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

J.D.Skinner, D.G .Moss & D.C. Skinner
Johannesburg Zoo, South Africa

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INTRODUCTION

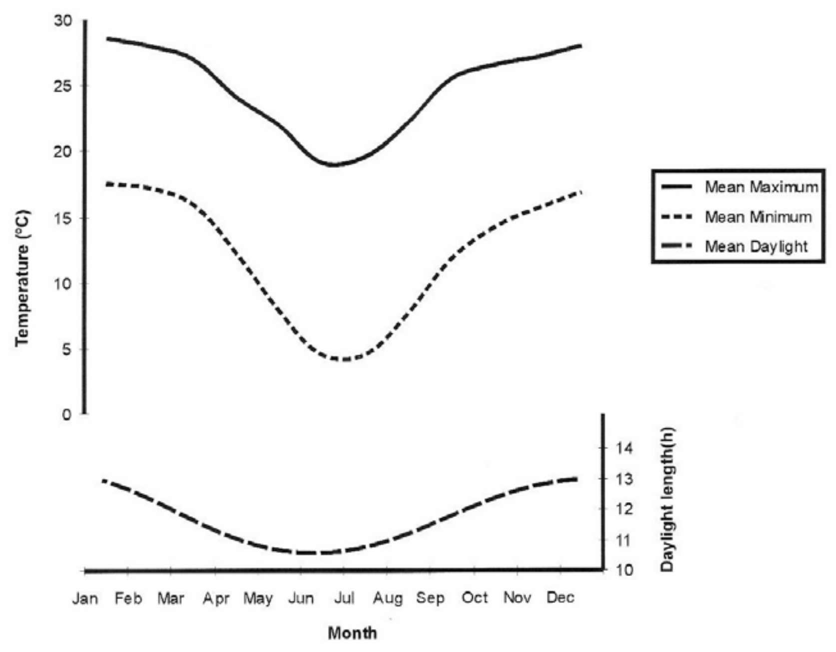
Birth records of mammals born in captivity have been published (e.g. Zuckerman, 1953; Brand, 1963) and are an important source of information on reproduction in species independent of nutritional constraints. In this paper, we enlarge on records of 31 species of South African mammals, which have bred 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 Figs 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 1330m 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, Vereniging, 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.

[Fig.1]



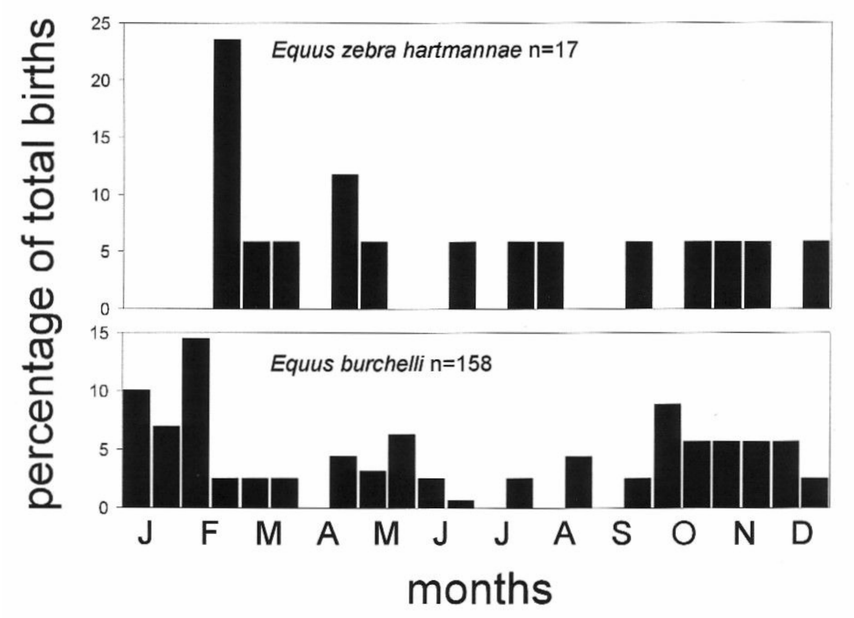
RESULTS AND DISCUSSION

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.

