ANNUAL REPRODUCTIVE CYCLES IN SELECTED AFRICAN MAMMALS IN RESPONSE TO ENVIRONMENTAL CUES

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Introduction

The assumption that natural selection is an optimising process, means that reproductive seasonality in mammals evolved to maximise gene survival. Although the constraints usually imposed on optimality theory are applicable, it can be assumed that periodicity in reproduction represents an adaptation to fluctuation in the availability of potentially limiting resources. In areas where these fluctuations in primary production are the result of a predictable seasonal climatic cycle, such as seasonal rainfall, a seasonal reproductive cycle becomes a viable strategem. Seasonal reproduction involves the temporal placing of *mating, gestation, parturition, lactation* and *weaning* in such a way to make maximum use of fluctuating resources (Skinner *et al.*, 1984).

In order to ensure that the young are born during favourable environmental conditions, the initiation of reproductive activity has to commence some time before the favourable season, or during it, depending on the duration of gestation. Larger mammals will tend to initiate reproductive activity earlier than small mammals, as gestation length usually increases with size (Rowlands & Weir, 1984). A number of environmental cues operate as proximate causes to initiate reproductive activity.

A large variety of African mammal species are seasonal breeders (Fairall, 1968 ; Smithers, 1983). The thrust of this paper is not to review the occurrence of seasonal breeding, but rather to examine some factors that influence their seasonal reproductive cycles by referring to five interesting examples. The reproductive cycles of three of these is controlled by the *photoperiod.*

Impala and *Blesbok*

Impala *(Aepyceros melampus)* and blesbok *(Damaliscus dorcas)* occupy habitats in *southern Africa* which are characterised by a *predictable climatic cycle* of dry winters and wet summers. In order to capitalise on this fixed climatic cycle, they respond to the *shortening daylength* to initiate breeding, conforming to the model proposed for the *Suffolk ewe* by Karsch *et al.* (1984). The central mechanism in this model is the *"LH pulse generator",* which processes both external and internal environmental signals. After attaining puberty at 16 months, ewes experience a maximum of two oestrous cycles annually, most conceiving during the first cycle.

Another environmental factor that has a profound effect on the expression of seasonality in *impala* and *blesbock,* is *social status.* The ability of males of these two species to respond to photoperiodic cues is complicated by the individual animal's social status. In anaesthetised males, an LH-RH challenge resulted in higher testosterone responses in territorial than bachelor males (Fig. 1).
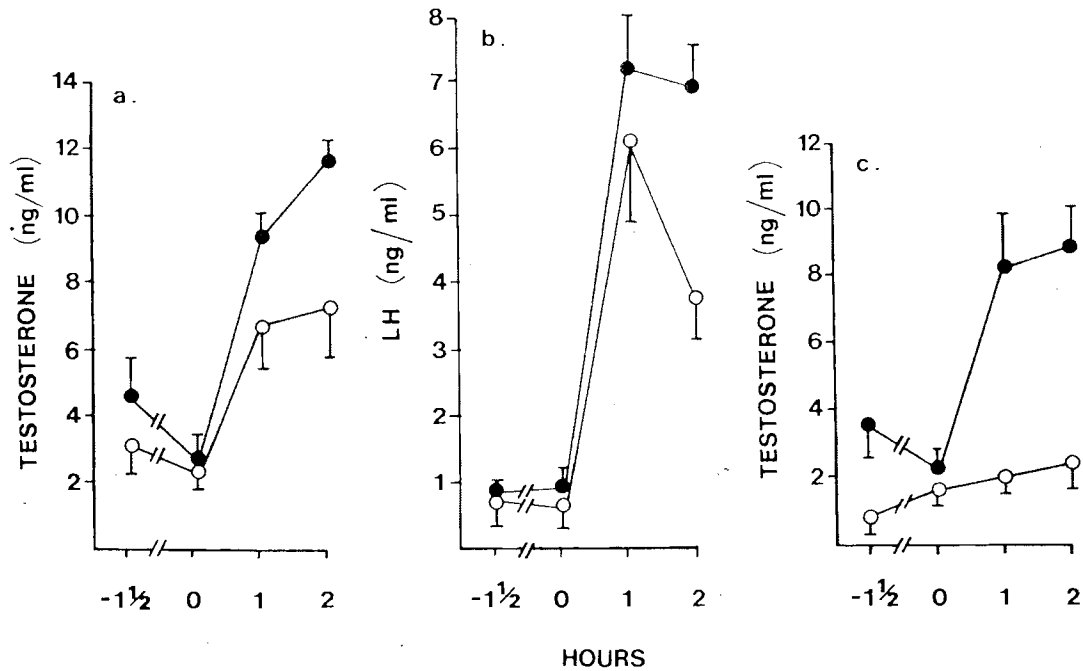
Figure 1.- Peripheral plasma *testosterone* concentrations in (a) territorial (●) and bachelor (o) blesbok and (c) territorial (●) and bachelor (o) impala at capture (-1 h) and 0,1 and 2 h after injection of 50 μg *LH-RH* (oh). Equivalent LH concentrations for blesbok are shown in (b). From Illius *et al.* (1983).

