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Breeding phenology in relation to NDVI variability in free-ranging African elephant

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The phenology of reproduction is often correlated with resource availability and is hypothesized to be shaped by selective forces in order to maximize lifetime reproductive success. African elephants have the distinctive life history traits of a 22 month gestation and extended offspring investment, necessitating a long-term strategy of energy acquisition and reproductive expenditure to ensure successful offspring recruitment.

We investigated the relationship between the reproductive phenology of a wild elephant population and resource availability using remotely sensed Normalized differential vegetation index (NDVI) data as a measure of time-specific primary productivity and hence forage quality.

The initiation of female elephants' 3+yr reproductive bout was dependent on conditions during the season of conception but timed so parturition occurred during the most likely periods of high primary productivity 22 months later. Thus, the probability of conception is linked to the stochastic variation in seasonal quality and the phenology of parturition is related to the predictable seasonality of primary productivity, indicating elephants integrate information on known current and expected future conditions when reproducing.

Juvenile mortality was not correlated with ecological variability, hence female fecundity rather than calf mortality appears to drive demographic processes in the study population.

Extreme climatic events, such as those associated with the El Niño-Southern-Oscillation (ENSO), acted to synchronize female fecundity in the population. This study suggests that the relationship between fecundity and ecological variability instigates the characteristic demographic fluctuations in elephant populations, rather than the mortality-driven fluctuations observed in many ungulate populations.

The link between population dynamics and temporal distribution of resources has been the focus of increasing research prompted by the availability of long time-series studies (Saether 1997). These studies indicate that while population growth in ungulates is most sensitive to adult survivorship, high temporal variation in juvenile recruitment typically drives variability in population growth rates (Gaillard et al. 2000). Variation in recruitment is strongly impacted by limiting factors caused by environmental stochasticity or population density (Gaillard et al. 1998). The ability to time reproductive activity to coincide with periods of increased resource availability can help to cover the energy costs of reproduction and, thus, can increase juvenile survivorship and lifetime reproductive success (Pianka 1976, Kennish 1997). As such, it is not surprising that the breeding phenology of many species is closely related to temporal variation in food availability (Drent and Daan 1980, Kennish 1997, Madsen and Shine 2000, Sinclair et al. 2000, Rubenstein and Wikelski 2003, Langvatn et al. 2004).

Reproductive timing may be shaped by resource needs and ecological conditions during parturition, conception, or a combination of both. Many studies of the factors influencing reproductive activity in ungulate populations have focused on parturition

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events, probably in relation to the importance of offspring survivorship to population dynamics (Gaillard et al. 2000) and the high cost of lactation (Oftedal 1984). Additionally, conception in many mammals (e.g. large ungulates) is not obvious, making research on the factors influencing conception more difficult to study. In order to understand the proximate cues for reproductive timing, however, the factors influencing the timing or rate of conceptions, e.g. female condition, should be distinguished from those influencing the timing of parturition, e.g. offspring survivorship (Stearns 1992). Variation in reproductive effort in relation to resource fluctuations within and across years can offer insight into the tradeoffs between current and future reproduction (Rivalan et al. 2005).

The reproductive phenology of a species is influenced both by ecological factors and life history constraints (Clutton-Brock 2002). Savanna elephants *Loxodonta africana* exhibit life history traits characteristic of large ungulates in that they are strongly iteroparous, have low annual fecundity and high annual adult survivorship, produce only one offspring per reproductive bout, and have long generation times. Compared to most ungulates, however, elephants exhibit a unique combination of life history traits that impact their ability to respond to temporal variability in ecological conditions or other factors influencing population demographic fluctuations. Each reproductive bout in an elephant includes the longest gestation period experienced by any terrestrial mammal (ca 656 d), extended parental care of young in which weaning typically occurs after 2 yr, and overlapping, dependent offspring necessitating extensive, long term energy investment in offspring (Laws 1969, Douglas-Hamilton 1972, Moss 1988). In respect to these life history constraints, we do not expect seasonality nor environmental stochasticity to impact conception probabilities or the timing of parturition. It is interesting, however, that recruitment rates in African elephant populations have been shown to vary widely across years, resulting in cyclic patterns in age distribution (Douglas-Hamilton 1972, Laws et al. 1975, Moss 2001).

