 or 3·0 years were compared.

Modelling steps and design

The significant indices of season-specific ecological quality, determined from the analysis on complete population knowledge, were correlated with the demographic information estimated using the calf age index. The relationship was then used to develop a regression-based model to estimate the season-specific proportion of females conceiving (conception rates). Data on season-specific conception rates (conceptions resulting in birth per female per season) were available for 13 seasons (7 years). We used the first six seasons for model building and parameter estimation and the remaining seven seasons for model validation.

Thereafter, we expanded our model to predict the time-specific distribution of conceptions by combining the intraseason temporal distribution of conceptions with the predicted seasonal number of conceptions in the population. The intraseason distribution of conceptions was estimated from our data set of known conception events (based on calf birth) occurring within the first six seasons. Based on our data set of known conceptions, females have been shown to time conceptions according to average wet season onset rather than specific wet season onset (G. Wittemyer, H. B. Rasmussen, I. Douglas-Hamilton, unpublished data), allowing a function describing the temporal distribution of season-specific

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Table 1. Models based on different NDVI and rainfall indices compared using Akaike's information criteria. Models are ranked by ΔAICc, which indicates the difference between each model and the model with the lowest AICc (rank 1). The model based on $NDVI_{max}$ (ranked 1) outperformed the model based on the three rainfall indices (ranked 6) with a ΔAICc = 59·40 between the two models. Models with ΔAICc < 2 are equally plausible given the data (Burnham & Andersen 1998)

Rank	Model	Log likelihood	Parameters (n)	Model χ^2 P	AICc	ΔAICc	w_i
1	$NDVI_{max}$	−411·29	1	< 0·0001	824·94	0·00	0·37
2	$NDVI_{max}$, $Rain_{tot}$, $Rain_{dur}$	−408·46	3	< 0·0001	825·59	0·64	0·27
3	$NDVI_{max}$, $Rain_{tot}$	−410·71	2	< 0·0001	826·62	1·68	0·16
4	$NDVI_{max}$, $Rain_{dur}$	−410·79	2	< 0·0001	826·78	1·84	0·15
5	$NDVI_{max}$, $Rain_{tot}$, $Rain_{dur}$, $Rain_{max}$	−407·95	4	< 0·0001	828·90	3·96	0·05
6	$Rain_{tot}$, $Rain_{dur}$, $Rain_{max}$	−437·84	3	< 0·0001	884·35	59·40	< 0·01
7	$Rain_{tot}$, $Rain_{dur}$	−439·93	2	< 0·0001	885·06	60·12	< 0·01
8	$Rain_{tot}$	−447·57	1	< 0·0001	897·50	72·56	< 0·01

Table 2. Model likelihood and coefficients for the best logistic regression models based on pure rainfall and pure NDVI indices

	Parameters	d.f.	Coefficients	SE	Wald	P
NDVI model						
	$NDVI_{max}^{-1}$	1	−1·684	0·15	125·13	< 0·001
	Constant	1	3·58	0·37	92·30	< 0·001
Whole model	Log likelihood	d.f.	Average residual	Percentage correct estimated	Chi square	P
	−411·29	1	0·084	70%	150·77	< 0·001
Rainfall model						
	$Rain_{tot}^{-1}$	1	−175·68	31·03	32·1	< 0·001
	$\ln(Rain_{max})$	1	0·477	0·25	4·11	= 0·043
	$Rain_{dur}$	1	−0·013	0·003	16·68	< 0·001
	Constant	1	−0·259	1·21	0·046	= 0·830
Whole model	Log likelihood	d.f	Average residual	Percentage correct estimated	Chi square	P
	−437·84	1	0·15	59%	97·71	< 0·001

conception events to be incorporated into the model. The first six seasons (97 conception events) were used to obtain the distribution of time delay between average seasonal onset and conceptions. To evaluate the accuracy of the distribution model for intraseason conceptions, the known number of total conceptions per season for the last seven seasons (43 months) was distributed using this model and compared with the actual distribution. Thereafter, the distribution model was applied to the estimated number of total conceptions per season based on our regression model, and the distribution of estimated conceptions was compared with the actual (observed) distribution. Both actual and predicted numbers of conceptions were calculated as monthly sums (± 15 days). In all regressions involving fractional data, the data were logit transformed.

