Ecological cues, gestation length, and birth timing in African buffalo (*Syncerus caffer*)

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We examined annual variation in the timing of conception and parturition in the African buffalo (*Syncerus caffer*) and the synchrony of birth timing with resource cues, using 8 years of monthly birth, rainfall, and vegetation data, measured as Normalized Difference Vegetation Index (NDVI). Monthly births had the strongest significant correlations with NDVI and rainfall levels 12 and 13 months in the past, respectively. In addition, the synchrony of current year births corresponds most strongly to the synchrony of the previous year's NDVI distribution. Because the gestation period of buffalo has been estimated to be around 11 months, these findings suggest that improved protein levels, occurring approximately a month after the first green flush of the wet season, are either a trigger for conception or conception has evolved to be synchronous with correlated environmental cues that ensure females enter a period of peak body condition around the time of conception and/or parturition. With a gestation period of approximately 340 days, parturition occurs to take advantage of the period when forage has its highest protein content. A comparative analysis of gestation periods within the subfamily Bovinae indicates that African buffalo have a protracted gestation for their body size, which we suggest is an adaptation to their seasonal environment. We also found that interannual variation in the birth distribution suggests a degree of plasticity in the date of conception, and variation in the number of calves born each year suggest further synchrony at a timescale longer than a single year. *Key words:* birth synchrony, breeding ecology, NDVI, phenology. *[Behav Ecol 18:635–644 (2007)]*

Multiple hypotheses have been offered as explanations for birth synchrony in ungulates: 1) predator swamping through dilution or group protection of young (Estes 1976; Sekulic 1978; Estes RD and Estes RK 1979; Keech et al. 2000; Testa 2002); 2) optimization of social development as a cohort within a group (Brown 1985; Pfeifer 1985); or 3) timing births to coincide with periods of optimal environmental conditions (Rutberg 1987). These hypotheses are not necessarily mutually exclusive and may act in concert. Here we focus on the third hypothesis, which points to the role of resource availability as driving the timing of parturition in African buffalo (*Syncerus caffer*). Ungulates may time parturition to coincide with the availability of high-quality vegetation to support the energetic costs of lactation (Gaillard, Delorme, and Jullien 1993), to maximize the growth rate of neonates to assist predator avoidance (Clutton-Brock et al. 1982), and to replenish maternal reserves for future reproduction while conditions are optimal (Gaillard, Delorme, Jullien, and Tatin 1993; Keech et al. 2000). However, we hypothesize that buffalo are also conceiving while conditions are optimal, and due to a protracted gestation period of slightly more than 11 months, additionally benefit from good conditions at parturition.

African buffalo exhibit similar seasonal social ecology to many other ungulates, in which males form bachelor groups in the nonbreeding season to forage and improve their condition and then compete for mates in the breeding herd during the breeding season (Clutton-Brock et al. 1979, 1982;

Halley and Mari 2004). The social ecology of buffalo seasonal breeding aggregation depends largely on resource availability: a threshold appears to exist at which the foraging cost for males of remaining in the group outweighs the reproductive opportunity (Turner 2003; Turner et al. 2005). In arid and semiarid systems, it is suggested that herbivore aggregation is also limited by a patchy spatial availability of resources (Fryxell 1995) whose quality varies with very local rainfall. This seasonal and spatial restriction by resources may act to limit male reproductive opportunity within the breeding herd due to reduced feeding availability in a mixed herd and competing with other males for mating opportunities. In addition, buffalo cows must attain sufficient body condition to conceive and contend with the competing potential energetic costs of gestation, lactation, or tending of the prior year's calf (Prins 1996). African buffalo are highly gregarious and appear to have a social system within the breeding herd in which females and their offspring move together within a looser female hierarchy (Mloszewski 1983; Prins 1996), using a set of vocalizations and postures to maintain herd cohesion and order (Mloszewski 1983; Estes 1991). Calves have been reported to suckle for up to 18 months in some study areas (Prins 1996).

In accord with the principles of optimal foraging theory, to maximize reproductive output, an organism should maximize food quality: for herbivores, this means maximizing protein intake (Kennish 1997). For grazers in a semiarid ecosystem, protein is a limiting nutrient (Bell 1971; Owen-Smith 1982; Owen-Smith and Novellie 1982). Although described as a "supreme bulk grazer," and therefore able to consume a high quantity of matter (Owen-Smith and Cumming 1993), buffalo still lose condition as grass biomass increases due to a decrease in the protein content of their diet (Fryxell 1995). Prins (1996)

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found that African buffalo in Manyara National Park, Tanzania, conceive at peak cow condition and suggested that the long gestation of buffalo additionally means that calving coincides with good nutritional condition. However, a direct connection between maximum protein availability and conception has not previously been made for buffalo.

African buffalo have birthing seasons reported to coincide with the wet season in multiple sites (Grimsdell 1973; Sinclair 1977; Mloszewski 1983; Prins 1996; Turner 2003) and a gestation period with a mean of around 340 days (Bertschinger 1996). In a study of buffalo diet in Kruger National Park, it was shown that remotely sensed vegetation greenness (Normalized Difference Vegetation Index, NDVI) correlated highly with the proceeding month's level of fecal nitrogen in buffalo (Ryan 2006), a widely used proxy for dietary protein intake in both domestic and wild ungulates (Holechek et al. 1982; Leslie and Starkey 1985; Wofford et al. 1985; Bartiaux-Thill and Oger 1986; Hobbs 1987; Leite and Stuth 1990, 1992, 1995; Nunez-hernandez et al. 1992; Lyons et al. 1995; Wehausen 1995; Grant et al. 1996; Kucera 1997). NDVI provides us with an important measure of habitat quality in this system because the patchiness of rainfall and the difference between sustained low rainfall and periodic or episodic events are hard to distinguish with precipitation data (Scanlon et al. 2005). As reviewed by Pettorelli et al. (2005), NDVI is a well-established proxy for vegetation productivity and phenology. The body condition of adult female buffalo, both with and without a calf at foot, coincided with peak monthly remotely sensed NDVI values in Kruger National Park (Ryan 2006).

Therefore, we hypothesize that conception occurs around peak protein content in the vegetation, 1 month after the peak NDVI, when buffalo cows are in peak condition, whereas parturition occurs within a month of the peak protein content 1 year later. This hypothesis is supported by our data; however, insufficient information exist to fully distinguish the individual roles of rainfall and protein content in forage.