Using time-specific conception rates recorded over a seven year period from an individually identified, wild elephant population in northern Kenya, we explore the relationship between ecological conditions and mortality, reproduction and demographic fluctuations in this species. For herbivores >50 kg, it has been posited that fecundity of young females rather than juvenile survivorship may be the fitness component most sensitive to environmental perturbations (Gaillard et al. 1998, 2000). We test this hypothesis on the largest terrestrial herbivore by exploring the relationships between remotely sensed NDVI (Normalized differential vegetation index), a measure of spatially explicit vegetative productivity (Goward and Prince 1995), and time-specific reproductive rates and mortality (Pettorelli et al. 2005). Specifically, we test the hypotheses that 1) female fecundity in this long lived species is not influenced by variation in ecological conditions, as may be expected in relation to the long duration of gestation and inter-calf intervals; 2) juvenile mortality is sensitive to variation in ecological conditions, a relationship found in many ungulate species (Gaillard et al. 2000); and 3) within season reproductive phenology synchronizes parturition events with the average seasonal peak in vegetation productivity, allowing females to synchronize early lactation and its associated high energy costs (Oftedal 1984) with the expected peak in plant growth.

Material and methods

Demographic data

Demographic changes have been monitored since 1997 in the individually identified elephant population inhabiting the semi-arid Samburu National Reserve in northern Kenya (Wittemyer 2001, Wittemyer et al. 2005). Between November 1997 and August 2004, 265 births were recorded within the group of 172 most frequently observed (i.e. seen within the study area at least 9 months of each year) and hence best known females of breeding age. Breeding age was defined as starting at 9 yr, since ca 98% of primiparous births in this species occur after this age (Moss 2001). Almost all births are believed to have been recorded during this period, as few of the studied females' inter-calf intervals exceeded the 4.5 yr average recorded in other populations (Moss 2001). Females that died during the study period were excluded from analyses from the point when her reproductive status was not known (pregnant/non-pregnant). In general, juvenile mortality rates were low during the study period, averaging 2.1% per annum (Wittemyer et al. 2005). Analysis of juvenile mortality was conducted on individuals five years and younger. Mortalities were recorded when known individuals were found dead or, more typically, when a mother was repeatedly observed without her calf (see Wittemyer et al. 2005 for description).

Using the aging techniques established with known aged elephants (Moss 1996, 2001), the birth date of calves less than one month old can be estimated accurately to within one week, providing detailed longitudinal data on the timing of reproductive events. The estimated ages at the first sighting of calves used in this study averaged 12 ± 15 (SD) d, with 253 of the 265 calves (95%) being observed less than one month after the estimated parturition date. In order to approximate the date of conception for the known parturition events, we subtracted the average gestation period of 656 d (ca 22 months) from the estimated date of birth (Moss 1983). Age estimates of mature individuals based on physical appearance were within ±5 yr of the age based on molar progression (Rasmussen et al. 2005). Therefore, breeding females were binned into 5-yr age classes for analysis in logistic regression models (described below).

The short duration (4–6 d) of behavioral estrus (Moss 1983) resulted in few estrus events being recorded relative to the number of known births, demonstrating our record of estrus events is incomplete. Therefore, analysis of conceptions in this study was based on back dating known parturition events. To evaluate if prenatal mortality influenced results, prevalence of prenatal mortalities was assessed using a smaller data set of observed estrus events. Estrus activity was defined by the observations of mate guarding/mating by males and distinct estrus behavior by females (Moss 1983). We compared observed estrus events occurring during a 4.5-yr period (from November 1997 to March 2002 containing 9 wet seasons) with estimated conception dates to assess the robustness of relying on parturition data for the calculation of conception probabilities. A total of 31 behavioral estrus events were observed. Two (6.5%), however, were erroneous as they occurred during mid pregnancy despite male elephants attempting to mate with the females. Thus, our analysis is conducted on the 29 potentially true estrus events (ranging from 0 to 6 events per cycle).

