

Contrasting timing of parturition of chital *Axis axis* and gaur *Bos gaurus* in tropical South India – the role of body mass and seasonal forage quality

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Seasonal variation in forage availability and quality is understood to affect the annual timing of parturition in large herbivores. In India—where seasonal monsoonal rains define variation in forage availability and quality—chital *Axis axis* exhibit stronger seasonality in parturition than the larger gaur *Bos gaurus*. We hypothesized that this difference can be explained by forage requirements determined by body mass. We developed a model to simulate changes in leaf biomass and nitrogen content based on plant available moisture and nutrients, and calibrated our model with field data. Our results show that the minimum forage nitrogen content required by lactating gaur was available throughout the year, but that required by lactating chital was available for less than 40% of the year, i.e. during the early wet season, which coincides with the annual peak period of chital births. The three to four month spread of chital births, which begins in the dry season, implies that the period of highest quality is also important for females to replenish maternal reserves for future reproduction and help maximize the growth rate of neonates. This spread also indicates low synchrony of chital births and suggests that predator swamping was less important in influencing their timing of parturition. As monsoonal rain exhibits annual temporal variation, we analyzed our model under different rainfall patterns while keeping the total annual rainfall constant. We found that the difference between the durations of how long forage quality is available to satisfy the minimum requirements of lactating gaur and lactating chital is similar for all simulated patterns. This insensitivity to variable rainfall patterns lends support to our hypothesis that forage requirements determined by body mass is one plausible explanation for the variation in parturition strategies among large herbivores species.

Many animals live in environments where the availability and quality of food follow cyclical patterns of seasonal variation. In the temperate zone, food of adequate quantity is available only during the summer and not in winter. In tropical regions with seasonal rainfall, abundant food of high quality during the wet season is replaced by less abundant food of low quality during the dry season. This seasonality in food availability and quality is understood to influence the timing of parturition of mammalian herbivores (Rutberg 1987, Wittemyer et al. 2007). The ‘seasonality’ hypothesis proposes that mammalian herbivores time their parturition with durations of optimal food availability to support the increased energetic and nutritional requirements of lactating females (Prins 1996, Gaillard et al. 2000), and/or maximize the growth rate of neonates to enhance their predator avoidance (Clutton-Brock et al. 1982), and/or replenish maternal reserves for future reproduction (Bronson 1989, Keech et al. 2000).

Multiple studies have highlighted the seasonality of parturition in herbivores in the temperate zone (Post and Stenseth 1999, Post et al. 2003, Barboza and Reynolds 2004, Langvatn et al. 2004, Loe et al. 2005). In the tropics, studies from African regions with seasonal variation in food

availability have shown that small and medium sized herbivores follow breeding cycles (Western 1979, McNaughton and Georgiadis 1986, Ogutu et al. 2010): mating occurs in the late wet/early dry season, and after a seven to nine month gestation period, parturition occurs during the early/mid wet season. The peak in parturition of these small and medium African herbivores in the early/mid-wet season coincides with the period of highest plant quality (Mduma et al. 1999). With limited photoperiodic influence on oestrous cycles in the tropics, the timing of ovarian activity/parturition cycles of small and medium sized tropical herbivores is understood to have evolved to satisfy the increased nutritional demands of females in late pregnancy and early lactation to nurture their offspring and themselves (Western 1979, Bronson 1989, Owen-Smith et al. 2005). That this behaviour is common in smaller-bodied herbivores is explained by the fact that smaller-bodied herbivores are more constrained than larger-bodied herbivores to feed on forage of higher quality (Demment and Van Soest 1985).

In much of tropical India forage production follows a seasonal (monsoonal) rainfall regime. The chital *Axis axis* (adult female ~ 50 kg), a widely distributed deer species in

India, exhibits seasonality in its annual parturition (Schaller 1967, Raman 1998). However, a larger sympatric herbivore species, Asia's largest bovid species the gaur *Bos gaurus* (adult female ~600 kg), does not have a well-defined parturition annual cycle and calves throughout the year (Schaller 1967, Prater 1997, Ahrestani et al. 2011). Both species have gestation periods – eight months for chital and ~ nine months for gaur – that fall within the range of African species that follow the 'late wet/early dry season mating and early/mid wet season parturition' pattern. Therefore, the goal of this study was to better understand why chital and gaur, despite their similar gestation periods, have different parturition strategies.

Body mass is fundamental to a large herbivore's forage quantity and quality requirements. The forage requirements of chital are different from that of the much heavier gaur; chital require less quantity, but much higher quality forage to survive than do gaur (Demment and Van Soest 1985, Owen-Smith 1988, Van Soest 1994). The well-studied large herbivore assemblage in Africa suggests that there exists a positive relation between species body mass and non-seasonal parturition, i.e. most large-bodied herbivores tend not to have a well-defined annual peak and exhibit parturition throughout the year (Appendix 1). Given that chital are constrained by high quality forage more than gaur, and that non-season parturition is more common in larger-bodied herbivores, we hypothesized that the difference in the impact that body mass has on the forage quality requirements of chital and gaur respectively contributes to why chital exhibit a seasonality in their annual parturition and gaur do not.

To test our hypothesis we collected data on the parturition timing of both chital and gaur from a field study and existing literature. We modelled the seasonal pattern in primary production nutrition based on plant available moisture and nutrients, and calibrated our model with field measurements of forage quantity (grass biomass) and quality (N content of grass leaves) at different times during the year. Based on known relationships between a herbivore's body mass and its nutritional requirements, we investigated whether seasonal variability in forage quality would influence smaller species (like chital) and not larger species (like gaur) to time their parturition with the primary production cycle. Since India's monsoonal rainfall varies annually, we analyzed our model for three different rainfall regimes: 1) the observed bimodal rainfall pattern containing the southwest and northeast monsoon, 2) the rainfall pattern with a reduced northeast monsoon, and 3) with a reduced southwest monsoon.

Material and methods

Parturition data of chital and gaur

We collected field data to determine the monthly calf (<6 months) to adult female ratio of both chital and gaur between March 2006 and August 2007 in two contiguous Tiger Reserves in South India, Mudumalai (329 km²; 11°32'–43'N, 76°22'–45'E) and Bandipur (880 km²; 11°36'–57'N, 76°13'–52'E). Most data were collected from a 200 km² study area (Fig. 1) that was split equally between the two reserves. Given the difficulty in observing animals in forested areas, and the fact that both species were more

tolerant of humans in vehicles than on foot, the majority of data were collected using an open-topped jeep while systematically sampling the study area along its 50 km road network. The sampling effort for the study period exceeded 2500 km and was restricted mainly to dawn and dusk, times when both species were both active and visible (Ahrestani et al. 2011). Identification and classification of animals were based on the detailed information provided by Schaller (1967) and Ahrestani and Prins (2011) for chital and gaur respectively. In general it was easy to identify adult females and calves of both species. The total sample size (that included all ages of both sexes) was 6773 and 1790 (with a monthly average of 616 and 163) for chital and gaur respectively. We found chital parturition to peak during February–May, while gaur appeared to calve throughout the year (Fig. 2).