To further explore the observed phenomenon that African buffalo conceive and give birth in optimal conditions, we compare their gestation period with other members of the subfamily Bovinae to assess whether they demonstrate a protracted gestation that allows for a synchronized annual cycle of conception and parturition. This is consonant with a hypothesis that although this is a "relaxed" (Rutberg 1987) seasonal environment as compared with Northern climes, there has been sufficient selective pressure for African buffalo to evolve extended gestation beyond a physiological expectation for their bodyweight.

The occurrence of droughts in this system can alter the timing of wet season onset, which can result in lowered vegetation production and palatability of standing grass. The plasticity of the breeding season in mammals subject to a highly variable climate may be greater than those that have evolved with reliable resource cues. In a study by Sinclair et al. (2000) and studies by Rutberg (1984), 1987), a data set was summarized from a period in 1977 (Sinclair 1977), in which 49 birth events were recorded. With our data that includes 786 births during a period spanning 1993–2001, we are able to evaluate the potential for a response to annual variations in ecological resource cues.

METHODS

Study site

The Klaserie Private Nature Reserve (KPNR) is located in the Limpopo Province of South Africa, bordering Kruger National Park on its western boundary (24°3–22′S, 31°2–19′E; 303–535 m above sea level; 57 800 ha) (Figure 1). The main geolog-

ical substrate is granitic gneiss, part of the extensive granalitic system underlying most of the country. The climate follows a subtropical savanna pattern: both annual temperature and rainfall follow a unimodal distribution (Figure 2). Mean annual rainfall for this study period is 574 mm. We define 2 main seasons based on rainfall and temperature: a hot wet "summer" season from October to March and a cool dry "winter" season from April to September. In this study, our years are from October to October, with the year (19XX) assigned as the calendar year for January. KPNR contains the range of 3 main herds of buffalo. The range and habitat selection of these buffalo are summarized in a prior study (Ryan et al. 2006).

Births

A data set containing 786 calving events by month for one herd were recorded by one of us (C.U.K.) between 1993 and 2001.
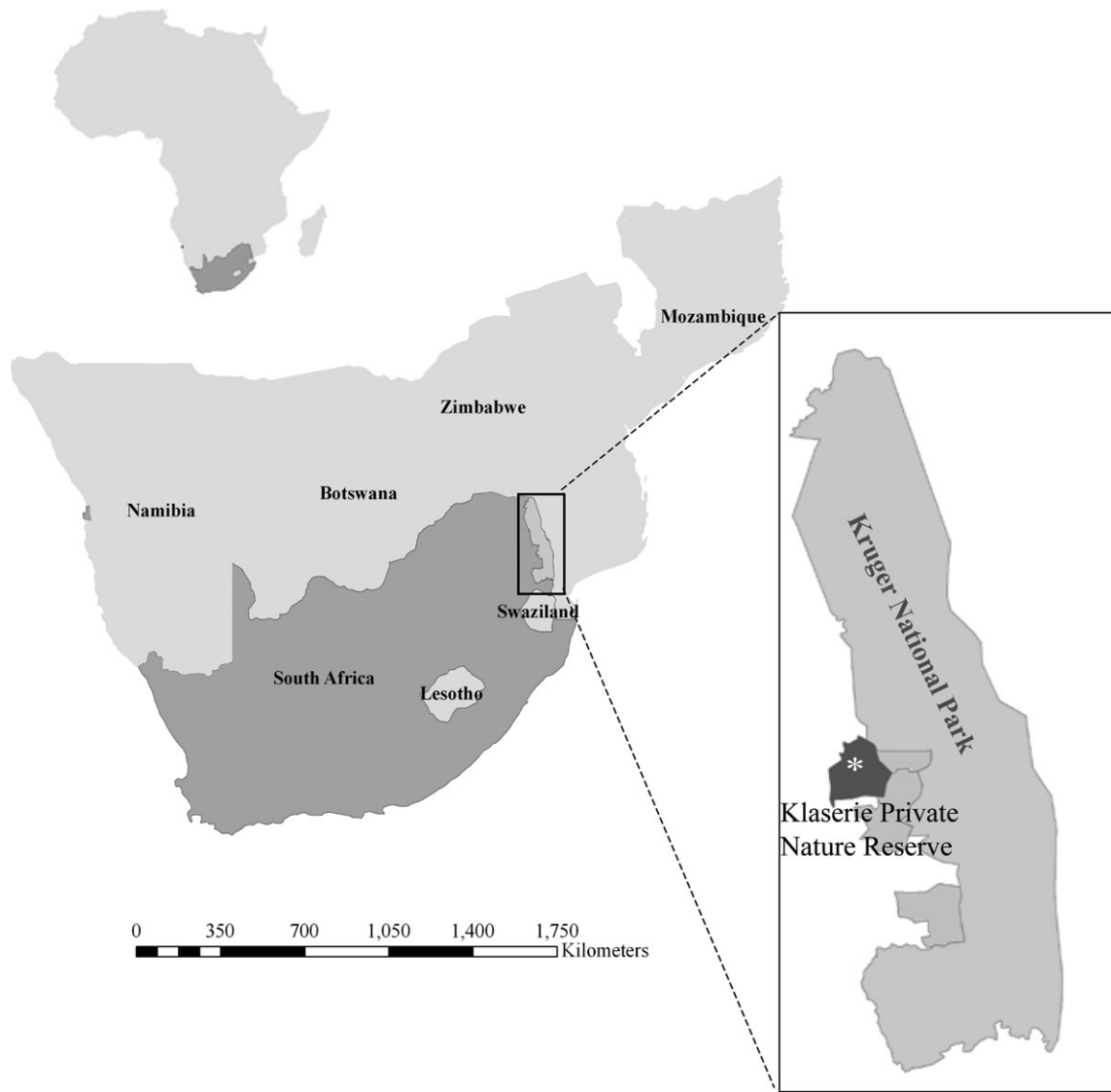
Precipitation

Mean monthly rainfall was taken from a maximum of 7 stations throughout KPNR. These data were transcribed from logbooks into Excel and monthly averages calculated to create a monthly distribution of rainfall through the study period (Figure 3).