Index of ecological variability

NDVI (Normalized differential vegetation index) is a remote sensing index value, calculated as the ratio between red and near infrared reflection, highly correlated with green biomass (Goward and Prince 1995). NDVI acts as a direct assessment of the spatial and temporal variability in vegetation growth (Diallo et al. 1991, Rasmussen 1998). We have shown previously that elephant reproduction is better predicted by NDVI than rainfall (Rasmussen et al. 2006). Thus, we use NDVI as a surrogate for primary productivity to explore the relationship thereof on the timing of elephant reproductive activity. Because our study system receives two distinct periods of rainfall per year, in April and November, we focus on the relationship between variability in primary productivity and reproduction both within a seasonal cycle (where two cycles occur per year) and between cycles across the seven-year study (13 cycles in total).

We used 10-d composite NDVI values recorded by the NOAA AVHRR (Advanced very high resolution radiometer; 1995–2001) and SPOT (Satellite probatoire d'observation de la terre; 1998–2004) systems to measure time-specific vegetation productivity. To cover the study period NDVI values from these two

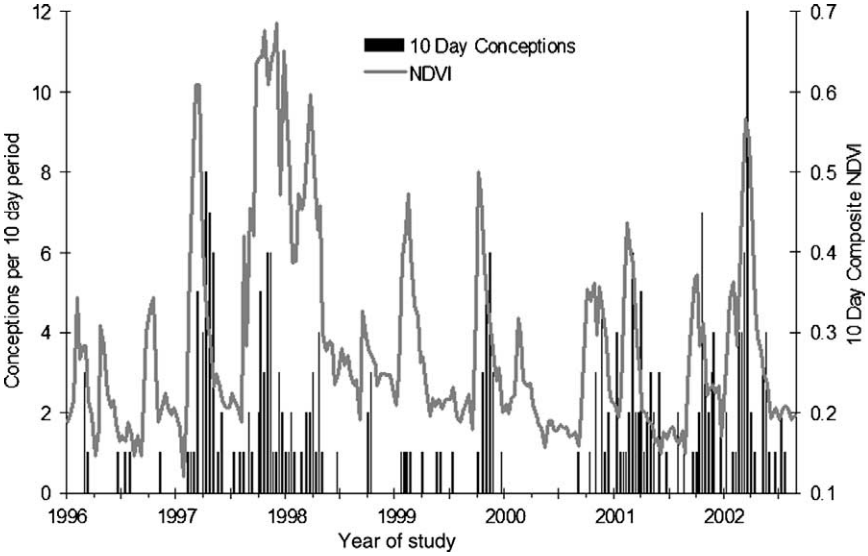

Fig. 1. The mean 10-d composite NDVI values (gray line) for the core study area and total number of conceptions 10-d^{-1} interval (black bars; calculated by subtracting 656 d gestation period from known time of birth). The high NDVI values and corresponding number of conceptions in 1997–1998 resulted in few non-pregnant females available during the following 22-month period. The relatively low NDVI values associated with the April 2000 "drought" occurred concurrently with the only season with 0 conceptions.

systems were calibrated and combined using a 2-yr overlap (Fig. 1). We calculated mean NDVI values for each 10-d period for a 1158 km^2 region covering the population's core area, defined by the 95% kernel isopleth (Worton 1989) calculated using hourly GPS data collected from 12 breeding females tracked for 10–14 months between 2001 and 2003. Vegetation productivity is most accurately estimated by NDVI when values are averaged over a generalized large area (du Plessis 1999). We found both maximum and minimum NDVI values in the core area were closely correlated with average values per 10 d period, demonstrating that average values were representative of variability in productivity across the core area. Each wet/dry cycle was defined as starting with an increase in the mean NDVI values >1 standard deviation above the dry season baseline (i.e. the mode of the distribution of composite NDVI values during the study period) and lasting until the next increase of one standard deviation (i.e. encompassing contiguous wet and dry seasons).