Model definition

We developed a model to simulate the monthly variation in leaf biomass and nitrogen content annually as our hypothesis was dependent on the annual variation of plant quality. The model aims to show whether decreases in forage quality, i.e. nitrogen content of the leaves, coincide with absence of births in chital and gaur. The model consisted of two parts: we first modelled the monthly variation in leaf biomass production over a year, which we then used to simulate the monthly variation in leaf nitrogen content (the main parameter of interest) over a year. Table 1 lists the parameters used in the model, their symbols, interpretation, units, and values. We modelled the growth of leaf biomass to include losses due to senescence and grazing. We assumed that local plant growth is limited by available soil nitrogen and moisture. We modelled growth of only grass leaves as they are preferred by herbivores (Prins and Van Langevelde 2008). The change in leaf biomass (P in $g\ m^{-2}$) was modelled as

$$\frac{dP}{dt} = rnP - g(P)P - bhP \quad (1)$$

where n is the plant available soil moisture content (PAM), r the specific growth rate of leaf biomass per unit of available soil moisture, $g(P)$ the loss rate due to senescence, h the herbivore density, and b the specific consumption rate of the herbivores. We assumed a density-dependent loss rate due to senescence so that $g(P) = aP$, where a is the specific density-dependent loss rate.

Similar to the seasonal pattern of leaf biomass, the content of nutrients in this biomass increases due to uptake by the plants and decreases when the plant loses leaves as a result of both senescence and grazing. Uptake of nutrients is modelled as a saturating function of aboveground biomass as we assume that older grasses invest more in structural material (stems) and less in organs to acquire resources (Beever et al. 2000). The change in nitrogen content (N in $g\ m^{-2}$) is

$$\frac{dN}{dt} = u \frac{P}{P+k} s - mN - bhN \quad (2)$$

where u is the maximum uptake rate of nutrients, k the leaf biomass where the uptake of nutrients is half of u (half saturation constant), s the available soil nutrients (PAN), m the



Figure 1. Map of the dry and moist deciduous regions of the study area that were located in Bandipur and Mudumalai Tiger Reserves, south India.

specific loss rate of nutrients due to senescence. We assume that a nutrient pulse F (temporarily increasing s) is available from accumulated plant detritus and animal dung at the beginning of the wet season that benefits the growth of young shoots, which are very nutritious for herbivores (McNaughton 1985, Scholes and Walker 1993).

Model calibration and sensitivity analysis

To calibrate the model, we measured live leaf biomass and nitrogen content from August 2006 to July 2007 in

a grassland located in a wildlife resort bordering Mudumalai Wildlife Sanctuary, south India ($11^{\circ}55'N$, $76^{\circ}63'E$; Fig. 1). Mudumalai hosts a diverse assemblage of herbivores including Asian elephant *Elephas maximus*, gaur *Bos gaurus*, sambar *Cervus unicolor*, chital *Axis axis*, muntjac *Muntiacus muntjac*, four horned antelope *Tetracerus quadricornis* and Indian spotted chevrotain *Moschiola meminna*. The study site experiences alternating wet (May–November) and dry (December–April) seasons. The wet season is bimodal as it receives precipitation from two monsoons: the southwest monsoon (May–August) followed by the northeast monsoon

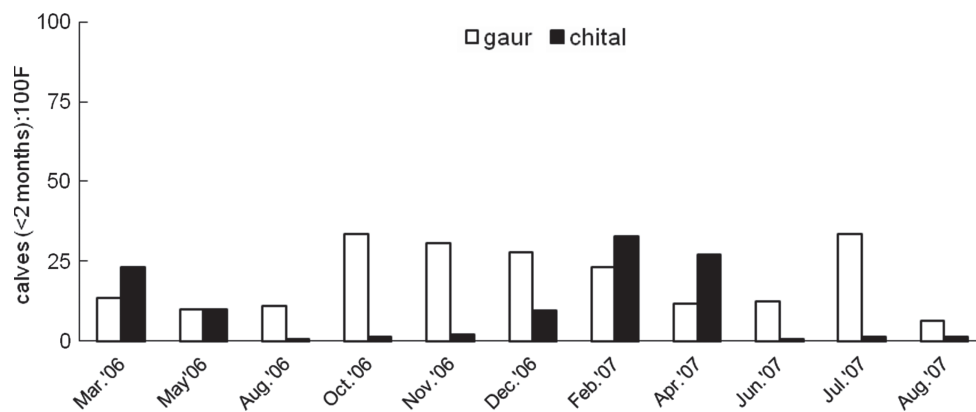


Figure 2. Comparison of the ratio of calves (<2 months): 100 female found for gaur *Bos gaurus* and chital *Axis axis* in Mudumalai and Bandipur National Parks, south India, March 2006–August 2007.

Table 1. Used symbols, their interpretation, units and values.

Symbols	Interpretation	Units	Values	Sources	Model sensitivity to $\pm 10\%$ change in parameter values
P	aboveground live leaf biomass	g m^{-2}	0–300	field measurements	–
N	nutrient content of leaves	g m^{-2}	0–2.5	field measurements	–
n	plant available soil moisture content (PAM)	mm month^{-1}	0–150	field measurements	–
r	specific growth rate of plant biomass per unit available soil moisture	mm^{-1}	0.6	Gambiza et al. 2000	–2.9%–2.9% for N –10.1%–9.9% for P
h	herbivore density	g m^{-2}	10	Ahrestani unpubl.	–0.2%–0.1% for N –0.2%–0.2% for P
b	specific consumption rate of herbivores	$\text{m}^2 \text{g}^{-1} \text{month}^{-1}$	0.02	Murray 1995	–0.2%–0.1% for N –0.2%–0.2% for P
a	specific density-dependent loss rate	$\text{m}^2 \text{g}^{-1} \text{month}^{-1}$	0.3	Gambiza et al. 2000	–3.6%–3.7% for N –10.5%–9.1% for P
u	maximum uptake rate of nutrients	$\text{m}^2 \text{g}^{-1} \text{month}^{-1}$	0.1	Risser and Parton 1982	–6.0%–5.9% for N no change for P
k	plant biomass where the uptake of nutrients is half of u	g m^{-2}	25	estimated	–3.3%–2.9% for N no change for P
s	available soil nutrients (PAN)	g m^{-2}	8	de Mazancourt et al. 1999	–22.2%–18.9% for N no change for P
m	specific loss rate of nutrients due to senescence	month^{-1}	0.3	Similar as a	–5.7%–4.9% for N no change for P
F	nutrient pulse at beginning of wet season	g m^{-2}	15	de Mazancourt et al. 1999	–5.4%–5.7% for N no change for P

(September–November). Rainfall in Masinagudi (2 km north of the experiment site) during the study period (Aug 2006–Jul 2007) was 730 mm, which was below the last 15 year (1991–2005) average of 860 mm. Mean annual temperature was 16–18°C, reaching its maximum of 28–30°C in April–May and dropping to its minimum of 5–6°C in December–January. Soils were slightly acidic with low nitrogen content, and were sandy loam on the surface with a gravelly clay substrate.