The lower LH-response to LH-RH in bachelor than territorial blesbok males suggests that *social stimuli* affect the responses of pituitaries through the action of *prolactin* (Keverne, 1979 ; McNeilly, 1980). A social effect on the LH-pulse generator through the *pineal gland* and *melatonin* cannot be excluded at this stage (Rieter, 1980).

Rock Hyrax

The herbivorous seasonal breeding rock hyrax *(Procavia capensis)* lives in rocky areas throughout Africa. The rock hyrax has a variable mating season which corresponds with latitude. In general, the mating season is later and longer in duration and parturition takes place later in the lower latitudes (Millar, 1971).

Due to its wide distribution, the rock hyrax inhabits a wide range of habits in southern Africa and is therefore subject to considerable variation in *food availabiliti.* Nutrition appears to affect the onset of *puberty* and *litter sizes* decrease in years, and areas, of diminished rainfall (Millar, 1971). In an experiment to determine the effect of different planes of nutrition on *spermatogenesis* and *androgenesis* in males during the mating season (Millar & Fairall, 1976), it was found that lower planes of nutrition caused decreased reproductive activity (Table 1). *Testicular weight, seminiferous tubule diameter* and *plasma testosterone concentration* were all significantly lower in hyrax fed the low-plane diet, while plasma and pituitary *LH* were lower, but not significantly so. Hypothalamic *LH-RH* did not differ between the low and high-plane diets.

TABLE 1

Comparison of *testicular activity* and hormone concentrations in sexually active hyrax on a high or low plane of nutrition and wild sexually quiescent hyrax (no in parentheses) - From Millar & Fairall (1976).

	Sexually active hyrax		Sexually quiescent hyrax (5)
	High plane (3)	Low plane (3)	
Weight of testes (g)	86,2 ± 8,2[ab]	48,2 ± 5,2[ac]	5,6 ± 1,8[bc]
Seminiferous tubules diameter (μm)	192,3 ± 0,3[ab]	143,2 ± 7,6[ac]	67,0 ± 3,9[bc]
Plasma testosterone (ng/ml)	13,6 ± 3,2[ab]	2,5 ± 0,6[a]	1,18 ± 0,06[b]
Plasma LH (ng/ml)	5,5 ± 2,8	1,0 ± 0,3	2,9 ± 2,0
Pituitary LH (μg/gland)	210,7 ± 40,5[b]	147,3 ± 11,7[c]	63,5 ± 21,9[bc]
Hypothalamic LH-RH (ng/gland)	16,5 ± 4,3[b]	21,5 ± 7,3[c]	101,6 ± 13,9[bc]
Plasma cortisol (ng/100ml)	6,6 ± 0,7	5,6 ± 1,2	3,4 ± 1,1

Values are means ± S.EM. ; means bearing identical superscripts differ significantly (p 0,05) by Students t-test.

*Expressed in terms of NIAMDD-ovine-LH-S18.

The interpretation of these results is difficult, mainly due to the low samples sizes. However, the inverse relationship between hypothalamic LH-RH content and plasma LH concentration in this species (Table 1) suggests that the nutritional effects on reproduction are primarily due to alterations in the secretion of LH-RH (Millar & Fairall, 1976) by the LH-pulse generator.

Porcupines

Our fourth example refers to Africa's largest rodent, the Cape porcupine *(Hystrix africaeaustralis)*. They are catholic in their habitat requirements, and are found throughout southern Africa. Porcupines are predominantly nocturnal and avoid environmental extremes by sheltering in subterranean burrows, rock crevices and caves (Skinner *et al.* 1984).