Statistical analysis

We used multiple factor logistic regression within a linear mixed model framework (Carlin et al. 2001) to assess the effect of ecological variability (as measured by NDVI) on female fecundity (hypothesis 1). Females were included in the analysis starting at the onset of the wet/dry cycle following parturition and ending during the wet/dry cycle during which conception occurred (i.e. excluding pregnant periods). Because data included multiple measures of individual reproductive status (conceiving or not conceiving), female identity was incorporated as a random effect in the model. The bimodal response variable of conceiving/non-conceiving during each wet/dry cycle was regressed against predictor variables of ecological conditions and individual specific variables to control for the influence of experience and reproductive history on fecundity. Covariates used in the model include two NDVI indices of season specific primary productivity, the maximum NDVI value and duration of elevated NDVI values above the dry season baseline, and three individual specific variables, female age group, number of seasons since last parturition date, and calf mortality. Calf mortality was a binary variable and recorded as "0" in seasons when the female's previous calf was alive or "1" when the previous calf had died prior to the mother's successive conception date (i.e. when a calf's death could influence the timing of a female's conception). Interaction variables of age × reproductive interval and NDVI × reproductive interval were included in the model. Exclusion of variables was tested using likelihood ratio tests, after which log likelihood values were compared between the full and reduced model.

To determine the effect of ecological variability on juvenile mortality (hypothesis 2), the correlation between season specific juvenile mortality (mortality of calves <5 yr) and wet/dry cycle maximum NDVI was assessed using Spearman rank correlation. Additionally, the influence of calf mortality on conception rates was assessed in the mixed model logistic regression as described previously.

Analysis of the relationship between the timing of conceptions and peaks in vegetation productivity within wet/dry cycles was used to test hypothesis 3. If parturition is targeted to coincide with average seasonal peaks in primary productivity, then conception dates should occur on a static calendar date (given a fixed gestation period) regardless of variation in the seasonal onset of pulses in vegetation productivity – i.e. a delay in the occurrence of conceptions will occur in early-starting as compared to late-starting seasons. To evaluate if the delay between seasonal onset and conceptions varied between seasons, the number of days between the actual start of seasonal pulses in vegetation productivity (defined previously) and conception dates were compared across wet/dry cycles using a Kruskal Wallis test. To evaluate if the variation in delay was related to the relative time of seasonal onset, the correlation between the median delay of conceptions from the wet/dry cycle onset and the difference between the number of days of the actual wet/dry cycle onset and the average start date over all wet/dry cycles during the study was assessed. Some wet/dry cycles had too few conceptions to estimate accurately the timing of conceptions. Thus, we limited this analysis to wet/dry cycles containing 10 or more events ($n=9$). We examined the residual autocorrelation from an ordinary least squares (OLS) regression model of the time series to ensure independent distribution of the data (Fox 2002). The partial autocorrelation function (PACF) for this analysis demonstrated residuals were not significantly correlated at any lag, therefore OLS regression results are reported. All statistical analyses were conducted using S-Plus (Venables and Ripley 1999).

Results

The numbers of conceptions in the study elephant population varied markedly across wet/dry cycles (Fig. 1), as did the numbers of non-pregnant females due to their 22 month gestation period. In contrast to our prediction for hypothesis 1, the maximum NDVI value during a wet/dry cycle was a significant factor in our model of female conceptions (Table 1). The duration of increased NDVI, however, was not significant ($\chi^2=0.559$, $p=0.455$) and was therefore removed. The fixed effects of

Table 1. The results from a multiple factor logistic mixed effect model, in which the individual was incorporated in the model as a random effect, indicate female fecundity is significantly impacted by the maximum seasonal NDVI value in addition to female age, calving interval, and calf mortality of individuals and two interaction variables (age with calving interval and NDVI with calving individual). The duration of elevated NDVI values per season (Duration NDVI) did not significantly add to the model and was subsequently removed.