While keeping the amount of annual rainfall the same, we tested our model under two different rainfall regimes: a reduced northeast monsoon (yearly average of 825 mm) and a reduced southwest monsoon (yearly average of 852 mm).

We also analysed the sensitivity of the model for the selected parameter values by changing these values by $\pm 10\%$ and observing their effect on the model's results.

Analysis of daily requirements

The daily requirements for maintenance, pregnancy and lactation for chital and gaur were derived from known allometric relationships (Table 2). Assuming that ruminant herbivores consume about 2% of their body mass on a dry matter basis every day (Murray 1995), we can estimate the daily required nutrient concentration as daily requirements divided by daily intake. This means that chital need 1.22%

Table 2. Nutritional requirements of chital and gaur per day.

Activity	Nutrient (unit)	Allometric function	Chital (50 kg)	Gaur (600 kg)	Source
Maintenance	energy (kJ d^{-1})	$293 \times W^{0.75}$	5510	35521	2
	N (g d^{-1})	$0.65 \times W^{0.75}$	12.22	78.80	2
	P (g d^{-1})	$0.02 \times W^{1.0}$	1.00	12.00	2
	Ca (g d^{-1})	$0.024 \times W^{1.0}$	1.20	14.40	2
	Na (g d^{-1})	$0.009 \times W^{1.0}$	0.45	5.40	2
Pregnancy	energy (kJ d^{-1})	$440 \times W^{0.75}$	6600	42552	3, 4
	N (g d^{-1})	$0.78 \times W^{0.75}$	14.67	94.56	1
	P (g d^{-1})	$0.038 \times W^{1.0}$	1.90	22.80	1
	Ca (g d^{-1})	$0.047 \times W^{1.0}$	2.35	28.20	1
	Na (g d^{-1})	$0.013 \times W^{1.0}$	0.65	7.80	1
Lactation	energy (kJ d^{-1})	$513 \times W^{0.75}$	8273	53342	3
	N (g d^{-1})	$1.01 \times W^{0.75}$	18.99	122.44	1
	P (g d^{-1})	$0.08 \times W^{1.0}$	4.00	48.00	2
	Ca (g d^{-1})	$0.096 \times W^{1.0}$	4.80	57.60	2
	Na (g d^{-1})	$0.036 \times W^{1.0}$	1.80	21.60	2

Sources: 1) Agricultural Research Council Working Party 1980, 2) Prins and Van Langevelde 2008, 3) Bauman and Currie 1980, 4) Bell et al. 2005.

Notes: The calculation for energy requirement for pregnant and lactating females was estimated as 20% and 50% greater than basal requirement. The calculation for N requirement for pregnant females was calculated as 20% greater than basal requirement, but for lactating females the N requirement was calculated as the average of the requirement of cows weighing 500 kg and producing 5–40 liters of milk with fat 40 g kg^{-1} .

and gaur 0.66% N for maintenance; chital need 1.47% and gaur 0.79% N for pregnancy; and chital need 1.89% and gaur 1.02% N for lactation. For other elements the requirements for both species are the same; requirements are a function of body mass raised to the power 1 and hence the body mass multiplier for these requirements is a linear relationship (for example, chital and gaur both need 0.1% P for maintenance). Herbivores can meet their daily energy requirements by adapting their foraging times (Shipley et al. 1994); during periods of low forage availability, herbivores can forage longer to meet their energy requirements. We assumed therefore that herbivores in our study area met their daily energy requirements throughout the year, and postulate that the differences in timing of parturition between chital and gaur can be explained by differences in nitrogen supply in plants.

Results

Using ordinary least square regression we fitted a non-linear function to represent rainfall over the year (Fig. 3); we ln-transformed rainfall and fitted a polynomial function (up to the 6th power) with month as independent variable ($n = 12$, adjusted $R^2 = 0.99$, constant = -5.631 ($t = -16.175$, $p < 0.001$), and regression coefficients for month = 5.572 ($t = 18.784$, $p < 0.001$), for month² = -1.021 ($t = -14.245$, $p < 0.001$), for month³ = 0.064 ($t = 12.055$, $p < 0.001$) and for month⁶ = -7.423×10^{-6} ($t = -10.088$, $p < 0.001$). The regression coefficients month⁴ ($t = 1.028$, $p = 0.344$) and month⁵ ($t = 1.146$, $p = 0.295$) were not added to the model. This relationship was used as PAM in the model (Eq. 1) to predict the annual pattern in forage availability (the amount of leaf biomass, Fig. 4), and forage quality (the nitrogen content in leaves, Fig. 5).

Comparing the daily requirements with that of the simulated available leaf nitrogen content shows that gaur meets its requirements for all activities (maintenance, pregnancy and lactation) throughout the year. For chital, however, this

pattern is different: chital meet their requirements for approximately 86% of the year for maintenance, for approximately 79% of the year for pregnancy, and for only 37% of the year for lactation (Fig. 5).

For both the modified rainfall regimes (a reduced north-east monsoon and a reduced southwest monsoon) we again fitted a polynomial function with month as the independent variable (Fig. 6). In these rainfall scenarios, we simulated leaf biomass and the leaf nitrogen content over time (Fig. 6). In both these two scenarios gaur could meet their requirements for all activities throughout the year. For chital, however, it was again different: chital met their maintenance requirements for approximately 86% of the year (for both scenarios), pregnancy requirements for 75–78% of the year (for both scenarios), and for lactation 39% (scenario reduced northeast monsoon) and 31% (scenario reduced southwest monsoon) of the year.

The sensitivity analysis of the model for changed parameter values ($\pm 10\%$) demonstrated that the model's outcomes for N, the nutrient content of the leaves, are especially sensitive to changes in the value of s , the available soil nutrients (PAN) (Table 1). Changes to the other parameters, however, did not significantly alter the model's outcome of either N or P (Table 1).