Remotely Sensed Vegetation Data

NDVI data from National Oceanographic and Atmospheric Association's (NOAA's) Advanced Very High Resolution Radiometer (AVHRR) sensor aboard weather satellites processed by the Global Inventory Monitoring and Modelling Studies group (GIMMS) at the National Aeronautical and Space Administration (NASA) at a scale of 8 km^2 were downloaded from the Africa Data Dissemination Service (ADDS) (Pinzon 2002; Pinzon et al. 2004; Tucker et al. forthcoming). We use these data as a measure of the change in vegetation quality in the reserve. These data were imported into Agricultural Research Centre (ARC)/INFO 8.0 (Environmental Systems Research Institute 2000a) and ArcGIS 8.3 (Environmental Systems Research Institute 2000b), using ArcMap for visual assessment of available images. For viable images (no cloud cover over KPNR, no image corruption), 0–3 images per month were used to create monthly average grids of data clipped to the KPNR, using an Arc Macro Language (AML) script. We converted the raw 8-bit data (256) to the conventional scale (−1 to 1), where vegetated land usually takes on values in the range 0.1–0.7 (Pinzon 2002; Pinzon et al. 2004; Tucker et al. forthcoming). These monthly average values were averaged across the reserve to derive a monthly mean value in a vegetation quality distribution (Figure 3).

Birth timing

To find the peak of the birth distribution, monthly average proportions of births in the years 1993–2001 were compared using an ANOVA with a post hoc Tukey–Kramer's HSD test for means. A generalized least-squares model was also fit to the births versus month and year in SPLUS for Windows to compare annual and intra-annual variance in births. To examine breeding at a finer scale, we took a set of 28 individually identified females that were followed through 7 consecutive years and calculated both an individual fecundity and a group proportion of birthing within a year. We did not have information on calf survival for these individuals, as would be necessary to formally test the effects of lactation or tending on

Figure 1
The study site: Klaserie Private Nature Reserve, South Africa.

conception, but we informally describe calving sequence for these individuals.

Environmental cue timing

We cross-correlated the resource cue (precipitation, vegetation) against the births over a 15-month window. We used a conservative backward stepwise regression ($P > 0.05$ to exit) to test the distribution of births against each of the lagged resource cues (0–15 month lagged) to identify the significant lags. We chose a backward stepwise regression as appropriate because we had prior assumptions from the cross-correlation about which time lags we were modeling, and a backward stepwise regression is initiated with all parameters (in our case, time-lagged cues) in a full model. In a mixed stepwise regression (0.05 to enter and 0.05 to exit), we achieved the same results, suggesting that we did not lose any significant parameter contributions in the selection process. In addition, we tested the parameter "year" in all models, with no significant results, so we do not report it in the model fit for this parameter.

Evenness of births and environmental cues

To quantify the evenness of births and environmental cues each year, we applied the method of Bronikowski and Webb (1996), which has been used in similar studies comparing ungulate behavioral responses to rainfall variability (Sinclair et al. 2000; Brashares and Arcese 2002). The evenness index J^q is given as

$$J_t^q = \frac{1}{\log 12} \sum_{i=1}^{12} p_i^q(t) \log p_i^q(t),$$

where $t = 1994, \ldots, 2001$ and $i = 1, \ldots, 12$ denotes the month of the year (respectively, from October of year $t - 1$ to September of year t); $q = b$, r, and g, respectively, represents births, rain, and NDVI (greenness); and $p_i^q(t)$ is the proportion of births or environmental cue in the ith month of the tth year. Evenness ranges from 0 (e.g., all births or rain occur in one month) to 1 (same levels each month).

For purposes of comparison, we followed the methods of Sinclair et al. (2000) and compared the evenness measure of
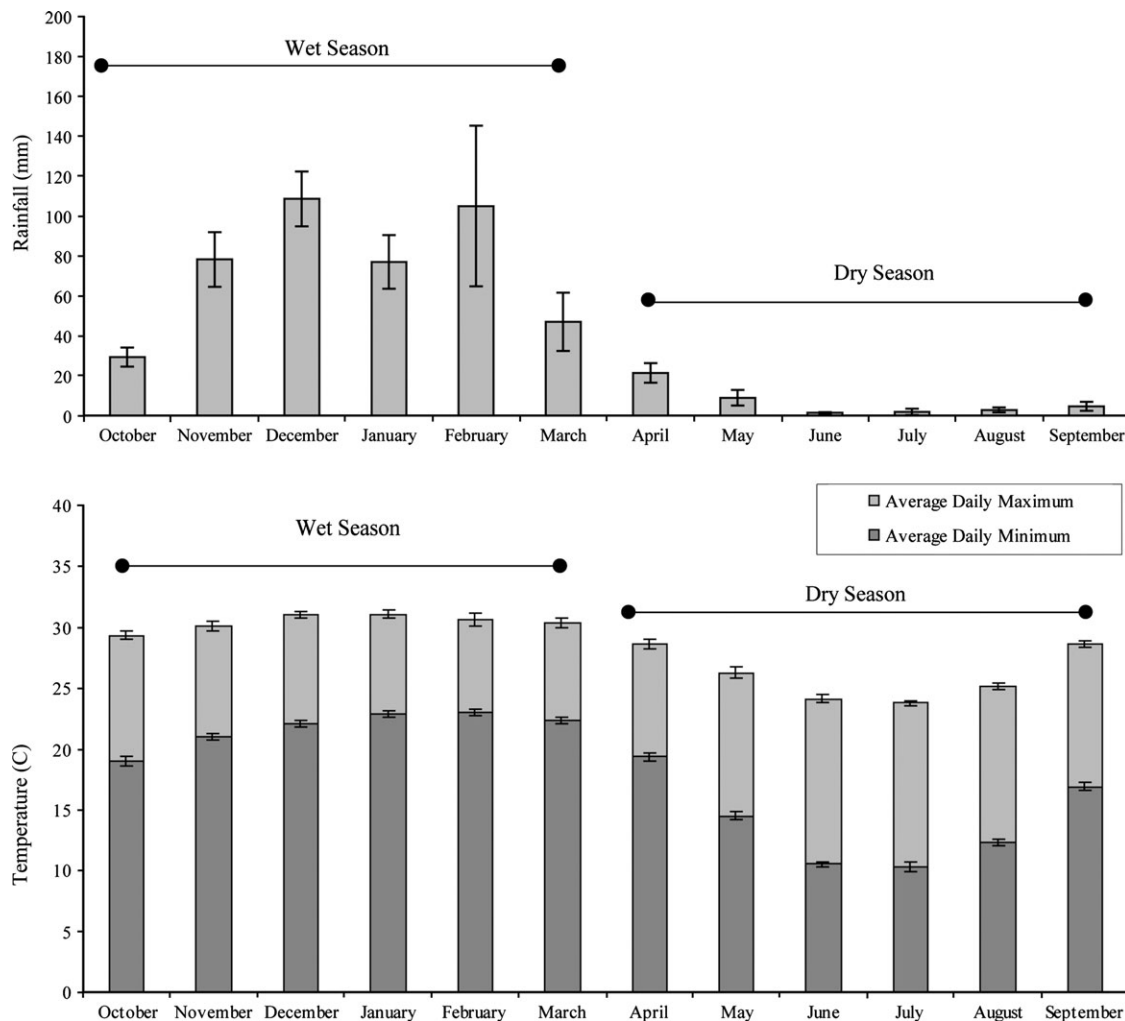
Figure 2
Rainfall and temperature (mean ± SE) of Klaserie Private Nature Reserve, 1991–2000 (adapted from Ryan et al. 2006).