Variables	Estimate	Standard error	Wald χ^2	p value	-Log Likelihood
Full model					−276.741
Maximum NDVI	−16.303	2.244	52.803	0.0000	
Duration NDVI	0.005	0.005	0.812	0.3680	
Age	1.125	0.317	12.550	0.0004	
Calving interval	−1.71	0.151	129.122	0.0000	
Calf death	1.763	0.551	10.239	0.0014	
Age × interval	−0.273	0.051	28.540	0.0000	
NDVI × interval	1.918	0.876	4.796	0.0280	
Reduced model					−277.151
Maximum NDVI	−14.841	1.507	96.948	0.0000	
Age	1.154	0.315	13.410	0.0003	
Calving interval	−1.691	0.148	130.415	0.0000	
Calf death	1.784	0.552	10.443	0.0012	
Age × interval	−0.273	0.051	28.474	0.0000	
NDVI × interval	1.853	0.873	4.512	0.0337	

individual age, interval since last parturition date, and calf mortality in addition to two interaction variables (interval × age and interval × NDVI) were significant (Table 1). NDVI and interval were the strongest covariates in the model (Fig. 2). Population conception rates ranged from 0.0% in one of the poorest cycles to 58.1% during the wet/dry cycle with the greatest maximum NDVI values. Of the combined births recorded over the 7-yr study (13 wet/dry cycles) over 55% were conceived during the four best cycles and <15% in the six poorest.

The effect of vegetation productivity on the proportion of successful pregnancies could result from high rates of prenatal mortality following conception in poor seasons or condition dependent estrus. To distinguish between these possibilities, we assessed the proportion

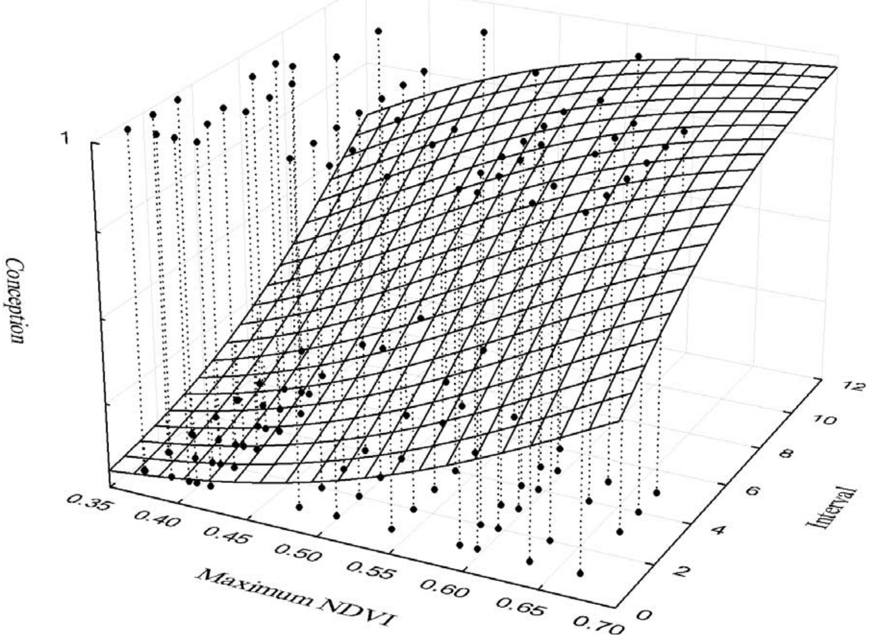

Fig. 2. Multiple factor logistic regression models in a mixed model framework demonstrate the importance of the fixed effect covariates of NDVI and interval since previous birth (Interval). As NDVI and the interval since a female's last calf's birth increase, a greater proportion of females conceive. Points represent multiple conception/non-conceiving events.