[Fig.2]

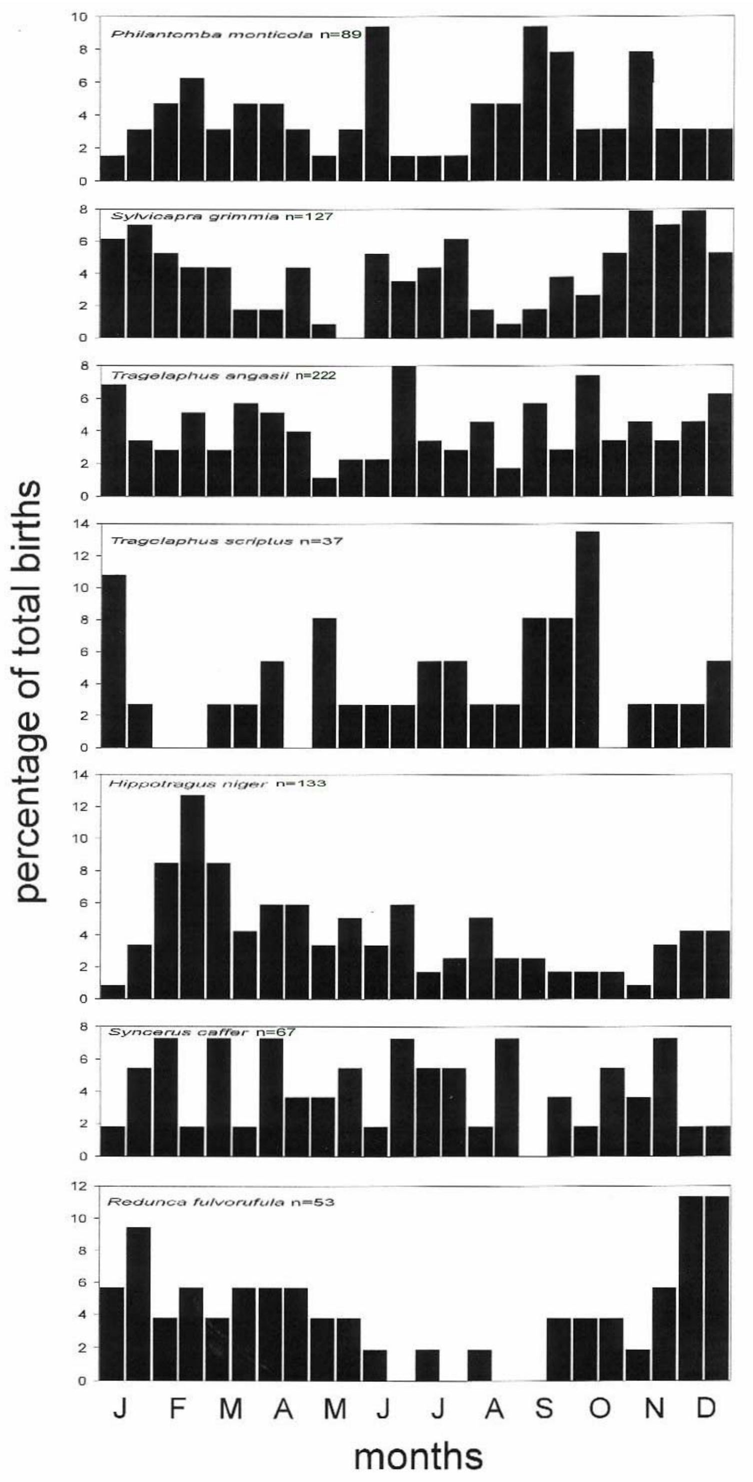


The aseasonal breeding ruminants can predictably be divided into the browsing antelope (Fig.3) and including certain grazers: sable antelope *Hippotragus niger*, buffalo *Syncerus caffer* and mountain reedbuck *Redunca fulvorufula,* as well as arid-adapted species (Fig.4). The mini-ungulates, blue duiker *Philantomba monticola* and common duiker *Sylvicapra grimmia* (Fig.3), breed throughout the year in captivity. Similarly, 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* (Fig.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* (Fig. 3) showed no seasonal tendencies in captivity. In the wild in Mocambique and adjoining KwaZulu/Natal, Nyala breed throughout the year (Tello & van Gelder, 1975; Anderson, 1984) as do wild bushbuck in Zimbabwe (Simpson, 1974).

[Fig. 3]



Remarkably, and in contrast to the situation in the wild, sable antelope bred throughout the year (Fig.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).

