Inherent seasonality in the breeding seasons of African mammals: evidence from captive breeding

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Breeding records from zoos provide a virtually untapped source of information for determining reproductive patterns of species unconstrained by nutritional variables and may be important in planning conservation strategies for rare species for which little "wild" data exist. In this study, we have analysed records of births in the National Zoological Gardens, Pretoria, from 1917 to 2001 for two species of zebras, 20 species of bovids, seven species of carnivores, the white rhinoceros and the hippopotamus. The zebras and pachyderms are aseasonal breeders, whilst the bovids show some variation. The African buffalo breeds throughout the year as do sable antelope in captivity, mountain reedbuck and all the arid-adapted species. The grazers tend to be seasonal, while browsers, with the exception of the kudu, tend to be aseasonal. Four species of felids and the spotted hyaena have an aseasonal breeding pattern but the African wild cat and wild dog are more seasonal. Possible reasons for the different patterns are discussed, with particular reference to the role of environmental cues.

INTRODUCTION

Birth records of mammals born in captivity have been published (e.g. Zuckerman, 1953; Brand, 1963) and are an important source of information on reproduction in species independent of nutritional constraints. In this paper, we enlarge on records of 31 species of South African mammals, which have bred at the National Zoological Gardens, Pretoria. The object of the present paper is to illustrate an inherent seasonality gleaned from breeding records from the past 84 years, to compare, where possible, breeding patterns in captivity with those in the wild and to discuss the implications for conservation.

METHODS

Birth data were obtained from the Zoological Gardens in Pretoria (25°45'S; 28°15'E), where they had been diarised by keepers. Relevant data for the period 1917 to 2001 were extracted and are displayed histographically (see captions to Figures 1–7). The base of each histogram represents half-monthly class intervals and the number of births recorded for each species in each interval is presented as the percentage of the total number of births for that species. A species was considered to exhibit a seasonal pattern of breeding if the percentage of births occurring within a 4-month time period in summer exceeded 75 % of the total number of annual births for that species.

The National Zoological Gardens, Pretoria, are situated at an altitude of 1330 m with the annual temperature and day length shown in Figure 1. Rainfall is irregular and is not shown because the animals were fed artificially and rations did not vary over the course of a year. Herbivores received lucerne, hay and antelope cubes (16% protein, Epol, Vereeniging, South Africa), while carnivores received a basic meat ration plus a supplement of Iams cat food (Iams South Africa, Midrand, South Africa). The period over which records were taken is included in the captions to the relevant figures and the number of recorded births is also shown. Data are shown for herbivores, carnivores and megaherbivores. For purposes of discussion, data are presented according to breeding pattern and not according to taxonomic order.

RESULTS AND DISCUSSION

Herbivores

Aseasonal breeders

In Figure 2, the aseasonal distribution of births for the mountain zebra *Equus zebra hartmannae* and plains zebra *E. burchellii* are illustrated. Some 30% of mountain zebra foals were born in February and, similarly, 30% of plains zebras were born in January/February. Gestation length is 364 days in mountain zebras and reports vary from 336 to 390 days for plains zebras (Brown, 1936; Skinner & Smithers, 1990). In the wild at Etosha National Park, Namibia, 81% of mountain zebra births occurred between November and April with a peak in December (Westlin-van Aarde *et al*., 1988). Plains zebras in the Kruger National Park showed a foaling peak in December/January with over 85% of all births taking place from October to March (Smuts, 1974). It would appear, therefore, that in captivity, with a "constant" food supply, there is a tendency for births to peak in summer and in the wild, where there is a summer rainy season with its consequent positive effect on grazing, for this tendency to be accentuated.

The aseasonal breeding ruminants can predictably be divided into the browsing antelope (Figure 3) and including certain grazers: sable antelope *Hippotragus niger*, buffalo *Syncerus caffer* and mountain reedbuck *Redunca fulvorufula*, as well as arid-adapted species (Figure 4). The mini-ungulates, blue duiker *Philantomba monticola* and common duiker *Sylvicapra grimmia* (Figure 3), breed throughout the year in captivity. Similarly,

ISSN 0035 919X – Trans. Roy. Soc. S. Afr. 57 (1&2). 2002. Pages 25–34.