of estrus events that resulted in births from observations of behavioral estrus events (Moss 1983) during the first nine seasons of the study. Estrus events were not correlated with the number of non-pregnant females ($R^2 = 0.120$, $y = 0.023x + 1.696$, $p = 0.317$). Observed estrus events were correlated with the number of conceptions carried to term ($R^2 = 0.674$, $y = 0.133x + 0.752$, $p = 0.0067$) and positively but not significantly correlated with maximum wet/dry cycle NDVI values ($R^2 = 0.355$, $y = 10.978x - 2.0639$, $p = 0.090$). Of the 29 observed estrus events, six (20.7%) did not result in calf birth 21-22 months later. Of these, four females gave birth approximately 16 weeks later than the estimated birth date from the observed mate-guarding event corresponding to a delay of one ovarian cycle (Hodges 1998). It appears these females failed to conceive during the mate-guarding event, experienced their full ovarian cycle, and subsequently ovulated and conceived. In 3 of the 4 cases, this missed estrus event and subsequent conception occurred within the same wet/dry cycle (thus not affecting the results in our analysis). In the last two cases, females gave birth more than four years after the observed mate-guarding event (corresponding to the duration of two full pregnancies). This suggests that the calf was carried to term but lost before it was observed or the estrus observation was erroneous (Material and methods).

Juvenile mortality of calves younger than 5 yr was generally low, 2.1% for the whole population (Wittemyer et al. 2005), and not correlated with maximum NDVI values during the wet/dry cycle when mortality occurred (Spearman's $\rho = -0.368$, $p = 0.195$), indicating that ecologically variability did not induce variation in population growth via influencing juvenile recruitment in contrast to our prediction for hypothesis 2. Although calf mortality did significantly impact female fecundity (Table 1), only 9 calves died prior to their mother's subsequent conception. These 9 events represent ca 3% of the total conceptions, thus the impact of calf mortality on population demographics via its effect on female fecundity was negligible.

Estimated conception dates occurred a median of 76 d (inter-quartile range: 52–98 d) after the cycle onset and a median of 38 d (IQR range: 15–63 d) after the seasonal NDVI peak (maximum wet/dry cycle NDVI value), with 86% percent of all conceptions taking place after the peak in vegetation productivity when NDVI values were declining. Since the gestation period is 22 months, this delay resulted in parturition events coinciding with the initial increases of NDVI associated with the onset of wet cycles occurring a median of only 4 d before the wet/dry cycle onset (IQR: −27–27 d) in support of our prediction for hypothesis 3. The difference between conception dates and the actual date of wet/dry cycle onset (1st increase in NDVI values) per season varied significantly across wet/dry cycles (Kruskal-Wallis test: $\chi^2 = 34.126$, $DF = 7$, $p < 0.001$). The differences between the date of wet/dry cycle onset and median conception date for each cycle were negatively correlated to that cycle's relative start date ($R^2 = 0.658$, $y = -0.717x + 72.55$, $p = 0.008$; Fig. 3), indicating females conceive later in early starting cycles and earlier in late starting cycles. Hence, this analysis of estrus and parturitions indicates a very low level of prenatal mortality.