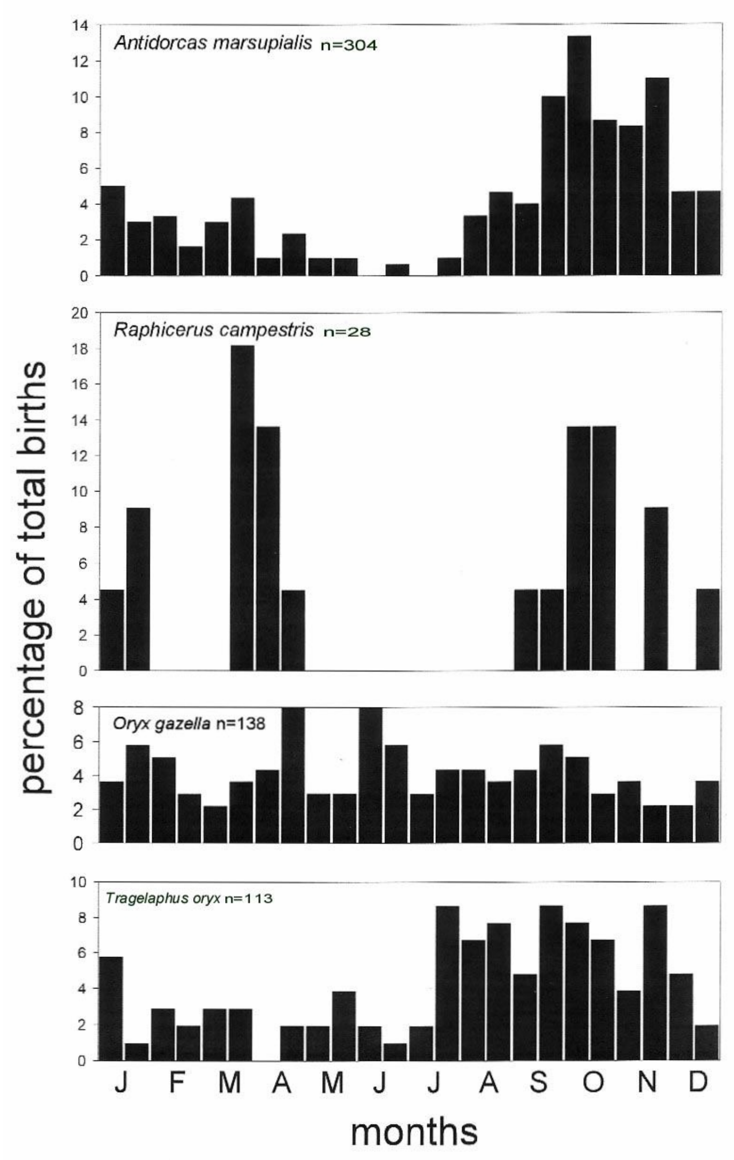
In captivity, buffalo breed throughout the year, although most births occur in the summer months. However, 88% of births occurred between December and May and only 12% of 155 births in the remaining six months in a captive breeding program at Sololo Private Nature Reserve in the Lowveld, (L. Hunt, unpublished). 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* (Fig.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 (Fig.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 *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 *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, 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 *et al.,* 1977). This indicates some interplay between environmental factors and the importance of rainfall 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 (Fig.4) although eland tended to calve more in the second half of the year. Zuckerman (1953) also found 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 *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 *et al.,* 2001).

[Fig.4]



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 (Fig.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, van Zyl & Oates, 1974). In the Kalahari Gemsbok National Park, 85% of blue wildebeest calves were born in December/January (Skinner, 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 *et al.,* 1974). Again, compared to the pattern in captive hartebeest, this may be due to differences in nutrition or the "ram effect" (Skinner, Jackson & Marais 1992; Marais & Skinner, 1993; Skinner, Cilliers & Skinner, 2002) which may be more accentuated in the wild. This may also have been the case for blesbok at Rietvlei.