Discussion

Our results highlight the contrast in the time periods when available plant nitrogen is above the minimum required by chital and gaur for maintenance, pregnancy and lactation. The model suggests that the decrease in forage quality, i.e. nitrogen content of the leaves, coincides with absence of births in chital. These results suggest that gaur are not constrained to time their parturition to satisfy nitrogen requirements in the study area, while chital are. We know that large mammalian herbivores respond strongly to the availability of nutrients in seasonal environments (Jarman 1974, Moen et al. 2006)

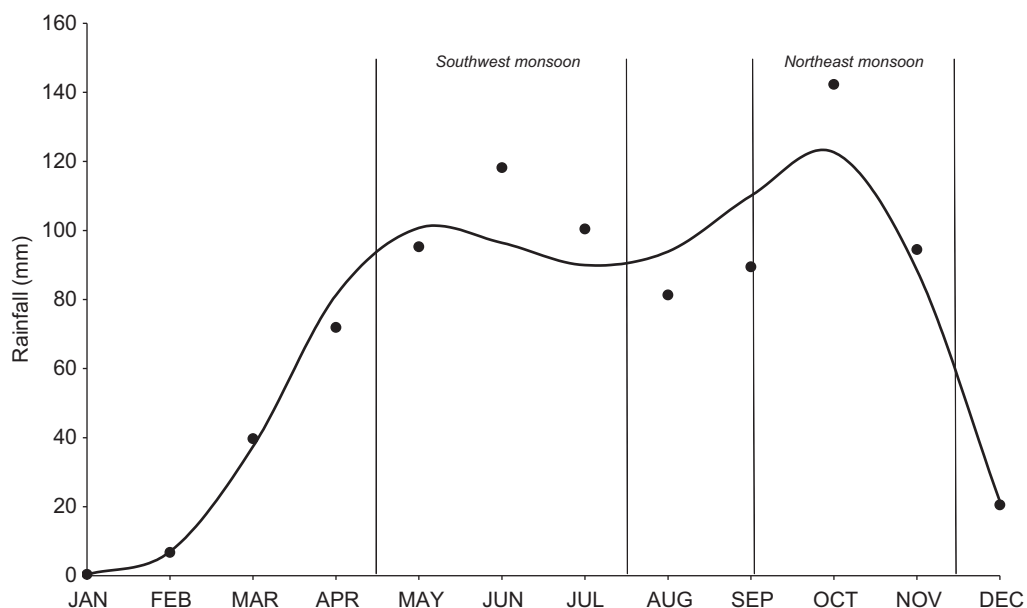


Figure 3. Measured rainfall (dots) and the fitted relationship (see text for statistical details) to be used in the model.

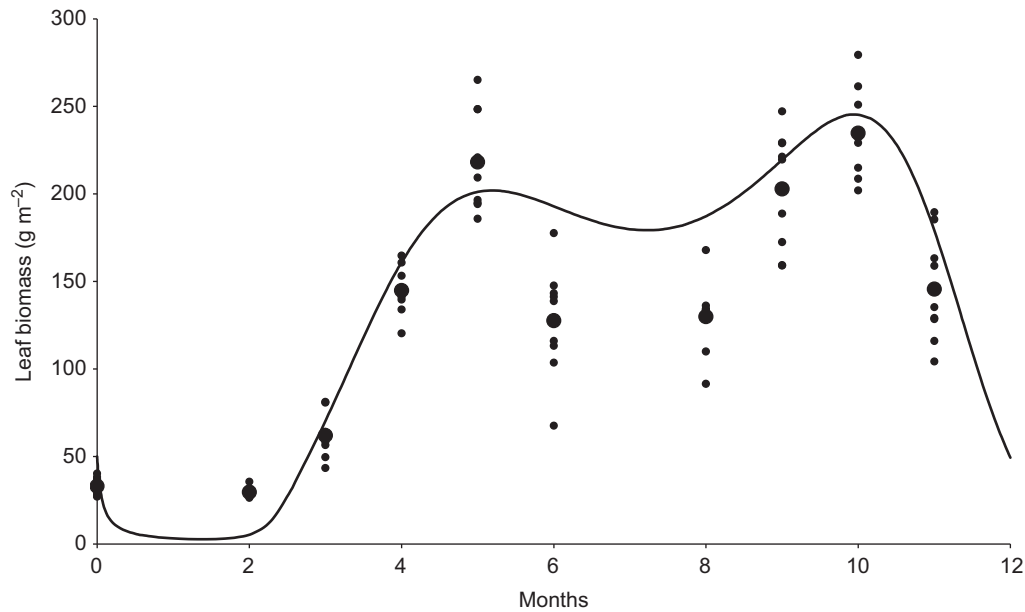


Figure 4. Measured (dots, large dots represent the means) and simulated amount of leaf biomass during the year (0 = January).

and that the availability of nitrogen is considered to be a key driver of their forage selection, especially smaller body-bodied species (Demment and Van Soest 1985, Van Soest 1994). Therefore, it is likely that the impact body mass plays on forage selection is one reason why gaur have a less pronounced annual peak in their parturition when compared to chital.

As with most species guilds, there is a continuum from capital to income breeders within the large herbivore species guild (Jöhnsson 1997). This continuum is positively related to body mass; smaller-bodied species are more inclined to be income breeders while larger-bodied species are capital breeders (Stearns 1992). While there exists little data to validate this proposition for tropical species, a positive relation between body mass and increasing reproductive success has been demonstrated for large herbivores in the

temperate zone; Festa-Bianchet et al. (1998) found a positive relation between an ewe's body mass and her reproductive success in their study of the capital breeder bighorn sheep *Ovis canadensis*. Given that chital are one order of magnitude smaller than gaur, it is safe to assume then that chital are more inclined to be income rather than the capital breeders. Coupling this assumption, i.e. that chital are income breeders, with the fact that chital have a greater dependence on high quality forage underscores the greater need that chital have in timing their parturition with the season of highest forage quality when compared to gaur.

The study area's chital population's parturition peak timing (February–April) overlapped with the early wet season, the season when available plant quality was above the minimum required by lactating chital females. By satisfying

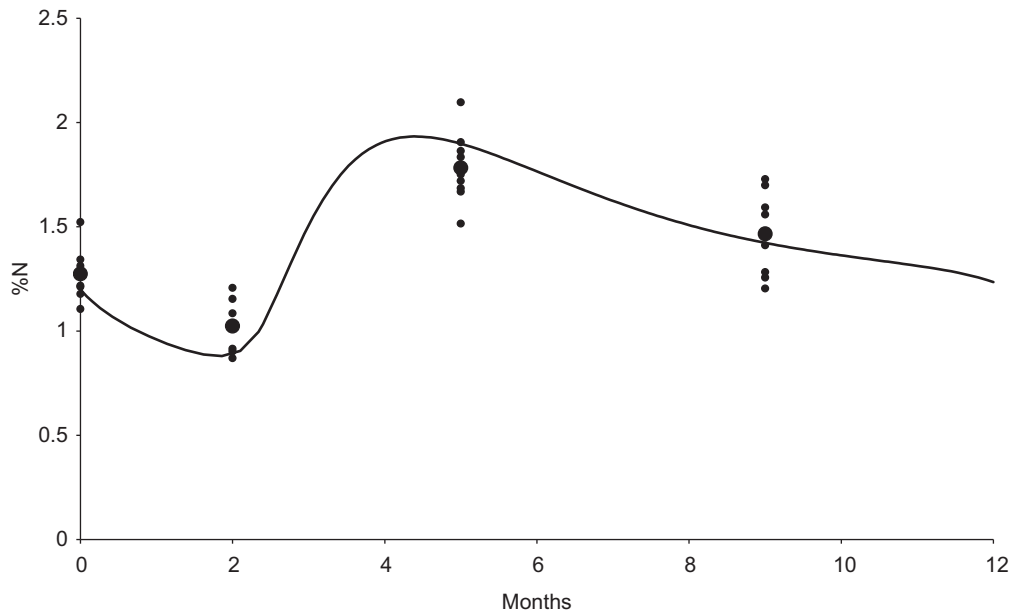


Figure 5. Measured (dots, large dots represent the means) and simulated leaf nitrogen content during the year (0 = January).