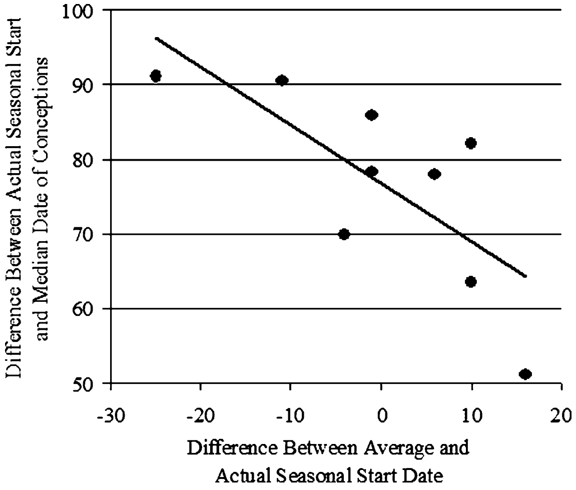

Fig. 3. The median delays of conceptions occurring per wet/dry cycle are negatively correlated with the relative start date of that cycle – the difference between the average and actual seasonal start date. In cycles where the initial increase in NDVI values occurred later than average (positive values on the x-axis), the average date of conceptions for that cycle occurred earlier (lower values on the y-axis). Thus, females are generally conceiving later in early starting seasons and earlier in late starting seasons ensuring births occur around the average date the rains begin. The four seasons with <10 births were excluded from this analysis.

Discussion

Our study of reproductive phenology in a wild elephant population indicates that conception probabilities, and therefore female fecundity, are positively affected by the seasonal specific level of primary productivity as measured by remotely-sensed NDVI, while controlling for experience and reproductive history of females (Table 1). This effect of ecological conditions did not seem to be linked to variation in prenatal mortality acting on a fixed proportion of conceptions. The time-specific numbers of observed estrus/mate-guarding events were not correlated with the number of non-pregnant females but weakly correlated to NDVI and significantly correlated to the number of conceptions carried to term, indicating prenatal mortality in response to poor vegetation productivity is unlikely to drive the seasonal specific variation in pregnancies carried to term. The most likely cause of error in our analysis, at a maximum of 7% in our sample of estrus events, appears to be calves that die after birth but before we observe them. Hence the effect of ecological conditions on pregnancies carried to term is most likely a result of condition dependent estrus. Few conceptions occurred during wet/dry cycles when the maximum NDVI values were low (Fig. 2). The majority of conceptions, carried to term, occurred after the maximum level of vegetation productivity as indicated by peak NDVI values. Thus elephants consume the majority of high quality resources associated with the wet season prior to ovulation, and may forgo reproduction during seasons with poor ecological conditions. This is suggestive of a physiological threshold below which conceptions do not occur in elephants. These traits are characteristic of a capital breeding reproductive strategy, in which resources are stored prior to initiation of a reproductive bout (Drent and Daan 1980, Jönsson 1997, Festa-Bianchet 1998).

Contrary to conceptions, which are correlated with between-cycle variation, the timing of births in elephants is shaped by variation in primary productivity associated with the predictable annual transitions between dry and wet periods. The median delay between onset of primary productivity pulses and conception dates varied significantly between wet/dry cycles, indicating the temporal cue for elephant estrus is not simply the onset of wet seasons. The median delay between the dates of specific wet/dry cycle onset and the corresponding median conception dates were negatively correlated with the relative onset of that cycle (Fig. 3). Intra-season conception phenology results in parturition at the average onset of increased primary productivity, thereby synchronizing the highest energy costs of post-partum maternal care with high quality ecological conditions ensuring that high quality resources are available to cover the cost of early lactation. Such a trait is typically associated with the income breeding strategy (Jönsson 1997). The mechanism by which elephants time these events is not clear since specific seasonal onset is not the cue. It seems reasonable to assume they use a general environmental stimulus such as photoperiod or temperature to time reproduction. However, photoperiod does not seem likely because reproductive activity occurs twice a year in relation to the two wet seasons, which are separated by approximately 6 months. Furthermore, the study area is situated half of a degree north of the equator such that day length varies by <30 min across the year. Temperature, also, does not appear to be the cue as most conceptions occur during the January "hot" season or during the June "cold" season, though temperatures in the equatorial study area do not fluctuate substantially across the year.