Results

EFFECT OF QUALITY MEASURES ON CONCEPTION RATES

For all models a significant effect of quality indices on conceptions was found (the eight highest ranked models are shown in Table 1). The log likelihoods (LL) of these models were compared and ranked using the AICc weights (w_i) (Anderson, Burnham & Thompson 2000). The one-parameter model based purely on $NDVI_{max}$ had

the overall best (lowest) AICc score (824·94) (ranked first in Table 1; model parameters shown in Table 2). The best model based purely on rainfall (ranked sixth in Table 1) contained all three rainfall indices but with $Rain_{tot}$ having the largest effect (model parameters shown in Table 2). Despite being based on more parameters, this purely rainfall-based model had a lower overall likelihood compared with the $NDVI_{max}$-based model (LL rainfall −437·84; LL $NDVI_{max}$ −411·29) and a higher deviation between observed and predicted proportions of available females conceiving than the $NDVI_{max}$-based model (average deviation NDVI model 0·084; rainfall model 0·15). This poorer performance was reflected in the much higher ΔAICc score relative to the highest ranked $NDVI_{max}$ model (ΔAICc = 59·40, w_i < 0·01). All models based purely on rainfall, without using the NDVI index, had w_i < 0·01, and the model based only on $Rain_{tot}$ was the lowest ranked of the compared models (Table 1). Models incorporating both $NDVI_{max}$ and rainfall parameters (ranked second to fifth in Table 1), with ΔAICc < 2 and thus equally plausible given the data (Burnham & Andersen 1998), were not significantly better than the single-parameter $NDVI_{max}$ model. In Fig. 5 the untransformed regression lines of predicted conception proportions based on $NDVI_{max}$ (a) and on the strongest rainfall index ($Rain_{tot}$) (b) are shown together with observed R_{avail}. The extreme point in the relationship between rainfall and R_{avail} occurred during
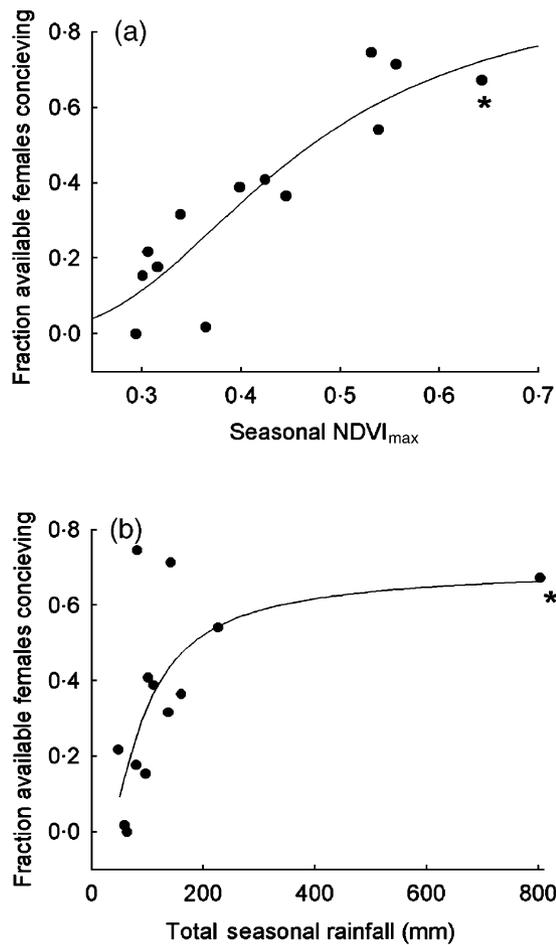
Fig. 5. Untransformed relation between maximum recorded seasonal NDVI (NDVI$_{max}$) (a) and the strongest rainfall index (Rain$_{tot}$) (b) vs. the fraction of available females conceiving during each season ($n = 13$). El Niño season indicated with *.

the El Niño season, with very high rainfall (indicated with * in Fig. 5). This season, however, was not an 'outlier' using NDVI as a quality measure, suggesting that this was a valid data point. Excluding this season from the analysis of rainfall did not alter the overall results.