births with that of each resource, both within the same year and the preceding year, using a ratio of $J_{births}/J_{resource}$. The ratio that most closely approximates 1 is the indication of similarity of birth and resource similarity (Table 1).

Evidence of protracted gestation

We collated data for gestation period in days (d), and body-weight (w) in kilograms for 24 of 25 members of the subfamily Bovinae (Myers et al. 2006), as taken from the Cetartiodactyla supertree of Price et al. (2005), using the software TREEVIEW and TREEedit (Page 1996). The phylogeny of the Bovinae is not well resolved, in particular, a reconstruction of the tribe bovini containing the African buffalo has not been resolved (Buntjer et al. 2002), although work is underway using mitochondrial DNA and Y-chromosomal sequences (Lenstra JA, personal communication), so a fully corrected analysis is not currently feasible. The genus *Syncerus* is monophyletic, and as this is an analysis at the subfamily level, we were comfortable, using a least-squares fit of log(d) versus log(w) at the genus level, to derive an allometric scaling equation (power law), $d = bw^a$, where a is the regression coefficient or slope and b is the intercept (Martin et al. 2005). To predict the expected gestation period for buffalo, we used the other 23 members of the Bovinae for which we have data to create the power law model,

using generic means, and then interpolated to examine where buffalo occur on the prediction interval. Because we had few data points in the regression ($n = 9$ genera), the prediction interval was quite wide, though we still retained the 2-tailed 95% prediction interval (but see [Garland and Ives 2000]) (Figure 4).

All statistics were run in SAS JMP 5.1 (SAS 1989–2003) or SPLUS 6.0 for Windows.

RESULTS

Birth timing

We found that across this study period, January is the peak month of birthing (Figure 5). An ANOVA with post hoc means comparisons showed that there is a 3-month peak from January to March wherein the mean proportion of births occurring in January is significantly higher than all other months, and February and March are significantly different from all other months but not from each other ($F_{ratio} = 23.96$, degrees of freedom [df] = 11, 95, $P < 0.0001$; Tukey–Kramer HSD, $\alpha = 0.05$). The generalized least-squares model showed that the intra-annual variability of births was significant, whereas interannual variance was not (ANOVA: model df = 83, intercept df = 1, $F_{ratio} = 160.93$, $P < 0.0001$; $F_{ratio} = 15.17$,
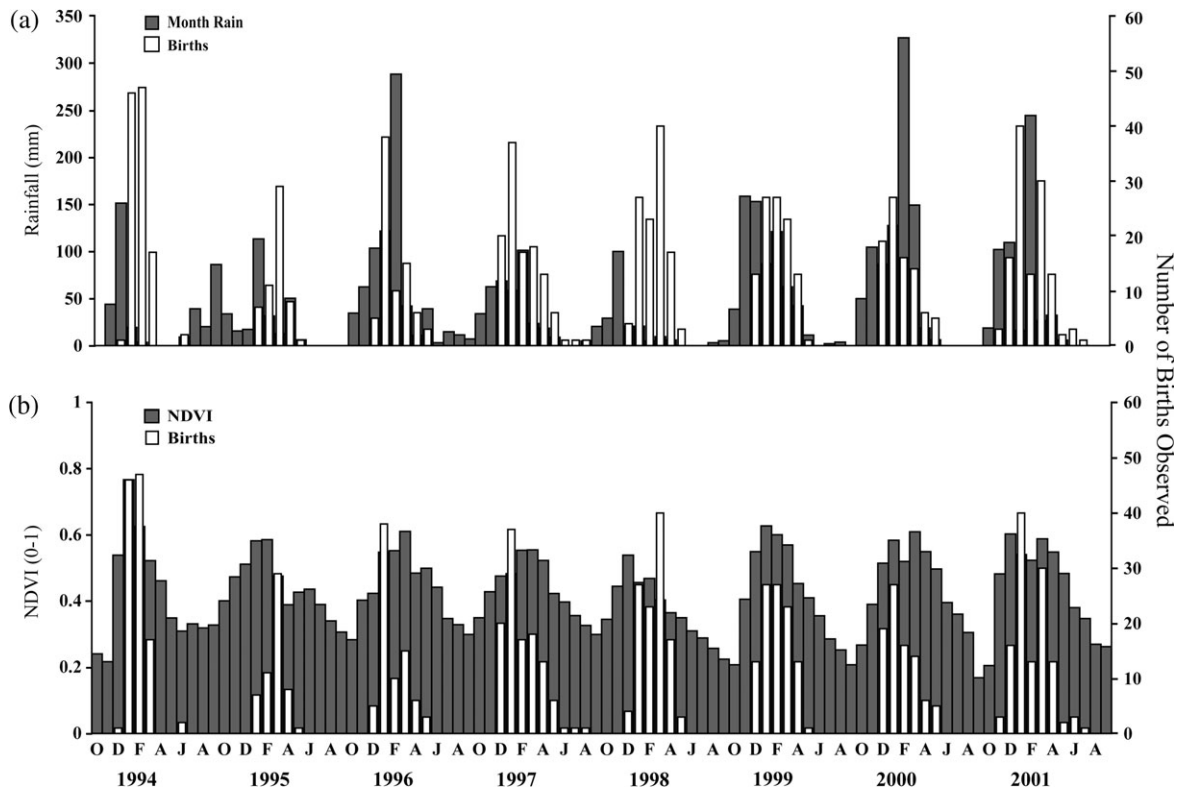
Figure 3
Monthly births (foreground, white), rainfall (millimeter) (background, black) (a), and NDVI (background, gray) (b) for the study period.