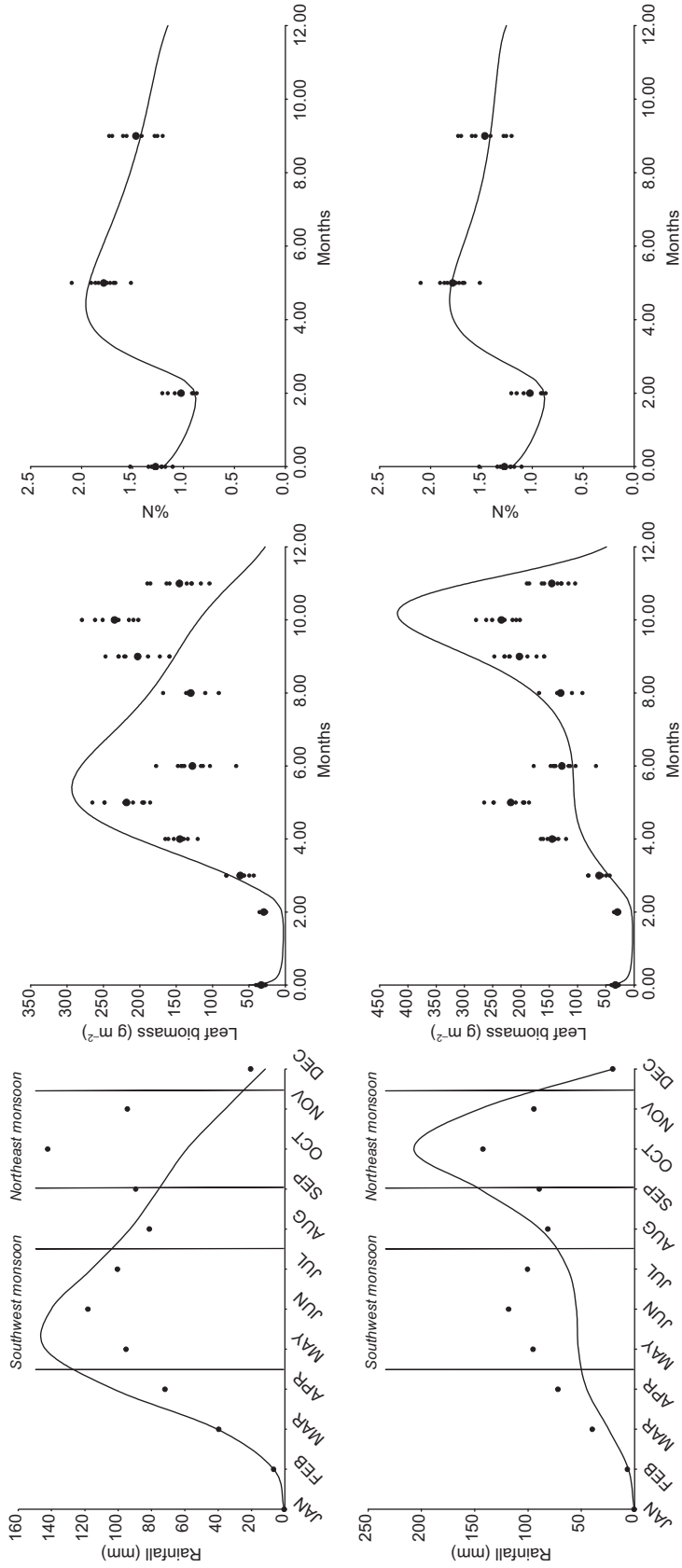


Figure 6. Measured (dots, see Fig. 3, 4 and 5) and simulated rainfall, leaf biomass and leaf nitrogen content during the year, for the two scenarios: rainfall pattern with a reduced Northeast monsoon (top row panels) and with a reduced Southwest monsoon (bottom row panels). For both scenarios, we fitted polynomial models using ln-transformed rainfall data. For the reduced Northeast monsoon ($n = 12$, adjusted $R^2 = 0.97$), we found the constant = -5.386 ($t = -8.337$, $p < 0.001$), and the regression coefficients for month = 5.175 ($t = 9.402$, $p < 0.001$), for month² = -0.860 ($t = -6.466$, $p < 0.001$), for month³ = 0.048 ($t = 4.898$, $p = 0.002$) and for month⁶ = -4.727×10^{-6} ($t = -3.462$, $p = 0.011$). The coefficients month⁴ ($t = 1.354$, $p = 0.225$) and month⁵ ($t = 1.546$, $p = 0.173$) could not be added to the model. For the rainfall pattern with a reduced Southwest monsoon, we found the regression model ($n = 12$, adjusted $R^2 = 0.99$) with the constant = -5.212 ($t = -16.938$, $p < 0.001$), and the coefficients for month = 5.283 ($t = 20.150$, $p < 0.001$), for month² = -1.040 ($t = -16.410$, $p < 0.001$), for month³ = 0.071 ($t = 15.126$, $p < 0.001$) and for month⁶ = -9.586×10^{-6} ($t = -14.737$, $p < 0.001$). The coefficients month⁴ ($t = 1.546$, $p = 0.173$) and month⁵ ($t = 1.546$, $p = 0.225$) could not be added to the model.

their nitrogen demands these females maintain their body condition and replenish their reserves for future reproduction (Bronson 1989, Keech et al. 2000) and improve their lactation ability and milk quality, which helps increase pre-weaning calf survival (Clutton-Brock et al. 1982, Rognum et al. 1983). The December to March annual peak found for other chital populations (Schaller 1967 – Kanha, India; Johnsingh 1983 – Bandipur, India; Raman 1998 – Guindy, India) suggests that the ‘seasonality’ of parturition in these chital populations helps replenish maternal reserves for future reproduction (Bronson 1989, Keech et al. 2000) and ensures continued growth of neonates (Clutton-Brock et al. 1982) more than it does to help to satisfy the requirements of lactating females.

Since nitrogen is the only element whose requirement is known so far to scale allometrically with a $3/4$ exponent rather than with an exponent of 1 (Prins and Van Langevelde 2008), nitrogen is therefore the only element whose requirement varies between species of different body mass. The linear allometric requirement functions of other nutrients – like P, K, Ca and Na – means that any variation in their availability impacts species of different body mass equally. This should not be, however, confused for the fact that nutrients such as P, K, Ca and Na are important for maintenance, pregnancy and lactation of large herbivores (Van Soest 1994).