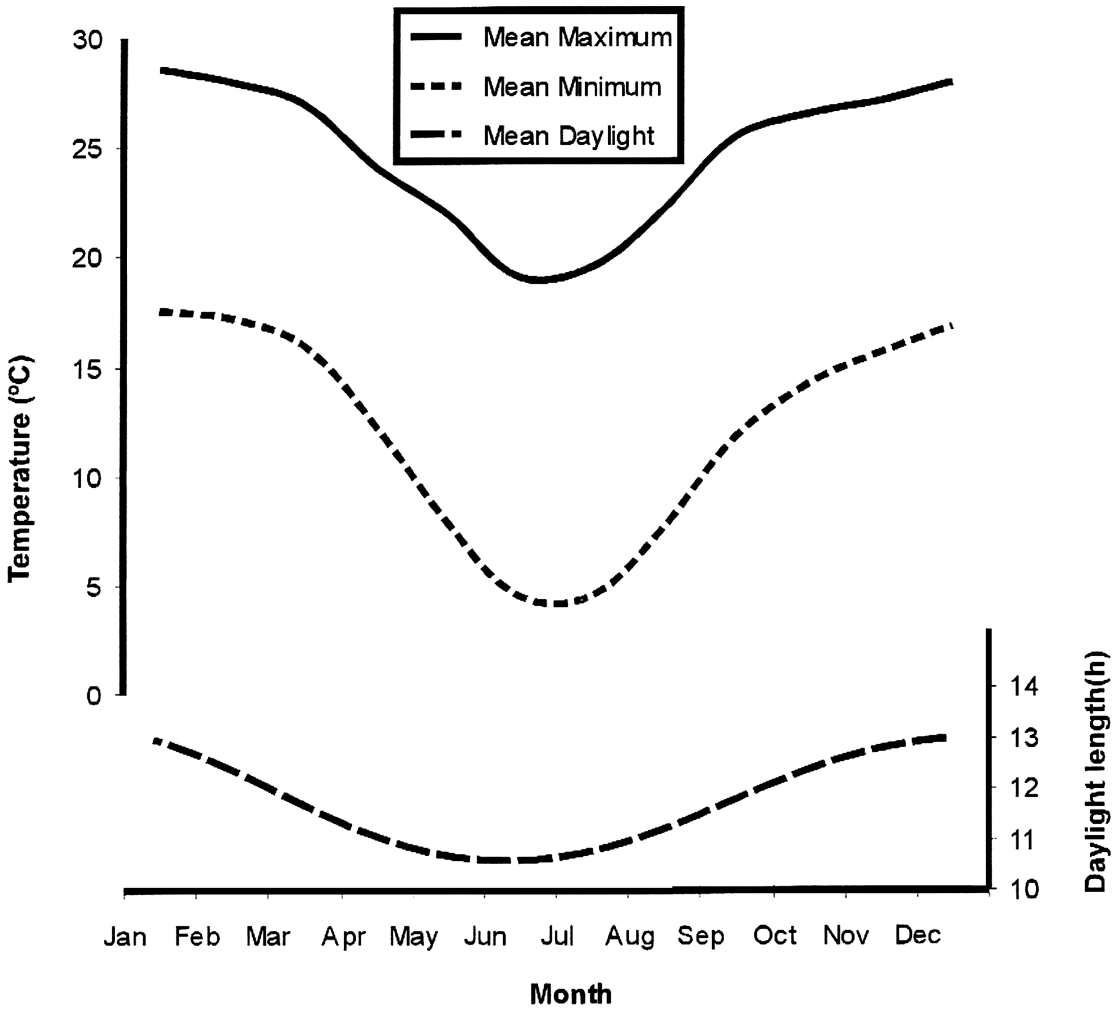

Figure 1. The annual temperature and day-length cycles at the National Zoological Gardens in Pretoria.

captive blue duiker in the East London Zoological Gardens, South Africa, were reported to breed throughout the year (Von Ketelhodt, 1973, 1977). In the wild in KwaZulu-Natal, Bowland (1990) has observed neonatal blue duiker in nearly every month, and common duiker lambs were reported to be born at any time of the year (Smithers, 1971).

Although captive steenbok *Raphicerus campestris* (Figure 4) show an apparent bimodal lambing pattern, the number of captive births was too few to portray an accurate picture. Wild steenbok in Botswana and Zimbabwe breed throughout the year (Smithers, 1971; Skinner & Smithers, 1990).