$P < 0.0001$; month: df= 11, $F_{ratio} = 23.97$, $P < 0.0001$; year: df = 1, $F_{ratio} = 1.06$, $P = 0.31$).

The group of 28 individually identified breeding females had an average individual fecundity (mean ± standard error [SE]) of 0.43 ± 0.02 calves/year. We found that the average proportion of females calving in a year is [mean (95% confidence interval (CI))] 0.43 (0.20–0.65). There was considerable interannual variability in the calving proportion and, in particular, 1998 appeared to be a particularly good calving year with 25 (89%) of the females calving (Figure 6). We bootstrapped the data from 28 females 10 000 times by rearranging each of the rows at random (i.e., each female's reproductive output for the 7-year period was held constant, but the years in which they had their calves was randomized). In none of these runs did 23 or more females reproduce at the same time

in any of the 7 years, and in only one did 22 females reproduce at the same time (the mode of this distribution is 12). This implies that the probability of observing 25 or more by chance of the 28 individuals reproducing, as was the case in 1998, is $P < 0.0001$.

The odds of having a calf in 2 consecutive years was 0.5 (prior year) and 0.58 (proceeding year), and of the females calving in 1998, 24% had calved the year previously and 20% calved in the following year. Seven individuals were observed to have calves in 3 consecutive years within this data set.

Environmental cue timing

Cross-correlations of the birth distribution from 1996 to 2001 against monthly rainfall and greenness (NDVI) lost

Table 1

Synchrony of births and resource cues

Year	n	J^b	J^r	J^b/J^r	J^b/J^{r*}	J^g	J^b/J^g	J^b/J^{g*}
1993			0.65			0.66		
1994	113	0.45	0.66	0.69	0.70	0.67	0.68	0.69
1995	56	0.23	0.70	0.34	0.35	0.69	0.34	0.35
1996	77	0.45	0.76	0.59	0.64	0.53	0.84	0.65
1997	114	0.66	0.82	0.81	0.88	0.99	0.67	1.25
1998	114	0.62	0.64	0.96	0.75	0.62	0.99	0.62
1999	104	0.64	0.77	0.84	1.00	0.84	0.76	1.04
2000	87	0.66	0.69	0.96	0.86	0.71	0.94	0.79
2001	121	0.65	0.63	1.03	0.94	0.73	0.89	0.92
Mean (±SE)	98 (8)	0.55 (0.05)	0.71 (0.02)	0.78 (0.08)	0.77 (0.07)	0.72 (0.05)	0.76 (0.07)	0.79 (0.10)

The number of births (n) and evenness indices (J^q) measuring synchrony for births ($q = b$), rainfall ($q = r$), and NDVI ($q = g$) each year; ratio measures of birth distributions with resource distributions of the same J^b/J^q and previous year J^b/J^{q*}. A ratio value of 1 is the maximum similarity between evenness values of births and resources.
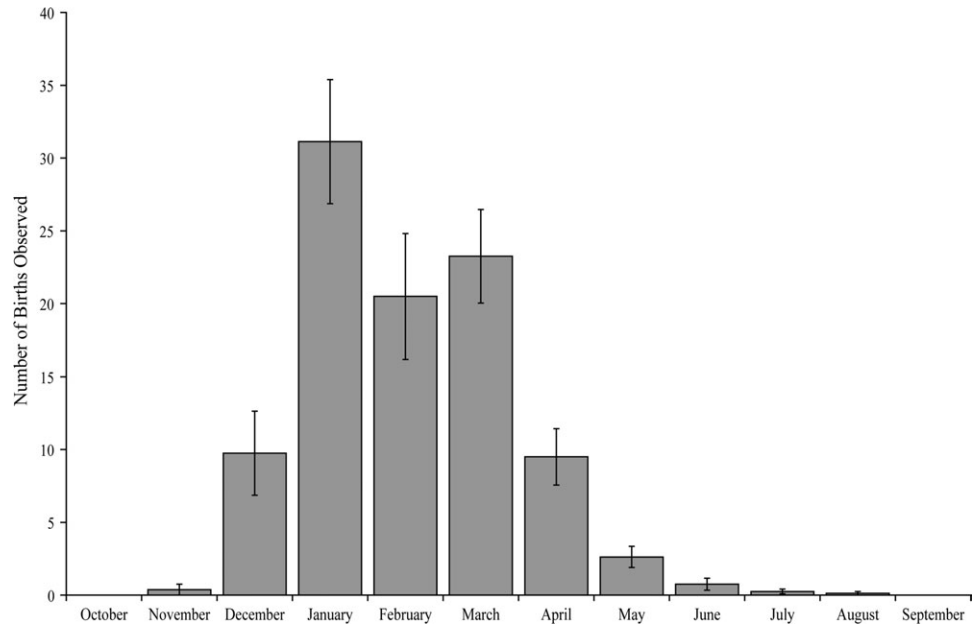
Figure 4
Average monthly proportion of births (mean ± SE) from 1993 to 2001.

significance (and meaning) at a 14-month lag. The highest correlation (Pearson's $r = 0.69$, $P < 0.0001$) is a 12-month lag in NDVI (1 year prior). For monthly rainfall, the highest correlation occurs at a 13-month lag (Pearson's $r = 0.57$, $P < 0.0001$). Positive correlations occur for both resource cues at a 0- to 3-month lag and between 10 and 14 for NDVI and 11 and 15 for rain, corresponding to the current and prior wet season months. These results support the idea that conception is tied to resources but that the extended gestation implies that the same high-quality conditions are realized at parturition a mean of 340 days later.