The seasonal variation in vegetative quality as a function of a plant’s fibre and lignin content is also critical in large herbivore forage selection (Prins and Beekman 1989). Body mass plays an important role within the context of fibre and lignin content too; smaller-bodied species (chital) are less tolerant of forage high in fibre and lignin content than are larger-bodied species (gaur). Both fibre and lignin are at their lowest during the early wet season and then increase over time till the next rains (Prins and Beekman 1989, Beever et al. 2000). The inverse relationship of forage quantity and quality means that the cyclic seasonal pattern of fibre and lignin contents is the inverse of the cyclic seasonal pattern of nitrogen content, i.e., in the wet season lignin and fibre contents are low while nitrogen content is high (optimal conditions for smaller-bodied herbivores), and in the dry season lignin and fibre are high while nitrogen is low (sub-optimal conditions for smaller-bodied herbivores). The fact that we tested our model under different rainfall scenarios, all of which consistency demonstrated a difference between gaur and chital, provides additional support to our proposition regarding the role that body mass plays in differentiating the breeding cycles between herbivore species of different body mass.

Despite the evidence that we have presented to support our proposition that body mass plays a role in differentiating chital and gaur parturition strategies, we acknowledge there exists other factors that determine large herbivore parturition strategies in the tropics. For example, different sized herbivores often forage on different plant components and species often vary the leaf:stem ratio of their seasonal forage intake (Owen-Smith 1988, Farruggia et al. 2006). These additional foraging variables need to be included while developing future models – we did not include these factors in our model as there exists little reliable data for both gaur and chital – to further our understanding of this subject. These more complex models might provide answers for why smaller-bodied species like the nyla *Tragelaphus angasii* (Appendix 1) do not

exhibit seasonal parturition and the African buffalo *Syncerus caffer*, a species similar to the gaur, exhibits seasonal parturition and gaur do not. So far there have been few studies that have focussed on explaining the inter-large herbivore species differences in parturition strategies.

Although the chital exhibited seasonality in parturition, there was low synchrony of births in the study population. Synchrony, which refers to the length over which births occur (Post 2003), was highlighted by Estes’ (1976) pioneering study which interpreted the high synchrony of births within a wildebeest population as predator swamping, i.e. reducing the risk of an individual young by increasing potential prey per predator. This ‘predation’ hypothesis also includes the added benefit that neonates derive from being born into congregating groups of vigilant mothers during the calving peak (Rutberg 1987, Böving and Post 1997). The ‘predation’ hypothesis, however, is not mutually exclusive from the ‘seasonality’ hypothesis; for e.g. the time of the year that the wildebeest choose to calve coincides with the period of highest plant quality. It appears, however, that in the case of chital predation is not the driving factor of the timing of their parturition because chital births were spread over three to four months.

In conclusion, this study presents a novel proposition, supported by evidence and validated by a model, that the impact body mass has on forage selection is one potential reason why large herbivore species of different body mass have different parturition strategies. We demonstrated that plant nitrogen content could be a seasonally limiting factor for smaller species like chital but not for larger species like gaur. The three to four months extended period of chital parturition indicates low synchrony and suggests that the chital population does not engage in predator swamping.

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References

- Agricultural Research Council Working Party 1980. The nutrient requirements of ruminant livestock. – Commonwealth Agricultural Bureaux, Slough, UK.
- Ahrestani, F. S. and Prins, H. H. T. 2011. Age and sex determination of gaur *Bos gaurus* (Bovidae). – *Mammalia* 75: 151–155.
- Ahrestani, F. S. et al. 2011. Life-history traits of gaur *Bos gaurus*: a first analysis. – *Mammal Rev.* 41: 75–84.
- Barboza, P. S. and Reynolds, P. E. 2004. Monitoring nutrition of a large grazer: muskoxen on the Arctic Refuge. – *Int. Congr. Ser.* 1275: 327–333.
- Bauman, D. E. and Currie, B. W. 1980. Partitioning of nutrients during pregnancy and lactation: a review of mechanisms involving homeostasis and homeorhesis. – *J. Dairy Sc.* 64: 1514–1529.
- Beever, D. E. et al. 2000. The feeding value of grass and grass products. – In: Hopkins, A. (ed.), *Grass: its production and utilization*. Blackwell, pp. 140–195.
- Bell, A. W. et al. 2005. Pregnancy and fetal metabolism. – In: Dijkstra, J. et al. (eds), *Quantitative aspects of ruminant digestion and metabolism*, 2nd ed. CABI, pp. 523–550.