Elephants, having long gestation periods and extended (multiple year) postpartum offspring investment, face an ecological conundrum regarding how to budget resources for reproduction when living in unpredictable environments. Elephant calves are generally not fully weaned until the birth of their sibling, meaning females are lactating at the time of conception and, at times, successive suckling calves may overlap. In combination with ecological conditions, the constraint of a dependent calf while conceiving appears to be the major factor influencing conception phenology of elephants. In our analysis, the interval since last parturition event and NDVI were strongly related to conception rates (Fig. 2). As is common in north temperate species, elephants parturition coincides with flushes in primary productivity within-seasons (Stearns 1992). The life history constraint of their extended reproductive bout, however, prevents elephants from predicting resource quality at the time of parturition based on conditions at the time of conception. In making the best of this constraint, elephants initiate their extended reproductive bout only when conditions are good and time the parturition to coincide with expected seasonal cycles of primary production. Thus, we suggest elephants maximize their use of experienced ecological conditions at the time of conception and rely on probabilistic resource availability during parturition when resource quality cannot be predetermined, employing distinct reproductive strategies during the different stages of reproduction.

Synchronicity in demographic parameters, necessary for the emergence of cyclic demographic fluctuations, are typically the result of variation in mortality in ungulate populations, driven by variability in food resources, population density, and predation pressure (Clutton-Brock et al. 1997, Gaillard et al. 2000). However, juvenile mortality rates in the study elephant population during the study period were low, averaging 2.1% per annum (Wittemyer et al. 2005). And mortality was not significantly correlated with seasonal NDVI values. Rather, the influence of cycle-specific primary productivity on conception rates has the effect of synchronizing reproduction in our study population. The El Niño-Southern-Oscillation (ENSO) resulted in a period of unusually high primary productivity in the study ecosystem during 1997 and early 1998 and to a less extent in 2002 (Fig. 1). This major perturbation in the dry and wet season primary productivity cycle strongly influenced elephant conception rates, acting to synchronize reproduction across the population. Additionally, poor rains and resulting low levels of primary productivity in 2000 associated with the La Niña phase of the ENSO resulted in no known conceptions, again affecting the synchronization of population reproductive activity. Thus, female fecundity rather than climatic or density driven mortality of juveniles appears to drive population fluctuations in the Samburu population, supporting the conclusions for ungulates >50 kg (Gaillard et al. 2000). Similarly, many elephant populations across Africa are experiencing high growth rates and low mortality (Blanc et al. 2003). Thus, time-specific recruitment in other elephant populations may not relate to mortality as found with the Samburu elephants. Rather, climatically-elicited synchronization in female fecundity can cause observed fluctuations in population age structure (Douglas-Hamilton 1972, Laws et al. 1975), though ecological differences between populations may elicit different demographic phenomena. Demography in plant communities have been ascribed to climatically driven variation in flowering (Inouye et al. 2002), but the implication of conception probabilities on such fluctuations in mammals is not commonly investigated. Identification of reproductively driven demographic variation as opposed to mortality driven is important for population management activities, such as sustainable harvesting and control regimes as well as recovery efforts.

The characteristic ecological variability and annual dry periods in savanna ecosystems when energy allocation is most strained may have disposed elephants to a capital breeding strategy, encouraging the development of energy buffers for periods of stress. The size of this species limits the cost of carrying excess energy stores (Jönsson 1997). However, due to their 22-month gestation period and the variability in ecological quality over a year, energy stores at the time of parturition are likely depleted pushing elephants towards a reliance on available resources during post-parturition lactation. Thus, elephants must rely on both energy stores and available resources to ensure successful offspring recruitment. Energy constraints in other species have also been shown to cause switching between stored and procured resources (Shanbhag 2003) or a mixed energy allocation strategy (Lourdais et al. 2002, 2003) to ensure successful reproduction. Investigation of the reproductive strategies employed by an organism during both the pre and post-natal phases of reproduction can serve to enhance understanding of the constraints impacting a species and can offer insight to the factors influencing population demographic cycles.

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