The two tragelaphines, the nyala *Tragelaphus angasii* and bushbuck *T. scriptus* (Figure 3), showed no seasonal tendencies in captivity. In the wild in Moçambique and adjoining KwaZulu-Natal, nyala breed throughout the year (Tello & Van Gelder, 1975; Anderson, 1984) as do wild bushbuck in Zimbabwe (Simpson, 1974).

Remarkably, and in contrast to the situation in the wild, sable antelope bred throughout the year (Figure 3). In the wild, sable calves were born in March in Zimbabwe (Child & Wilson, 1964); from January to early February in northern Botswana (Child, 1968); and births peak in February but calving continues to April in the Limpopo Province of South Africa (Skinner, 1985).

In captivity, buffalo breed throughout the year, although most births occur in the summer months. However, 88% of births occurred between December and May and only 12% of 155 births in the remaining six months in a captive breeding programme at Sololo Private Nature Reserve in the Lowveld (L. Hunt, unpublished). A similar seasonal pattern in breeding was reported in wild populations in Botswana, South Africa and Zimbabwe (Fairall, 1968; Pienaar, 1969; Carmichael *et al.*, 1977; Taylor, 1985).

Mountain reedbuck *Redunca fulvorufula* (Figure 3) also bred throughout the year with births peaking in December/January, which is similar to patterns in the wild (Skinner & Smithers, 1990).

Although captive springbok *Antidorcas marsupialis* bred throughout the year, 70% of the lambs were born between August and September (Figure 4), which reveals a strong seasonal skewing. This finding concurs with experimental studies on captive springbok that revealed a notable seasonality in the occurrence of oestrous cycles (Skinner, D.C. *et al.*, 2001). In contrast, the reproductive pattern of wild springbok is markedly influenced by environmental factors (Skinner & Louw, 1996): in the Lombard Nature Reserve (27°35'S; 2.5°30'E) (Skinner, J.D. *et al.*, 1974) springbok births are concentrated in the summer months with 80% of lambs being born between September and January; in the southern Kalahari (25°25'S; 20°36'E) most births occur in February/March following the rains (Skinner, J.D., unpublished) when there is a summer-rainfall pattern while, in the absence of rain, births tend to be scattered through the year; in the winter-rainfall region (29°40'S), all births occurred in July (mid-winter) (Skinner, J.D. *et al.*, 1977). This indicates some interplay between environmental factors and the importance of rain-