A series of backward stepwise linear regressions (SLR) yielded the following models for each resource. For monthly rainfall (r), the SLR selected lag 2, lag 11, and lag 13 as best explanatory variables, with most support for lag 13 ($F_{total} = 23.43$, $P = 0.0001$; $r_{lag\ 2}$: $F = 13.66$, $P = 0.0134$, $r_{lag\ 11}$: $F = 4.71$,

$P = 0.03$, $r_{lag\ 13}$: $F = 31.20$, $P < 0.0001$); $y = 0.06(r_{lag\ 2}) + 0.03(r_{lag\ 11}) + 0.09(r_{lag\ 13}) + 0.32$.

For NDVI (v) the SLR selected lag 1, lag 3, and lag 12 as most explanatory variables ($F_{total} = 51.81$, $P = 0.0001$; $v_{lag\ 1}$: $F = 31.00$, $P < 0.0001$; $v_{lag\ 3}$: $F = 24.36$, $P < 0.0001$; $v_{lag\ 12}$: $F = 12.28$, $P = 0.0007$); $y = 53.41(v_{lag\ 1}) - 35.86\ (v_{lag\ 3}) + 30.96\ (v_{lag\ 12}) - 12.27$.

Evenness of births and environmental cues

The distributions of births, rainfall, and NDVI across the study period are shown in Figure 3. The average evenness, J^b, for births over the study period was 0.55 ± 0.05 (mean ± SE), for rainfall it was 0.71 ± 0.02, and for NDVI it was 0.72 ± 0.5. The mean ratios of J^b/J^q suggest that the birth evenness is most similar to the prior year's vegetation (NDVI) measure of evenness (0.79 ± 0.10) (Table 1).
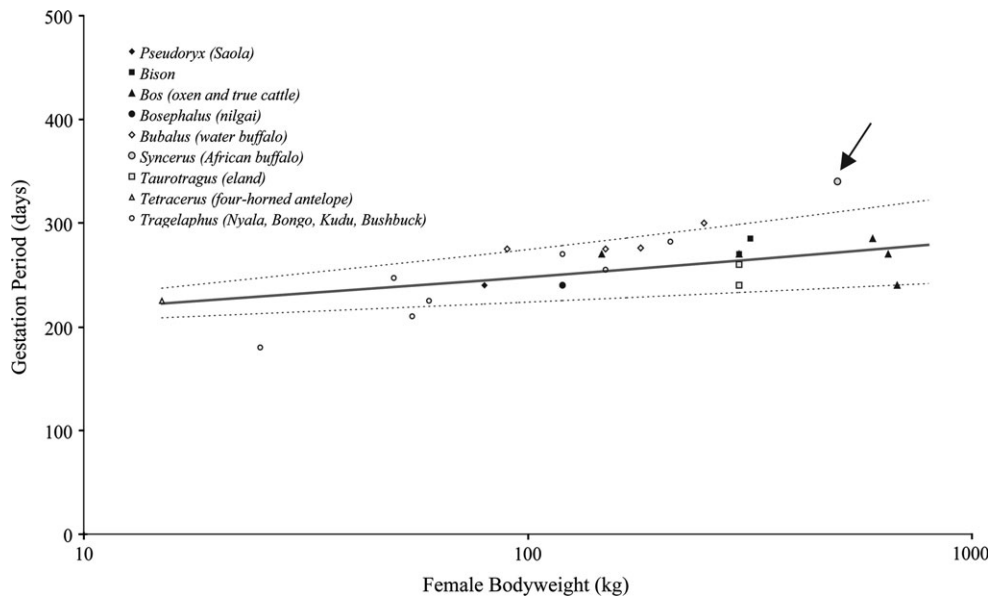
Figure 5
The relationship of gestation period (days) to female bodyweight (kilogram) for the subfamily Bovinae excluding African buffalo. The power law of log gestation (days) against log bodyweight (kilogram) at the level of genus is shown (solid line) with 95% PIs (dashed lines), with raw data for the 9 Bovinae genera, depicting the African buffalo (*Syncerus caffer*) (pointer).
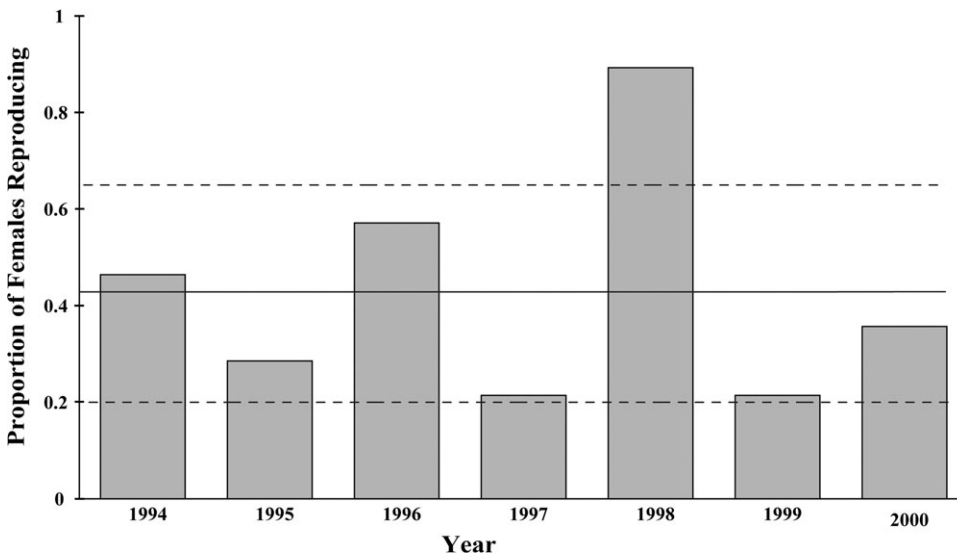
Figure 6
The proportion of 28 individually identified females calving in a given year (gray columns), with mean (solid line) and 95% CI (dashed lines)—note the high proportion of 89% in 1998.

Evidence of protracted gestation

The power law equation derived from the least-squares fit of log transformed gestation period (d) against female body-weight (w) at the genus level is $d = 5.25w^{0.057}$; ($a = 0.057 \pm 0.02$ [mean ± SE], $t = 2.94$, $P = 0.025$; $b = 5.25 \pm 0.097$ [mean ± SE], $t = 54.06$, $P < 0.0001$]. The estimate for African buffalo gestation with the individual estimate 95% prediction interval (PI) is 272 (95% PI: 237–310) days. Thus, the reported buffalo gestation period with a mean of 340–343 days (Sinclair 1977; Bertschinger 1996) is outside the 95% CI of its predicted range (Figure 5).