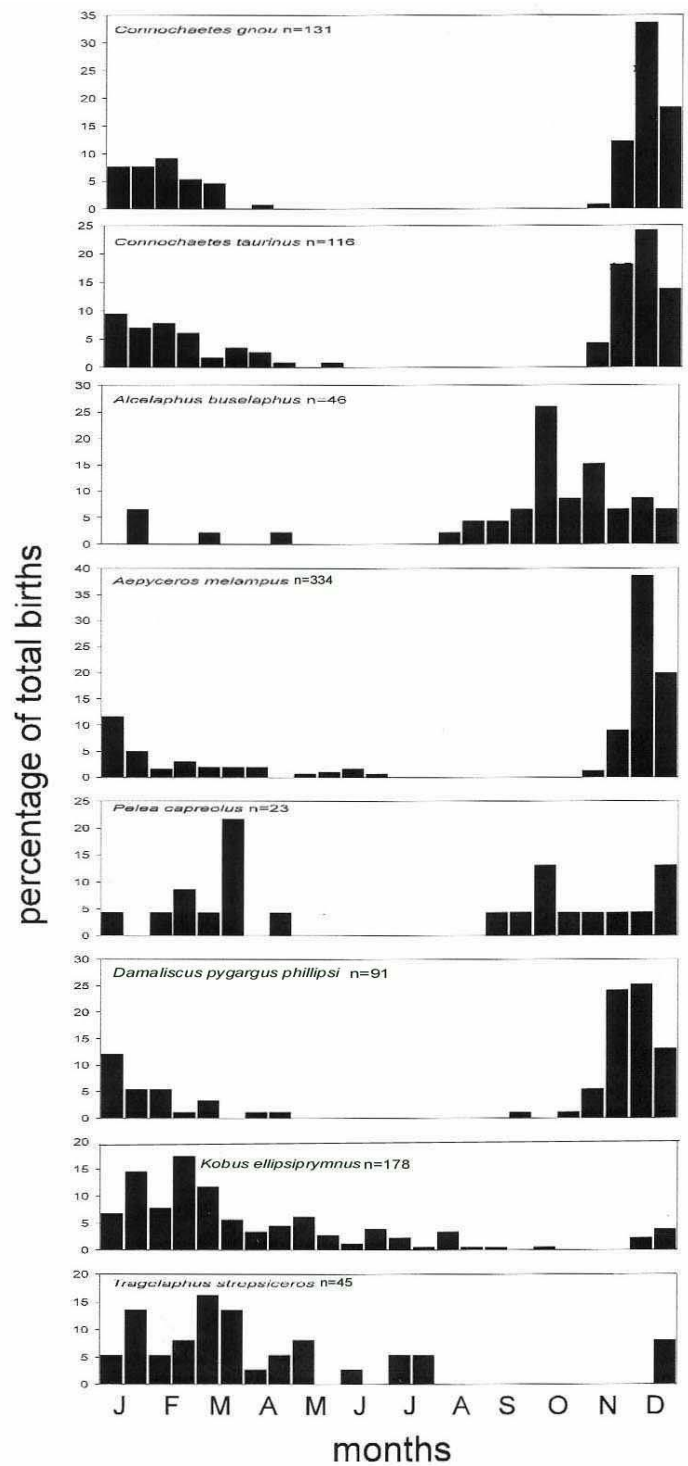
Although captive waterbuck, *Kobus ellipsiprymnus,* gave birth in all months except November, from August to October only three calves were born, 60% of births occurring in the first three months of the year. Wild waterbuck have been shown to breed seasonally throughout their range in southern Africa, with calving peaks in October and March (Pienaar, 1963; Fairall, 1968). Records of 13 roan antelope *Hippotragus equinus* births at the National Zoological Gardens between 1996 and 2002, show that all but two were born from January to April.

Captive impala *Aepyceros melampus* have a marked seasonal reproductive cycle and 70% of lambs were born in December/January, which mirrors the wild profile for this mixed feeder (Fairall, 1968; Skinner *et al.,* 1974) where 80% of lambs were born in December/January. However, in captivity there is a wider spread with the occasional birth as late as June (mid-winter) (Fig.5). Records of 34 births of captive black-faced impala *A. m. petersi* from Namibia, between 1996 and 2001 show similar marked seasonality with 68% of births occurring in December.

Although there was only a small number of captive grey rhebok, *Pelea capreolus,* these lambed from August to March with a gap in winter. These browsing antelope have an autumn rut in the wild (Skinner & Smithers, 1990) indicating seasonality. Indeed, at Sterkfontein Nature Reserve in the Free State, 94% of 32 births were in mid-summer (November-February), 72% peaking in December to January in 2000-2001 (A. Taylor, unpublished).