- Bøving, P. S. and Post, E. 1997. Vigilance and foraging behaviour of female caribou in relation to predation risk. – *Rangifer* 17: 55–63.
- Bronson, F. H. 1989. Mammalian reproductive biology. – Univ. of Chicago Press.
- Clutton-Brock, T. et al. 1982. Red deer: behaviour and ecology of two sexes. – Univ. of Chicago Press.
- de Mazancourt, C. et al. 1999. Grazing optimization and nutrient cycling: potential impact of large herbivores in a savanna system. – *Ecol. Appl.* 9: 784–797.
- Demment, M. W. and Van Soest, P. J. 1985. A nutritional explanation for body-size patterns of ruminants and nonruminant herbivores. – *Am. Nat.* 125: 641–672.
- Estes, R. D. 1976. The significance of breeding synchrony in the wildebeest. – *East Afr. Wildlife J.* 14: 135–152.
- Farruggia, A. et al. 2006. Diet selection of dry and lactating beef cows grazing extensive pastures in late autumn. – *Grass Forage Sci.* 61: 347–353.
- Festa-Bianchet, M. et al. 1998. Mass- and density-dependent reproductive success and reproductive success and reproductive costs in a capital breeder. – *Am. Nat.* 152: 367–379.
- Gaillard, J. M. et al. 2000. Temporal variation in fitness components and population dynamics of large herbivores. – *Annu. Rev. Ecol. Syst.* 31: 367–393.
- Gambiza, J. et al. 2000. A simulation model of miombo woodland dynamics under different management regimes. – *Ecol. Econ.* 33: 353–368.
- Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. – *Behavior* 48: 215–266.
- Johnsingh, A. J. T. 1983. Large mammalian prey–predators in Bandipur. – *J. Bombay Nat. Hist. Soc.* 80: 1–57.
- Jönhsson, K. I. 1997. Capital and income breeders as alternate tactics of resource use in reproduction. – *Oikos* 78: 57–66.
- Keech, M. A. et al. 2000. Life-history consequences of maternal condition in Alaskan moose. – *J. Wildlife Manage.* 64: 450–462.
- Langvatn, R. et al. 2004. Timing and synchrony of ovulation in red deer constrained by short northern summers. – *Am. Nat.* 163: 763–772.
- Loe, L. E. et al. 2005. Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. – *J. Anim. Ecol.* 74: 579–588.
- McNaughton, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. – *Ecol. Monogr.* 55: 259–294.
- McNaughton, S. J. and Georgiadis, N. J. 1986. Ecology of African grazing and browsing mammals. – *Annu. Rev. Ecol. Syst.* 17: 39–65.
- Mduma, S. A. R. et al. 1999. Food regulates the Serengeti wildebeest: a 40 year record. – *J. Anim. Ecol.* 68: 1101–1122.
- Moen, J. et al. 2006. Living in a seasonal environment. – In: Danell, K. (ed.), *Large herbivore ecology, ecosystem dynamics and conservation*. Cambridge Univ. Press, pp. 50–70.
- Murray, M. G. 1995. Specific nutrient requirements and migration of wildebeest. – In: Sinclair, A. R. E. and Arcese, P. (eds), *Serengeti 2: dynamics, management, and conservation of an ecosystem: based on papers at a workshop held in December 1991 at the Serengeti Res. Inst., Tanzania*. Univ. of Chicago Press, pp. 231–256.
- Ogutu, J. O. et al. 2010. Rainfall extremes explain interannual shifts in timing and synchrony of calving in topi and warthog. – *Popul. Ecol.* 52: 89–102.
- Owen-Smith, R. N. 1988. Megaherbivores: the influence of very large body size on ecology. – Cambridge Univ. Press.
- Owen-Smith, R. N. et al. 2005. Correlates of survival rates for ten African ungulate populations: density, rainfall and predation. – *J. Anim. Ecol.* 74: 774–788.
- Post, E. 2003. Timing of reproduction in large mammals: climatic and density-dependent influences. – In: Schwartz, M. D. (ed.), *Phenology: an integrative environmental science*. Kluwer, pp. 437–449.
- Post, E. and Stenseth, N. C. 1999. Climatic variability, plant phenology, and northern ungulates. – *Ecology* 80: 1322–1339.
- Post, E. et al. 2003. Synchrony between caribou calving and plant phenology in depredated and non-depredated populations. – *Can. J. Zool.* 81: 1709–1714.
- Prater, S. H. 1997. *The book of Indian animals*. – Oxford Univ. Press.
- Prins, H. H. T. 1996. Ecology and behaviour of the African buffalo: social inequality and decision-making. – Chapman and Hall.
- Prins, H. H. T. and Beekman, J. H. 1989. A balanced diet as a goal of grazing: the food of the Manyara buffalo. – *J. Afr. Ecol.* 27: 241–259.
- Prins, H. H. T. and Van Langevelde, F. 2008. Assembling a diet from different places. – In: Prins, H. H. T. and Van Langevelde, F. (eds), *Resource ecology: spatial and temporal dynamics of foraging*. Springer, pp. 129–155.
- Raman, T. R. S. 1998. Antler cycles and breeding seasonality of the chital *Axis axis* Erxleben in southern India. – *J. Bombay Nat. Hist. Soc.* 95: 377–391.
- Rognmo, A. et al. 1983. Effects of improved nutrition in pregnant reindeer on milk quality, calf birth weight, growth and mortality. – *Rangifer* 3: 10–18.
- Risser, P. G. and Parton, W. J. 1982. Ecosystem analysis of the tallgrass prairie nitrogen cycle. – *Ecology* 63: 1342–1351.
- Rutberg, A. T. 1987. Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. – *Am. Nat.* 130: 692–710.
- Schaller, G. B. 1967. *The deer and tiger*. – Univ. of Chicago Press.
- Scholes, R. J. and Walker, B. H. 1993. *An African savanna – synthesis of the Nylsvely study*. – Cambridge Univ. Press.
- Shiple, L. A. et al. 1994. The scaling of intake rate in mammalian herbivores. – *Am. Nat.* 143: 1055–1082.
- Stearns, S.C. 1992. *The evolution of life-histories*. – Oxford Univ. Press.
- Van Soest, P. J. 1994. *Nutritional ecology of the ruminant*. – Cornell Univ. Press.
- Western, D. 1979. Size, life history and ecology in mammals. – *Afr. J. Ecol.* 17: 185–204.
- Wittemyer, G. et al. 2007. Breeding phenology in relation to NDVI variability in free-ranging African elephant. – *Ecography* 30: 42–50.

Appendix 1

Parturition data of medium- and large-bodied tropical large herbivores.

Common name	Scientific name	Female body mass (kg)	Gestation period (months)	Birth period	References
Impala	<i>Aepyceros melampus</i>	40	6.5	seasonal (wet)	Skinner 1971, Fairall 1972, Bramley and Neaves 1972, Warren 1974, Murray 1982
Grant's gazelle	<i>Nanger granti</i>	42	7.5	seasonal (mid wet)	Walther 1972, Leuthold and Leuthold 1975, Sinclair et al. 2000
Hog deer	<i>Axis porcinus</i>	45	6	seasonal (late wet)	Dhungel and O'Gara 1991
Chital	<i>Axis axis</i>	50	7	seasonal (wet)	Schaller 1967, Raman 1998, this study
Southern reedbeek	<i>Redunca arundinum</i>	60	7.5	seasonal (wet)	Howard 1983
Puku antelope	<i>Kobus vardonii</i>	70	8	seasonal (wet)	Rosser 1987, 1989
Nyala	<i>Tragelaphus angasii</i>	90	7	perennial	Anderson 1979, Fairall 1968
Topi	<i>Damaliscus lunatus</i>	110	8	seasonal (late dry)	Duncan 1975, Sinclair et al. 2000
Lichtenstein's hartebeest	<i>Alcelaphus lichtensteinii</i>	140	8	seasonal (wet)	Skinner et al. 1973
Barasingha	<i>Rucervus duvaucelii</i>	160	8.5	seasonal (late wet)	Schaller 1967
Common wildebeest	<i>Connochaetes taurinus</i>	180	8	seasonal (early wet)	Estes 1976, Skinner et al. 1974, Sinclair et al. 2000
Sambar	<i>Cervus unicolor</i>	200	8	seasonal (wet)	Schaller 1967, Johnsingh 1983, Prater 1997
Greater kudu	<i>Tragelaphus strepsiceros</i>	210	9	seasonal (wet)	Owen-Smith 1984
Roan	<i>Hippotragus equinus</i>	250	9	seasonal (late wet)	Wilson 1975, Wilson and Hirst 1977, Erb 1993
Grevey's zebra	<i>Equus grevyi</i>	400	13	perennial	Smuts 1974, Rubenstein 1986
Eland	<i>Taurotragus oryx</i>	450	9	perennial (early wet)	Hillman 1979, Buys and Dott 1991, Rowe-Rowe 1994
African buffalo	<i>Syncerus caffer</i>	550	11	seasonal (wet)	Fairall 1968, Grimsdell 1973, Sinclair 1977, Taylor 1985
Gaur	<i>Bos gaurus</i>	600	9.5	perennial	Schaller 1967, this study
Giraffe	<i>Giraffa camelopardalis</i>	800	14	perennial	Hall-Martin et al. 1975, Langman 1977
Hippopotamus	<i>Hippopotamus amphibius</i>	1500	8	perennial	Laws 1984, Kayanja 1989
Black rhino	<i>Diceros bicornis</i>	1700	15	perennial	Hitchens and Anderson 1983, Owen-Smith 1984
White rhino	<i>Ceratotherium simum</i>	1800	16	perennial	Owen-Smith 1973, 1988
Asian elephant	<i>Elephas maximus</i>	4000	22	perennial	Sukumar 1992