DISCUSSION

The proposed mechanisms for birthing synchrony in ungulates (i.e., timing to good conditions for lactation, replenishing maternal reserves, and providing high-quality food for offspring) may all contribute to the synchrony and timing of births in this system.

In savanna ecosystems, the seasonality or variation of resource availability is largely predicated on rainfall. A cursory examination of Figure 3 shows the close relationship between rainfall and vegetation greenness in this system. However, it is clear that vegetation productivity and quality are subject to more than just precipitation (Scanlon et al. 2005). Vegetation greenness, measured as NDVI, lags the rainfall by 1 month, and crude dietary protein lags NDVI by 1 month. It is therefore unsurprising that the synchrony of births is similar to that of resources. We found moderate values of birth synchrony for this period ($J^b = 0.55 \pm 0.05$, mean ± SE), slightly more synchronous than the value found by Sinclair et al. (2000) of 0.695. In comparison, the rainfall in our system was more uneven, $J^r = 0.71 \pm 0.02$ (mean ± SE), versus 0.935 in the western Serengeti (Sinclair et al. 2000). Although a formal evenness analysis was not conducted, a comparison between Manyara and the Serengeti by Prins (1996) pointed out that at Manyara, 50% of the births occur over 17 weeks, whereas in the Serengeti, 50% occur over 7 weeks. Manyara has 2 consecutive wet seasons (short rains and long rains), and the standing groundwater is higher than in the Serengeti in the dry season, but the birth season still peaked in the long rains. Even in captive buffalo, birthing appeared to have a peak in the austral midsummer (Skinner et al. 2006). The seasonality of buffalo birth has been noted in populations of Cape buffalo, but data for the subspecies of forest buffalo, *Syncerus caffer nanus*, are very scant. It is assumed that as the same species, that reproduction is similar, and new data suggests that gestation is 11 months also, with potential seasonality in birthing (Korte L, personal communication).

Following the method of Sinclair et al. (2000), we found that the synchrony of births most closely approximated to that of the prior year's vegetation measure distribution, suggesting that there is a strong link between the pattern of resource distributions in 1 year and the proceeding birth distribution. In a similar finding, Visscher et al. (2004) suggested that because buffalo conceive into the late wet season in Kruger National Park, they may not be responding to prior rainfall but anticipating the green flush of grass in 11 months. But how could this timing occur? The idea that buffalo can use cues in the environment is not novel, whereas they are bulk grazers and they do exhibit selective grazing, preferring certain grasses over others (Macandza 2004; Turner et al. 2005). As a herd, buffalo may be capable of assessing the quality of grazing patches. In the Serengeti, crude protein was shown to decline with the maturation of grass, and Fryxell (1995) cited experiments wherein herbivores selected patches of intermediate biomass, suggesting that they are behaviorally capable of responding to the trade-off between abundance and quality. This supports the idea that the new, green leaf grass is the most nutritious and likely to be selected preferentially. However, it will still take time after the onset of the wet season for there to be sufficient biomass for buffalo cows to attain sufficient condition to conceive. Thus there will be a lag between rainfall and sufficient biomass and protein in grass to support conception.

In a comparison of a suite of African ungulate species, Sinclair et al. (2000) posited that birthing synchrony in buffalo evolved as predator satiation. This echoed Rutberg (1984, 1987) who asserted that buffalo calves are precocious "followers" rather than "hiders": part of large groups in open habitat, promoting defence against predators. However, the observed length of the buffalo birthing season, both in this study and others (Sinclair 1977; Prins 1996; Sinclair et al. 2000), is far longer than that of other follower species, corresponding to Rutberg's (1987) alternate hypothesis that the climate enables a longer birthing season, with peaks occurring at times of good nutritional condition. In addition, Sinclair (1977) noted that buffalo calves tend to hide with their mothers in the bush, away from the herd, after birth, refuting this

argument, although this is unusual for our system. Thus, it is more likely that the synchrony of buffalo parturition is driven by resource availability, which confers the additional advantage of predator swamping. We suggest that buffalo have individual behavioral adaptations to predation (hiding young calves, keeping them in the center of the herd, or providing them the protection of the whole herd) for protection of neonates, which may simply be a function of habitat. The open savanna would necessitate "following," whereas bushveld allows for "hiding."

We found that the availability and seasonality of resources around conception correlate with the birth distribution for this population. Due to an uncharacteristically long gestation period for the Bovinae of over 11 months, the condition of the mother at both conception and during lactation will be maximized at vegetation quality peaks. Our examination of gestation times within the subfamily Bovinae suggests that African buffalo have a protracted gestation period to take advantage of these resource peaks (see Figure 4). An adult female buffalo carries a calf for several months during the dry season in this system, followed by a period of lactation, in which her maternal resources will be depleted and her protein intake requirement may double (based on cattle estimates [Prins 1996]). Depending at what point in the gestation the female enters the dry season, the following sequence of life-history events could be affected. This points to a much larger and in-depth suite of questions regarding the sequence of energetics for which we do not currently have the data. An explanation for the longer gestation in African buffalo is that this is part of a larger suite of life-history traits, characterizing "K-strategists"—those species which have a late age of sexual maturity, a long life span, and large brain size (Lee 1997). This would emphasize the role of weaning and lactation time for buffalo, which can be quite long (Bertschinger 1996). However, the high rate of juvenile mortality in buffalo appears in contrast to this idea.

Over the 8 years of data presented here, births occurred in all months except October. The NDVI distribution is relatively even and does not change significantly for 3 months around its peak during the year, so we were cautious in making conclusive statements as to its role in cueing conception by specific month. However, we find that in our correlations with all resource cues, both in current and previous years, the strongest correlation corresponds to a 1-year lag with NDVI (an 11-month lag with protein). This represents the time at which buffalo breed. Thus, we infer that they come into breeding condition when the forage condition is optimal. Peak rainfall lags the greenest month of the year by a month, meaning that we see a birth peak month followed by a rainfall peak month. This was also found in buffalo in Hluhluwe-Umfolozi Park, to the south of Klaserie (Turner 2003), and is in fact the pattern seen in the study of Sinclair et al. (2000) in the Serengeti. In their study, "green biomass" was predicted by rainfall, and births lagged peak biomass by 1 month. We suggest that rather than parturition nearly corresponding to biomass, the Serengeti buffalo conceived at the Serengeti green biomass peak, and parturition was observed 11 months later. With a longer period over which to examine this relationship, it is possible to distinguish between the prior year and conditions at parturition. However, Sinclair et al. (2000) also found that the birthing peak for buffalo was around 5 months out of phase with the peak protein content of their forage. The rainfall season of Eastern Africa is different from that of Southern Africa leading to a different pattern of protein availability than we find in our system, and we therefore do not find the same corresponding lag. We posit that buffalo in our more subtropical system are reaching conception peak, whereas the protein content of available

grasses is highest, which coincides with the peak growing season.