The kudu *Tragelaphus strepsiceros* also breeds seasonally in captivity (Fig. 5) with a peak (30%) in March but calves were born as late as July (8%). Similarly in the wild it is a seasonally breeding browser. Calving begins in late December to early January, peaks in February, when grass is at its tallest, and continues for about another three months (Pienaar, 1963; Simpson, 1966).

[Fig.5]



Carnivores

Results for the seven carnivore species are presented in Figure 6. The distribution of births for leopards *Panthera pardus*, although the number is small, is very similar to that presented by Zuckerman (1953) and indicates no evidence of seasonality. In contrast, Bailey (1993) found in wild leopards that the peak (49%) in courtship activity in the Kruger National Park occurred in the late dry season from July through September and was lowest (9%) in the wet season from January to March. This resulted in the peak period of leopard births coinciding with the peak in impala births following which they were actively preyed on by leopards. Gestation in wild leopards lasts 106 days (le Roux & Skinner, 1989) and litter size in the National Zoological Gardens, Pretoria varied from one to three which was similar to records from London Zoo (Zuckerman, 1953). Le Roux & Skinner (1989) found the mean number of cubs for wild leopards was two *(n=5)*; similarly, Bailey (1993) gives a figure of two (*n=4*) from the same area.

Births for lions *P. leo* show an aseasonal distribution similar to the London Zoo's records (Zuckerman, 1953). They are prolific breeders in captivity, with up to three litters per year from a single female being recorded. Following a gestation period of 110 days (Zuckerman, 1993), the number of cubs per litter varied from one to five with an average of three compared to an average of two for London. In the wild, litter size averages two (n=19) with a range of one to four but up to six have been recorded (Rudnai, 1973; Patterson, 1988). Although in the wild they mate throughout the year, Smuts (1982) found births peaked between February and April coinciding with the period of availability of seasonally breeding prey species.

Caracal *Caracal caracal* births, although few in number, indicate no fixed breeding season. Litter size varied from one to three with an average of two. In the wild litters have been recorded in all months of the year with a peak between October and February following a gestation period of 79 days (Stuart & Wilson, 1988).

The small number of births of the African wild cat *Felis silvestris* showed a distinct seasonal distribution with no kittens being born between autumn and early summer. Smithers (1971), however, had a captive free-ranging female which produced four of eight litters in winter so the seasonal distribution we have found may be spurious and a result of a low sample size. Litter size for captive animals varied from one to five with an average of three.

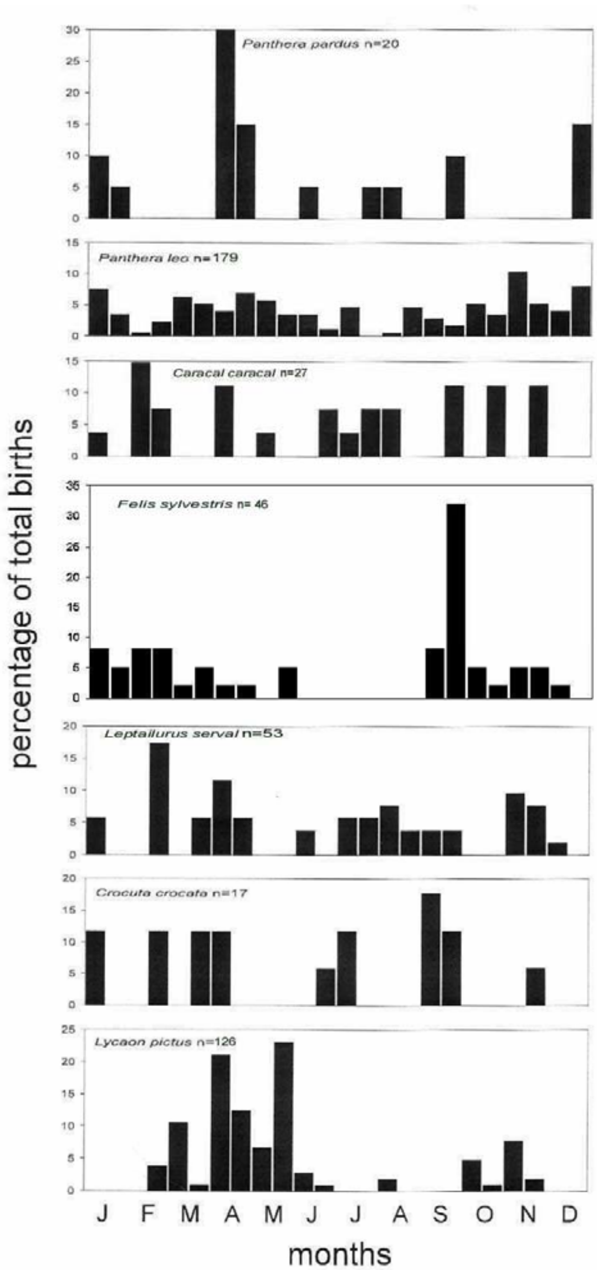
The serval *Leptailurus serval* breeds easily in captivity and the distribution of births is aseasonal. Following a gestation period of 68-72 days (Jones, 1952) litters averaging two kittens (range one to four) are born. In contrast, in the wild, gravid females have been taken from November to March (warm wet season) (Smithers, 1978). Mean number of foetuses was two (range 1-3; n=8).