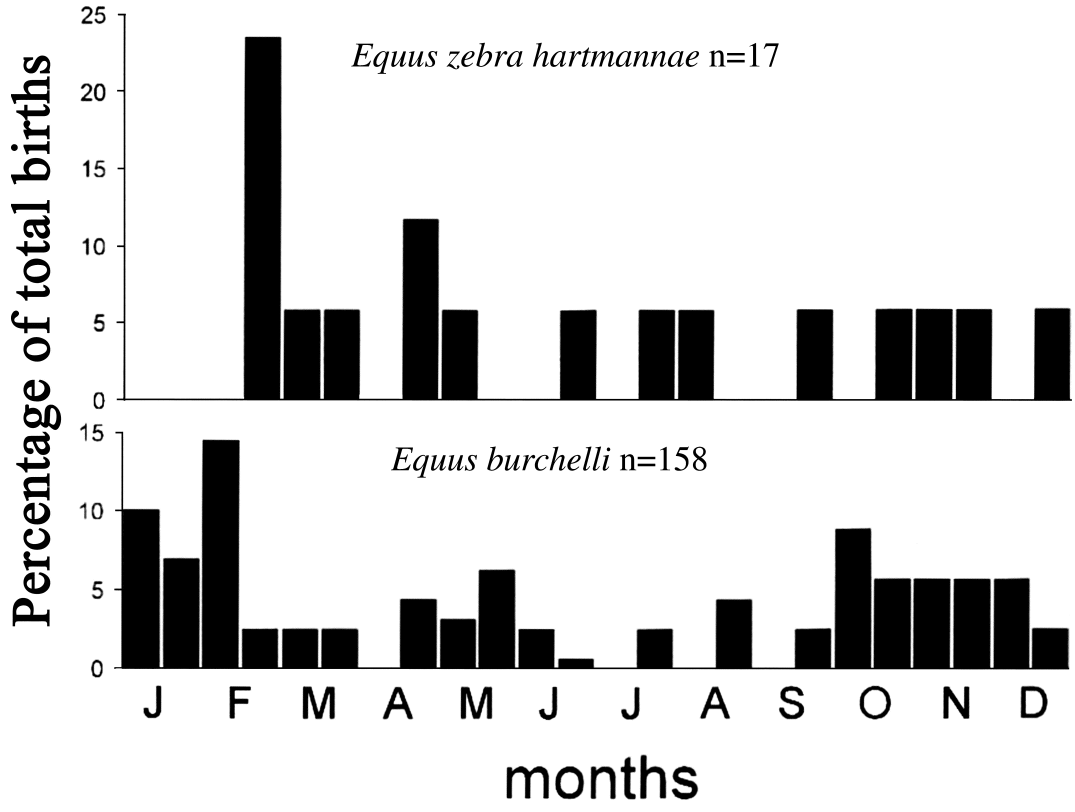

Figure 2. Half-monthly distributions for equid births; period in parentheses.

Equus zebra hartmannae	(1932–1996)
Equus burchellii	(1931–1996)

fall on breeding season through its influence on primary plant production.

Other arid-adapted species, namely the gemsbok *Oryx gazella* and the eland *Tragelaphus oryx*, showed a more even calving distribution (Figure 4) although eland tended to calve more in the second half of the year. Zuckerman (1953) also found that eland births at the London Zoo were concentrated in the spring and summer. In the wild, most eland births occurred in summer in the Lombard Nature Reserve (Skinner, J.D. *et al.*, 1974), with 30% of births taking place in November. In the same Reserve, wild gemsbok births peaked a month earlier. The cues influencing reproduction in these arid-adapted antelope are unknown but recent data suggest that environmental temperature could be a major factor (Skinner, D.C. *et al.*, 2001).

Seasonal breeders

The breeding pattern in many species of artiodactyls complies with Baker's (1938) hypothesis that the ultimate reason for timing of birth is neonatal survival. It is particularly important for grazers in seasonal rainfall areas to calve after the first rains to ensure that females can obtain adequate food for milk production. This pattern is innate and the cue for breeding is diminishing day length in such seasonal breeders. Mating takes place in autumn and calves are born in summer. In addition, day length helps synchronise births which has been suggested by Estes (1976) as a means of swamping predators.

It is not surprising therefore that the alcelaphines and their cousins show marked seasonality (Figure 5). In both the black *Connochaetes gnou* and blue wildebeest *C. taurinus* 65% of calves were born in the last six weeks of the year (November/December mid-summer) with a further 15% born in January. This captive breeding profile mirrors the wild, where 92% of births in black wildebeest occur in December/January in the Lombard Nature Reserve (25°35'S; 2.5°30'E) (Skinner, J.D. *et al.*, 1974). In the Kalahari Gemsbok National Park, 85% of blue wildebeest calves were born in December/January (Skinner, J.D., unpublished).

Similarly to the wildebeest, 65% of captive blesbok *Damaliscus pygargus phillipsi* calves were born in the last six weeks of the year (November/December) with a further 15% born in January. In wild blesbok in the Lombard Nature Reserve, 68% of calves were born in November/December and a similar but slightly earlier pattern was recorded at the Rietvlei Nature Reserve adjoining Pretoria (Du Plessis, 1972). Here births are extremely synchronised with 83% occurring within 10 days and this has been attributed to significant black-backed jackal *Canis mesomelas* predation.

The red hartebeest *Alcelaphus buselaphus*, which is more widely distributed in arid regions, shows a greater spread with 50% occurring in early summer (October/November). Wild red hartebeest calving in the Lombard Nature Reserve peaks earlier than in the wildebeest, with 80% of calves being born in October/November (Skinner, J.D. *et al.*, 1974). Again, compared to the pattern in captive hartebeest, this may be due to differences in nutrition or the "ram effect" (Skinner, J.D. *et al.*, 1992; Marais & Skinner, 1993; Skinner, D.C. *et al.*, 2002) which may be more accentuated in the wild. This may also have been the case for blesbok at Rietvlei.

Although captive waterbuck, *Kobus ellipsiprymnus*, gave birth in all months except November, from August to October only three calves were born, 60% of births occurring in the first