PREDICTIVE MODEL

The results on conception dates vs. calf age showed that females with calves less than 6 months could not be considered available, likewise almost all females with calves older than 3 years had already conceived (Fig. 3). To find the best estimate for females that were available based on coarser data accessible in less studied populations, the known fraction of females that were available ($F_{avail} = N_{avail}/N_{females}$) was correlated with the fraction calculated on females within three age classes of calves: 0·5–2·0, 0·5–2·5 and 0·5–3·0 years ($F_{avail(est)} = N_{0·5-x·x}/N_{females}$). F_{avail} and $F_{avail(est)}$ were compared (logit-transformed fractions) rather than actual numbers because of varying numbers of females between seasons. Females with calves between 0·5 and 2·5 years were the most strongly correlated with the actual numbers of available females [logit(F_{avail}) = 0·89 × logit($F_{avail(est)}$) + 0·6069, R^2

= 0·82, $P < 0·0001$] and were subsequently used for the estimate of the number of females available for reproduction ($N_{avail(est)}$). Data on the estimated numbers of conceiving/non-conceiving females ($N_{conceiv.}$ and $N_{avail(est)} - N_{conceiv.}$) from the first six seasons were regressed against NDVI$_{max}^{-1}$ using logistic regression (LL = −178·8, $\chi^2 = 73·5$, $P < 0·0001$), and a prediction of the proportion of available females conceiving was obtained from the regression equation by:

$$R_{avail(est)} = \exp(2·96 + NDVI_{max}^{-1} \times -1·68)/ \\ (1 + \exp(2·96 + NDVI_{max}^{-1} \times -1·68)) \qquad \text{eqn 2}$$

The estimated proportion of all females conceiving per season i ($R_{females(est)}$) was then calculated as:

$$R_{females(est)\ i} = F_{avail(est)\ i} \times R_{avail(est)\ i} \qquad \text{eqn 3}$$

where $R_{females(est)\ i}$ is the estimated proportion of females conceiving during season i (resulting in birth 22 month later); $F_{avail(est)\ i}$ is the fraction of all females with calves between 0·5 and 2·5 years in season i (estimate of available females); NDVI$_{max\ i}$ is the maximum 10-day mean NDVI value within season i; and $R_{avail(est)\ i}$ is the estimated proportion of available females conceiving during season i.

The actual (observed) season-specific proportion of females conceiving ($R_{females\ i}$) varied between 0 and 0·4 (Fig. 6). The median deviation of the modelled $R_{females(est)\ i}$ from the actual (observed) values was 0·073. The model had the highest deviations during the last three seasons. The deviation from observed rates was negatively correlated, although not significantly, to the fraction of known non-pregnant females with calves older than 2 years (F2+) (model deviation = −0·06 × logit(F2+) − 0·12, $R^2 = 0·34$, $n = 7$, $P = 0·17$).

We developed this model further to predict time-specific numbers of conceptions, which is nearly equivalent to the number of oestrus females in the study population as a result of low pre-natal mortality and high conception probability (G. Wittemyer, H. B. Rasmussen, I. Douglas-Hamilton, unpublished data). Combining the model for season-specific conception rates ($R_{females(est)}$ ($_i$)) from equation 3 with numbers of females in the population ($N_{females}$), the seasonal number of conceptions ($N_{conception(est)}$) was estimated:

$$N_{conception(est)} = R_{females(est)\ i} \times N_{females\ i} \qquad \text{eqn 4}$$