Husbandry of cheetahs *Acinonyx jubatus* at the De Wildt Cheetah Breeding Centre has been described elsewhere (Brand, 1980). Successful captive breeding has resulted in 230 cubs being born from 67 litters. Young are born to wild Cheetahs throughout the year but in captivity males were introduced to oestrous females only in April; females thought to be pregnant did not have another opportunity to mate until the following year (Meltzer, 1988).

Spotted hyaenas *Crocuta crocuta* are aseasonal breeders in captivity as indeed they are in the wild (Skinner & Smithers, 1990). In the Kruger National Park births peak during the latter half of summer which is to the advantage of the female and her litter as this is the time when equids and bovids have their young (Lindeque & Skinner, 1982). Litter size was one or two.

Wild dogs *Lycaon pictus* breed seasonally in captivity when litters are born in winter from April to June. The average gestation period was 72 days (n=7); the average litter size was seven (n=27) (van Heerden & Kuhn, 1985). In the wild in the Kruger National Park litter size varies from 2 to 19 and pups are born from April to September (Maddock, 1989).

[Fig.6]

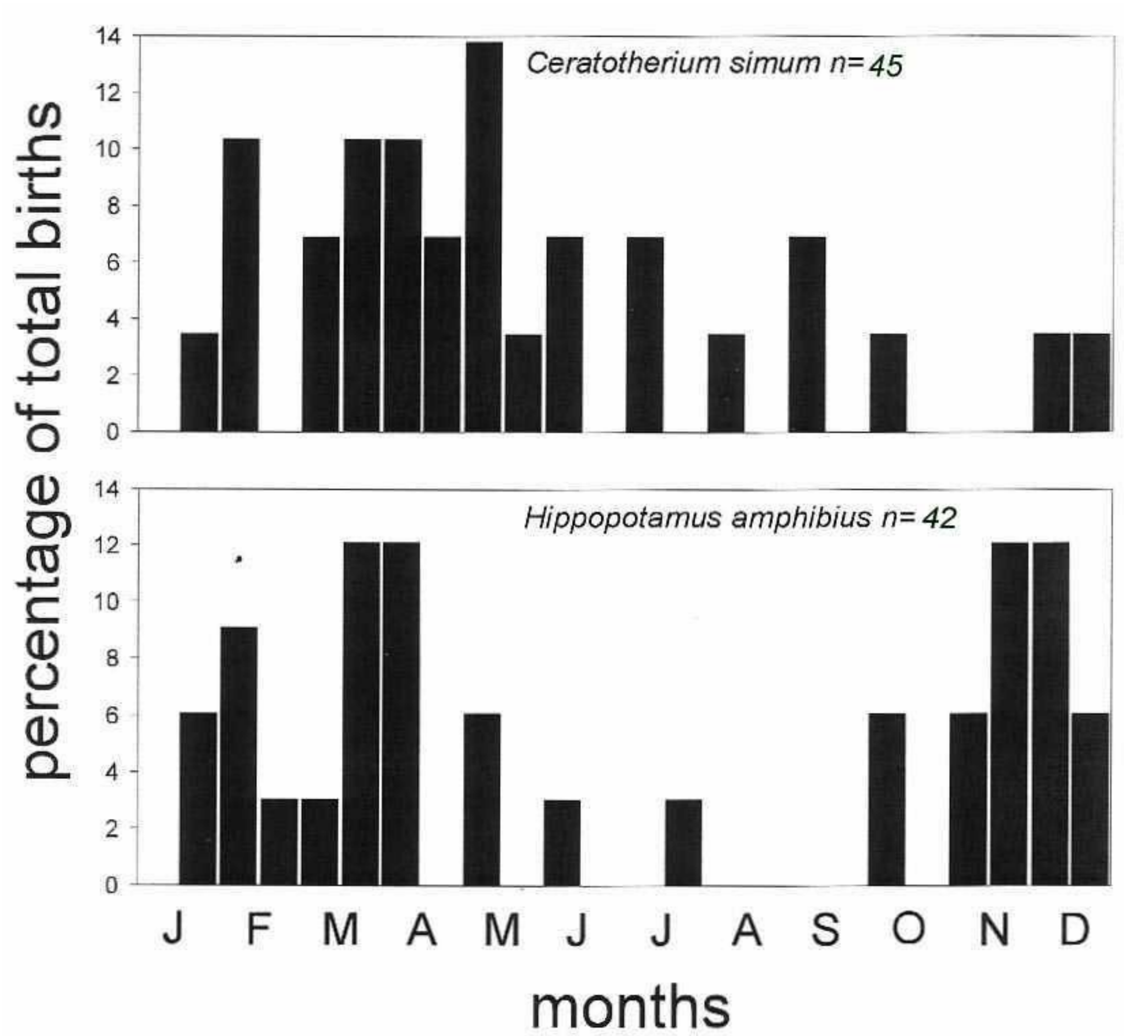


MEGAHERBIVORES

The birth distribution of the white rhinoceros *Ceratotherium simum* is aseasonal, although most captive births occur in autumn as is illustrated in Fig. 7. This is also true for white rhinos in the wild where, in KwaZulu/Natal, there are calving peaks in March and July. Owen-Smith (1988) suggests that it is the suppressant effect of an inadequate protein or energy balance which influences conception peaks rather than a stimulatory effect of high nutrition.

Reproduction in captive hippopotamus *Hippopotamus amphibius* (Fig. 7) is aseasonal, with birth occurring after a gestation period of 225-257 days (Brown, 1936; Asdell, 1964). In the Kruger National Park cows reproduce throughout the year but seasonal peaks may occur (Pienaar, van Wyk & Fairall, 1966; Smuts & Whyte, 1981).

[Fig.7]



CONCLUSIONS