References

- Anderson, J. L. 1979. Reproductive seasonality of the nyala (*Tragelaphus angasii*): the interaction of light, vegetation phenology, feeding style and reproductive physiology. – *Mamm. Rev.* 9: 33–46.
- Bramley, P. S. and Neaves, W. B. 1972. The relationship between social status and reproductive activity in male impala (*Aepyceros melampus*). – *J. Reprod. Fertil.* 31: 77–81.
- Buys, D. and Dott, H. M. 1991. Population fluctuations and breeding of eland (*Taurotragus oryx*) in a western Transvaal Nature Reserve. – *Koedoe* 34: 31–36.
- Dhungel, S. K. and O'Gara, B. W. 1991. Ecology of the hog deer in Royal Chitwan National Park, Nepal. – *Wildlife Monogr.* 119: 1–40.
- Duncan, P. 1975. Topi and their food supply. – PhD thesis, Univ. of Nairobi.
- Erb, K. P. 1993. The roan antelope (*Hippotragus equinus*), its ecology in the Waterberg Plateau Park. – MSc thesis, Univ. of Stellenbosch.
- Fairall, N. 1968. The reproductive seasons of some mammals in the Kruger National Park. – *Zool. Afr.* 3: 189–210.
- Fairall, N. 1972. Behavioural aspects of the reproductive physiology of the impala, *Aepyceros melampus* (Licht.). – *Zool. Afr.* 7: 167–174.
- Grimsdell, J. J. R. 1973. Reproduction in the African buffalo *Syncerus caffer* in western Uganda. – *J. Reprod. Fertil.* 19: 301–316.
- Hall-Martin, A. J. et al. 1975. Reproduction in the giraffe in relation to some environmental factors. – *E. Afr. Wildlife J.* 13: 237–248.
- Hillman, J. C. 1979. The biology of the eland (*Taurotragus oryx*) in the wild. – PhD thesis, Univ. of Nairobi.
- Hitchens, P. M. and Anderson, J. L. 1983. Reproduction, population characteristics and management of the black rhinoceros *Diceros bicornis* in Hlululuwe Corridor/Umfolozu Game Reserve Complex. – *S. Afr. J. Wildlife Res.* 8: 71–80.
- Howard, P. C. 1983. An integrated approach to the management of common reedbeek on farmland in Natal. – PhD thesis, Univ. of Natal.
- Kyanja, I. B. 1989. The reproductive biology of the male hippopotamus. – In: Jewell, P. A. and Maloiy, G. M. O. (eds), *The biology of large African mammals in their environment*. Clarendon Press, pp. 181–196.
- Langman, V. A. 1977. Cow-calf relationships in giraffe (*Giraffa camelopardalis*). – *Z. Tierpsychol.* 43: 264–286.
- Laws, R. M. 1984. Hippopotamuses. – In: MacDonald, D. (ed.), *The encyclopaedia of mammals*. Facts on File, pp. 506–511.

- Leuthold, W. and Leuthold, B. M. 1975. Patterns of social grouping in ungulates in Tsavo National Park, Kenya. – *E. Afr. Wildlife J.* 11: 369–384.
- Murray, M. G. 1982. The rut of the impala: aspects of seasonal mating under tropical conditions. – *Z. Tierpsychol.* 59: 319–337.
- Owen-Smith, R. N. 1973. The behavioural ecology of the white rhino. – PhD thesis, Univ. of Wisconsin.
- Owen-Smith, R. N. 1984. Spatial and temporal components of the mating systems of kudu bulls and red deer stags. – *Anim. Behav.* 32: 321–332.
- Owen-Smith, R. N. 1988. Megaherbivores. – Cambridge Univ. Press.
- Raman, T. R. S. 1998. Antler cycles and breeding seasonality of the chital *Axis axis* Erxleben in southern India. – *J. Bombay Nat. Hist. Soc.* 95: 377–391.
- Rosser, A. M. 1987. Resource defence in an African antelope, the puku (*Kobus vardonii*). – PhD Thesis, Univ. of Cambridge.
- Rosser, A. M. 1989. Environmental and reproductive seasonality of puku *Kobus vardonii* in Luangwa Valley, Zambia. – *Afr. J. Ecol.* 27: 77–88.
- Rowe-Rowe, D. T. 1994. The ungulates of Natal. – Natal Parks Board.
- Rubenstein, D. I. 1986. Ecology and sociality in horses and zebras. – In: Rubenstein, D. I. and Wrangham, R. W. (eds), *Ecological aspects of social evolution*. Princeton Univ. Press, pp. 282–302.
- Sinclair, A. R. E. 1977. The African buffalo. – Univ. of Chicago Press.
- Sinclair, A. R. E. et al. 2000. What determines phenology and synchrony of ungulate breeding in Serengeti? – *Ecology* 81: 2100–2111.
- Skinner, J. D. 1971. The sexual cycle of the impala ram (*Aepyceros melampus*). – *Zool. Afr.* 6: 75–87.
- Skinner, J. D. et al. 1973. The effect of season on reproduction of the black wildebeest and red hartebeest in S Africa. – *J. Reprod. Fertil.* 19: 101–110.
- Skinner, J. D. et al. 1974. The effect of season on the breeding cycle of plains antelope of the western Transvall Highveld. – *J. S. Afr. Wildlife Manage. Ass.* 4: 15–23.
- Smuts, G. L. 1974. Growth, reproduction and population characteristics of Burchell's Zebra (*Equus Burchei*) in the Kruger National Park. – DSc Thesis, Univ. of Pretoria.
- Sukumar, R. 1992. Asian elephant: ecology and management. – Cambridge Univ. Press.
- Taylor, R. D. 1985. The response of buffalo *Syncerus caffer* to the Kariba lakshore grassland (*Panicum repens*) in Matusadona National Park. – PhD thesis, Univ. of Zimbabwe.
- Walther, F. R. 1972. Social grouping in Grant's gazelle (*Gazella granti*) in the Serengeti National Park. – *Z. Tierpsychol.* 31: 348–403.
- Warren, H. B. 1974. Aspects of the behaviour of impala male (*Aepyceros melampus*) during the rut. – *Arnoldia* 27: 1–9.
- Wilson, V. J. 1975. Mammals of the Wankie National Park. – National Museums and Monuments of Rhodesia.
- Wilson, E. E. and Hirst, S. M. 1977. Ecology and factors limiting roan and sable populations. – *Wildlife Monogr.* 54: 1–111.