The intraseason distribution of conceptions during the first six seasons did not deviate significantly from a normal distribution ([normal(x, $\mu = 75·29$, $\delta = 34·11$): χ $P = 0·47$] $\chi^2 = 3·56$, d.f. = 4, $P = 0·47$; Fig. 7). By combining equation 4 with the temporal distribution of intraseason conception events (Fig. 7), a model of the monthly number of conceptions was obtained. The model starts at the average seasonal onset (day $i = 1$) until the 200th day of the season, thereby distributing 99% of the estimated conceptions:
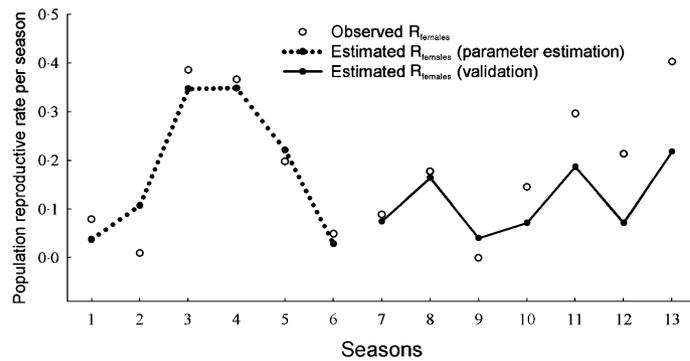
Fig. 6. Observed and predicted seasonal conception rates of adult females. The first six seasons were used for model building and parameter estimation and the last seven seasons for validation.
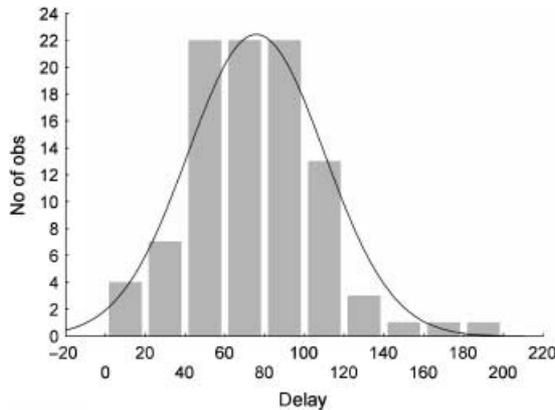

Fig. 7. The distribution of the time lag (days) between average seasonal onset and the estimated date of conception ($n = 96$) was normally distributed.

conception day $i =$

$$\int_{i-15}^{i+15} \text{Normal}(i;75 \cdot 29;34 \cdot 11) \times N_{\text{conception}} \quad i = (1\text{--}200) \qquad \text{eqn 5}$$

The distributions were slightly overlapping during late March–April, thus the total number of predicted conceptions was calculated as the sum of the two overlapping distributions at each time step.
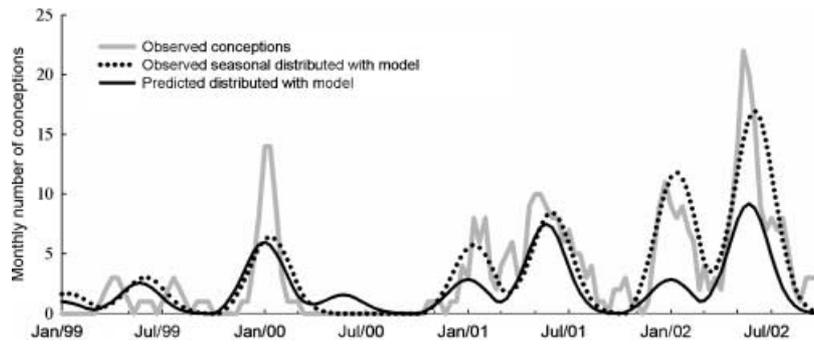
The distribution model (equation 5) was first evaluated by distributing the known number of seasonal conceptions ($N_{\text{conceptions}}$) monthly, and then comparing that distribution to the known monthly numbers of conceptions during the 43 months not used in the estimation of the distribution parameter. The predicted monthly number of conceptions (range 0–16) was significantly correlated with the observed (range 0–22) (observed = $0 \cdot 91 \times$ predicted + $0 \cdot 336$; $R^2 = 0 \cdot 67$; $n = 43$; $P < 0 \cdot 0001$), with 80% of months being within $\pm 2 \cdot 8$ and 90% within $\pm 3 \cdot 5$ conceptions.