Evolution of breeding seasons has undoubtedly played a role in the success of different species. In several wild aseasonally breeding ungulates there are birth peaks in the wet summer months compared to the captive cycle. This may indicate an influence of the seasonal nutritional cycle. However, in captivity, arid-adapted springbok and eland have a tendency to reproduce before the onset of the rains. This pattern may be influenced by an inherent circannual rhythm. It is difficult to explain why the sable antelope breeds aseasonally in captivity and seasonally in the wild other than that seasonal nutritional variations are responsible. When nutritional variations even out under captive conditions, sable antelope breed throughout the year. This does improve conservation prospects by ensuring a more rapid increase in captive population growth.

The seasonally breeding ungulates conform predominantly with Baker's (1938) hypothesis. Most probably their reproductive cycle evolved to be innate and reproductive hormonal secretions are controlled by day length (as in most seasonally breeding ungulates that have been investigated) and there is no apparent nutritional overlay apart from a small extension of the breeding season in some instances. It is interesting to note that such flattening has occurred in many breeds of sheep *Ovis aries* that are no longer subject to nutritional constraints. The kudu is the only species falling outside this ambit and it has been suggested that calves are born in late summer because the grass is long and they can be well hidden.

It is really not surprising that most of the captive larger carnivores, with a "constant" food supply, are all aseasonal reproducers apart from the African wild cat and wild dogs. In contrast, although still aseasonal, their wild counterparts all display birth peaks in the warm wet season when prey, particularly neonates, is more abundant. Wild dogs in the wild have a slightly longer winter-spring birth season. This may be explained by adaptation as wild dogs are coursing pack hunters. A neonate would provide only a tiny morsel for the pack which depends on the larger herbivores to satiate their appetite. In felids, reproductive success seems to be strongly influenced by prey availability - abundance in summer and, in the case of the African wild cat which feeds on rodents and other small animals, paucity in winter.