In years in which rainfall is low or has a very late onset, grass production and availability will also be low and/or late. As buffalo have evolved such that breeding season occurs during the wet season, years in which conception cues are not strong are likely to lead to less synchronized or disrupted birth patterns in the following year. The year 2000 had the highest rainfall of the entire study period. The birth distribution in 2001 had an early onset, with births occurring as early as November (Figure 3), which is unique in the data set but anecdotal given that this could have happened by chance. The population will likely reflect some abiotic effects that affect demography, even at this timescale. The area experienced a severe drought in 1992, 2 years prior to this study, in which there was a 60% decline in the buffalo population in the neighboring Kruger National Park (Mills et al. 1995), and a 53% decline in the buffalo counts for KPNR (Ryan et al. 2006). The lack of resources due to low rainfall years may drive prime females either into nonreproductive condition or cause them to leave the population, perhaps migrating to better habitat. This would likely result in fewer offspring in following years in this data set, regardless of phenological resource pattern. Although the data are sparse, 1995 and 1996 fall below the estimated lower 95% of births per year in this data set (95% CI: 79–117) at 56 and 77 births, respectively, which we can only suggest might be indicative of a lagged effect of the 1992 drought leading to low-quality breeding-age females (4+) and fewer births.

To attempt to account for the numerical fluidity of this population, we instead looked at a subset of data. An examination of the breeding success of 28 individually identified females with 7 years of complete records (1994–2001) reveals that, in 1998, 89% reproduced, compared with a mean proportion of 43% for the period (Figure 6). We found that within the data set, calving did not appear to be constrained by a birth in the previous year, with females equally or slightly more likely to give birth in consecutive years; a quarter of the females calved in 3 consecutive years. The lack of information on individual calf survival for these females does not allow us to fully examine whether these females were essentially released from the constraints of lactating by calf loss and thus able to regain condition prior to the next breeding season. Grimsdell (1973) noted that the duration of the calving interval in his study in Western Uganda depended on nutrition and that cows in better condition tended to produce more offspring. Calves can be weaned as early as 4–5 months of age (Bertschinger 1996); however, in this system, it has been observed that calves suckle up to at least the seventh month of the following pregnancy. This is supported by evidence given in Estes (1999) that females stop lactating in the seventh month of pregnancy despite observations of suckling continuing up to 15–18 months or until the next calf is born (Prins 1996; Apps 2000). This suggests that if a female can maintain body condition to meet the demands of gestation and lactation, a yearly calf is possible. The high rates of pregnancy, from 47% to 83% in 5 different parks reported for adult female buffalo (Bertschinger 1996), combined with high calf mortality (30–70%, Bertschinger 1996) suggest that early postpartum condition of both the mother and, perhaps more importantly, the resources, will drive population growth. Within this study period, 1998 had the lowest rainfall on record, without apparent immediate or following year effect on either the onset of births or the number of births in the overall population; however, of the 28 individuals that calved in 1998, only 20% produced calves in the following year. This suggests that the following dry season may have been too harsh for many of the cows to complete gestation again.

This indicates that although the seasonality of resources may influence the seasonality of birth events in the following year, the interaction between resource quality and fecundity is far more complex and may even operate at a timescale beyond the scope of this paper.

In addition, it is not just breeding females that rely on the resources and resource cues. In a study of buffalo in Hluhluwe-Umfolozi, Turner et al. (2005) suggest that males who join breeding herds face an energetic trade-off between obtaining sufficient food and engaging in reproductive activity. As the grass growing season tapers and the quality of food is reduced, it is likely that both sexes must face this trade-off. A habitat selection study (Ryan et al. 2006) showed that these buffalo range further in the dry season, most likely in search of forage that is still green. The combination of spending more time searching and more time ruminating would likely curtail reproductive activities after the wet season, although this may be a simplistic explanation.

Our findings of the close relationship between buffalo breeding ecology and seasonal availability of resources have further implications during periods of extreme conditions. A study of Alaskan moose with highly synchronized parturition suggested that they have adapted timing and synchrony of births to long-term patterns of climate and could not adjust to proximate resource changes (Bowyer et al. 1998). The authors concluded that this lack of proximate adjustment in the face of global warming could compromise the long-term viability of the population. It has been argued that greater birthing synchrony and a shorter breeding season will occur in temperate or subarctic climates (Rutberg 1987; Gaillard, Delorme, Jullien, and Tatin 1993; Gaillard et al. 1998; Rubenstein and Wikelski 2003), whereas tropical and subtropical habitats enable longer birthing periods (Rutberg 1987), except where predation provides a strong selective force (Estes 1976). Buffalo, with their extended birth season and a demonstrated capacity to adjust to the onset of seasonal forage availability, are less likely to suffer such dramatic impacts as their northern counterparts.

Despite the availability of more data than prior studies of buffalo birth seasonality, our study still spans a short period for this savanna ecosystem. The study period reflects the wetter second half of an interdecadal rain cycle (Ogutu and Owen-Smith 2003), yet has considerable annual variation in rainfall within the study period. This may create noise in the study system from which it is hard to untangle behavioral breeding responses. In addition, individual females do not breed every year, thereby confounding the analyses over a short period of time. In low rainfall years, cows may build condition on any and all available biomass and then conceive toward the end of the breeding season. This may in turn cause disruption in consecutive years due to females having dependent yearling calves during the next mating opportunity. Another possibility is that some cows may "skip" a bad year and be in high condition very early in the following mating season. Only with the availability of data sets, spanning 4 decades or more, can we hope to begin to capture the impacts of an 18-year interdecadal cycle on buffalo demography in the South African lowveld.

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