The same steps were applied to the predicted seasonal number of conceptions calculated using equation 4 ($N_{\text{conceptions(est)}}$). Here the monthly numbers of conceptions were also significantly correlated with the observed number of conceptions (observed = $1 \cdot 55 \times$ predicted +

$0 \cdot 18$, $R^2 = 0 \cdot 60$, $n = 43$, $P < 0 \cdot 0001$), with 80% being within $\pm 3 \cdot 1$ and 90% within $\pm 4 \cdot 8$ conceptions. The known monthly numbers of conceptions are shown in Fig. 8 together with the modelled distribution of known and predicted seasonal conceptions. The modelled distribution using the known seasonal number of conceptions generally followed the actual distribution in terms of both timing and peak height, whereas the distribution of the modelled predicted generally underestimated values as a result of the underestimation of seasonal number during the last two seasons.

Discussion

Both rainfall and NDVI were correlated with the proportion of available females conceiving per season, showing that elephant reproduction is highly influenced by interseason fluctuations in ecological conditions. However, the seasonal rainfall indices explained far less of the variation, with a log-likelihood of $-437 \cdot 84$, compared with the model based on the maximum seasonal NDVI value, with a log-likelihood value of $-411 \cdot 29$ (ΔAICc = 59·40), demonstrating that remotely sensed NDVI data are a better indicator of the conditions influencing reproduction than the traditionally used measure of rainfall. Indeed, combined models containing both rainfall and NDVI indices demonstrated that rainfall did not add to the overall explanatory power of the NDVI-based model. The relationship between rainfall and NDVI was sigmoidal (data not shown), suggesting that a certain threshold of rainfall is needed before triggering a response in the vegetation (foot of curve); likewise a saturation point is probably reached where any additional rain only marginally improves the conditions for vegetative growth (top of curve). The largest variation between rainfall and NDVI was found at intermediate rainfall levels, probably linked to differences in vegetative response related to how the season's rain fell (rainfall pattern) or other conditions affecting vegetation growth (du Plessis 2001; Wessels *et al.* 2004). The higher predictive power of NDVI suggests that during such seasons the level of vegetative growth rather than amount of rainfall causes the reproductive response observed in the study population.

Fig. 8. The temporal distribution of conception events obtained from calf births (grey line), the distribution of known seasonal number of conceptions based on the distribution model (dotted line), and distribution of estimated conceptions based on available females and 10-day NDVI values (black line).

The life-history traits of elephants necessitate the estimation of the time-specific proportions of available females in order to model the population demographic processes. In species with shorter gestation periods, where individual reproductive bouts occur seasonally or annually, such variability may not need to be incorporated in a demographic model. To estimate the number of available females, we used the number of females with calves between 0·5 and 2·5 years to parameterize our model. These coarser demographic data are available at the time of conception, 2 years before the birth of a calf, and are obtainable from populations not under intense monitoring through relatively simple collection protocols such as sample counts of female groups (see the Methods for description of ageing calves).

In our study the first six seasons covered the complete variation in observed vegetation productivity, measured by NDVI, and a subsequent rerun of parameter estimation using the complete data set only marginally changed correlation parameters. However, six seasons may be few for accurate estimation of parameters in some systems. The model based on $NDVI_{max}$ was able to trace the variation in observed, season-specific reproductive rates (range 0–0·4) and had a median deviation from observed values of only 0·07. The model generally underestimated the rates during seasons with large fractions of available females whose youngest calves were between 2 and 2·5 years old. Such females are probably more likely to conceive than females with calves between 0·5 and 2 years. This particularly occurred during the 2001 and 2002 seasons in which many females had 2–3-year-old-calves, a remnant effect from the high conception rates associated with the 1998 El Niño event. This indicates that a stage-specific model with age class-specific parameters for females with different aged calves could out perform our age-unstructured model. Such a model will require a larger, longer term data set to parameterize accurately each age class, and is therefore beyond the capacity of our current 7-year data set. The specific parameter values estimated in the current study may be partially population/area specific hence parameter validation to local conditions is needed before application of this model to other populations.