The megaherbivores have little to worry about when predation is considered. Very few young are preyed upon and yet there are still birth peaks in the wet summer months in the wild compared to the captive cycle. This indicates an influence of the seasonal nutritional cycle as a proximate factor influencing the occurrence of oestrus.

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FIGURE LEGENDS

Fig. 1 The annual temperature and daylength cycles at the National Zoological Gardens in Pretoria

Fig. 2 Half-monthly distributions for equid births; period in parentheses:
Equus zebra hartmannae (1932-1996)
Equus burchellii (1931-1996)

Fig. 3 Half-monthly distributions for aseasonal ungulate births; period in parentheses:
Philantomba monticola (1921-2001)
Sylvicapra grimmia (1924-2001)
Tragelaphus angasii (1939-2001)
T. scriptus (1926-1984)
Hippotragus niger (1932-2001)
Syncerus caffer (1929-2001)
Redunca fulvorufula (1933-1996)

Fig 4 Half-monthly distributions for arid-adapted aseasonal ungulate births; period in parentheses:
Antidorcas marsupialis (1923-1987)
Raphicerus campestris (1925-2001)
Oryx gazella (1937-1987)
Tragelaphus oryx (1916-2001)

Fig.5 Half-monthly distributions for seasonal births; period in parentheses:
Connochaetes gnou (1917-1996)
C. taurinus (1926-1996)
Alcelaphus buselaphus (1940-1996)
Aepyceros melampus (1917-2001)
Pelea capreolus (1939-1996)
Damaliscus pygargus phillipsi (1922-1996)
Kobus ellipsiprymnus (1925-1996)
Tragelaphus strepsiceros (1920-2001)

Fig. 6 Half-monthly distributions for carnivore births; period in parentheses:
Panthera pardus (1922-1996)
P. leo (1921-2001)
Caracal caracal (1937-1996)
Felis silvestris (1961-1996)
Leptailurus serval (1961-2001)
Crocuta crocuta (1982-1989)
Lycaon pictus (1929-2001)

Fig. 7 Half-monthly distributions for megaherbivore births; period in parentheses:

Ceratotherium simum (1967-2001)
Hippopotamus amphibius (1921-2001)

An in situ collaboration of trainers and researchers to condition semi-free-ranging black bears for reproductive physiology research

R. Cisneros, Senior Hospital Keeper
San Diego Zoo, California, United States of America
rcisneros@sandiegozoo.org

Introduction

Behavior husbandry training has become a standard tool for animal care professionals and has been incorporated into daily husbandry routines everywhere. Animal management strategies include behavior management as viable alternatives to physical or chemical restraint, crating or shifting animals, sample collection for research purposes, scale training for routine weight measurements, separation and calling to station, and a myriad of other animal husbandry related applications. Operant conditioning, for example, has helped provide a safer environment for elephant keepers through protected contact, allowing keepers to continue to care for their elephants without the use of physical discipline or aversive contact (Priest, 1991a).

In many cases, behaviors that are already occurring can be intensified with positive reinforcement (Pryor, 1984). This allows keepers to reinforce existing behaviors and make them available upon request when paired with a cue. Shaping behaviors can be effectively accomplished through successive approximations. Consistency, a well-developed training paradigm, effective reinforcers, and species-specific knowledge are tools that help develop a successful training regimen.

The concepts of training and conditioning can be applied in any setting. Its applications are carried over to all fields of animal care. Techniques in positive reinforcement are being applied to birds, mammals, and reptiles in zoo settings throughout the world. In many cases, zookeepers have used these techniques to help provide veterinary staff and researchers with blood and urine samples without the use of physical restraint or chemical immobilization. Operant conditioning can increase the reliability of treatment when used to shape behaviors conducive to treatment (Priest, 1990). Keepers and trainers at the San Diego Zoo conditioned a diabetic drill (*Mandrillus leucophaeus*) to allow insulin injections and venipuncture when it was discovered that the drill's diabetes was life-threatening (Priest, 1991b). Training diabetic primates for urine collection has allowed animal care staff to monitor ketone levels throughout the day for many diabetic primates at the San Diego Zoo.

While operant conditioning has been a successful tool for zookeepers and trainers, it is not restricted to the closed settings of the zoo environment. The principles of operant conditioning can be transferred out of the zoo setting and into the field with