Our study focused only on conception rates, as the accuracy and temporal resolution of elephant mortality data in our study population did not allow for any detailed modelling of time-specific mortality. However, observational evidence from the study system suggests that the same ecological variation governing reproductive rates affects mortality, especially among juveniles (Wittemyer *et al*. 2005). Thus, it is likely that a NDVI-based model could be used to predict mortality as well as conception rates. Such a model may be highly applicable to systems in which mortality is salient to population growth rates (Portier *et al*. 1998). Postponing reproduction for a single season because of poor vegetation productivity is less likely to affect the lifetime reproductive success of elephants than that of shorter lived ungulates with short-interval breeding cycles (Stearns 1992). In the latter system, females may attempt breeding regardless of specific seasonal conditions but with these conditions impacting offspring survival or future reproductive attempts (Trivers 1972). Despite these likely species-specific differences, the better predictive power of NDVI for our study system suggests that NDVI is a more accurate metric than rainfall for the analysis of links between ecological variability and demographic parameters such as mortality, reproductive rates and carrying capacity.

Time-specific information on the number of conceptions is important for population management (Gordon, Hester & Festa-Bianchet 2004) as well as behavioural studies of reproductive strategies and individual decision-making processes (Emlen & Oring 1977), but is often difficult to collect from free-ranging populations. By applying a temporal distribution model of intraseason conception events to the model predicting seasonal numbers of conceptions, the monthly number of conceptions in the study population could be predicted to within ±3·1 events with 80% confidence. The occurrence and duration of peaks in oestrus females were generally well predicted by this model (Fig. 8), but the actual peak sizes were not accurate because of the underestimation of seasonal conceptions during the last seasons. The level of accuracy attained in our fine scale temporal model is, however, useful for assigning categorical levels (low,

medium and high) of receptive females at a 1-month resolution. The resolution at which time-specific reproductive rates can be predicted in other systems will depend on the relationship between season-specific quality and conception probabilities in combination with the degree of variability in intraseason breeding phenology (Sinclair, Mduma & Arcese 2000).

Prior to its employment, the characteristics and limitations of NDVI in relation to the ecology of the system to be modelled should be considered. An ecosystem-wide measure such as NDVI (or rainfall) may be better for predicting the population processes of generalist herbivores compared with a specialist or frugivorous species dependent on specific plants or fruiting events. If population processes are regulated by factors unrelated to general vegetation productivity, such as predation or disease (Sinclair, Dublin & Borner 1985; Gasaway, Gasaway & Berry 1996), NDVI is not likely to be a good factor with which to compare ecologically related changes. NDVI only measures actively growing vegetation, therefore dry season or winter standing biomass cannot be directly measured using this index. In addition, NDVI cannot directly differentiate between vegetation types, so grazers and browsers may respond differently to the same NDVI values depending on which type of vegetation is responsible for the remotely sensed photosynthetic activity. In predominantly wooded areas and forests, the inter annual fluctuations in NDVI values are limited and weakly correlated with relative vegetation growth (Scanlon *et al.* 2002), particularly in respect to subcanopy growth, which cannot be evaluated by remote sensing. With these limitations in mind, which are also generally applicable to using rainfall as a proxy, NDVI can provide a better more direct measurement of the ecological quality influencing population dynamics of herbivore species. For practical purposes NDVI may also be more easily accessible in areas where few rainfall stations exist or detailed rainfall records are not available.

In conclusion, the results presented for a free-ranging elephant population demonstrate the utility of NDVI in predicting season-specific conception rates. Our results show that in this system remotely sensed NDVI data have much greater predictive power than the widely used rainfall proxy. These results are likely to be generally applicable to ungulates occurring in rainfall-dependent ecosystems and are promising for the use of remote-sensing data in demographic population models. NDVI data may offer an improvement over previous data sources for the estimation of harvesting and conservation protocols. Our method has further implications for behavioural studies of reproductive strategies and may provide better insight into the potential effects of climatic and direct human-induced changes in ecological conditions on the demographic dynamics of a population.

Acknowledgements

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