Porcupines in the semi-arid Karoo of southern Africa are strictly seasonal breeders. Litters are produced during the hot wet months between August and March when most (81.7%) of the annual rainfall (440mm) is recorded (Skinner *et al.*, 1984). The mean date of conception for this population is 21 september (± 18,6 days). Captive porcupines exposed to natural illumination and a constant food supply, breed throughout the year with females conceiving only once per annum. Furthermore females are *polyœstrous* but do not cycle while lactating and only conceive during the third to seventh 30-day cycle following the end

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of *lactation*. In considering the time interval of events from one conception to the next in the average female following Skinner *et al.* (1984) it is clear why females conceive only once a year (Fig. 2).
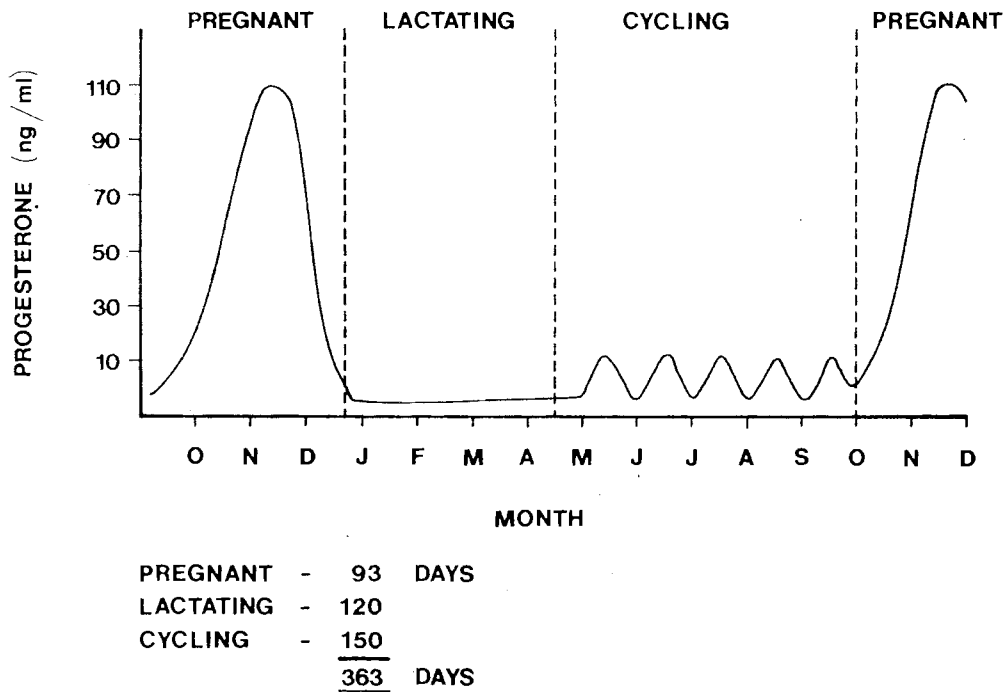

Figure 2.- Annual reproductive cycle of adult female porcupines. Adapted from Skinner *et al.* (1984).

The fact that this reproductive cycle lasts approximately one year in captivity, despite the food abundance, means that the infertile cycles must have some function in the general annual reproductive cycle. It has been postulated that these cycles, which show lower *progesterone* levels than fertile cycles, are important for the priming of the uterus (Van Aarde 1984). This period could also play an important role in providing an opportunity for the replenishment of resources following the extended gestation period characteristic of the hystricomorpha (Rowlands & Weir, 1974).

The occurrence of a seasonal pattern of reproduction in the species as a whole nevertheless indicates some kind of environmental selection pressure, with pregnancy normally occurring after the increase in primary production in spring, and lactation extending into the late summer when resources are plentiful (Fig. 2).

Springhaas

The *springhaas (Pedetes capensis)* is a large bipedal rodent of uncertain taxonomic position (McLaughlin 1967) occurring throughout southern Africa. Although capable of breeding throughout the year, in the highland grassland plateau the relationship between pregnant females and mean monthly *temperature* was highly significant ($r = 0,84$; $P < 0,001$; $n = 10$), the highest incidence of pregnancy occurring in the colder months. An accurate gestation length has not yet been recorded but indications are that it is about 80 days.

A peak in mating activity occurs in mid-winter but this is not reflected in any apparent seasonal cycle in testicular endocrine or exocrine function in males (Table 2), the full spermatogenic cycle being evident in all males.

TABLE 2

Mean ± s.d. plasma concentrations of LH and testosterone in male springhaas (adapted from van der Merwe *et al.* 1980).

Months	N	LH (ng/ml)	Testosterone (ng/ml)
Jan.-Feb.	6	0,73 ± 0,87	0,94 ± 0,58
June-Aug.	13	1,97 ± 1,34	1,90 ± 0,86
Sept.-Nov.	18	1,49 ± 0,88	1,74 ± 0,87

Although Coe (1969) considered *P. capensis* a seasonal breeder, the short *gestation* period would tend to preclude this unless nutritional cues are also important. Nutrition was adequate for the animals in our study area but temperature appeared to have an influence with significantly fewer births in the cold winter months. This may conversely be affected by the lower LH and testosterone levels in the hottest summer months when ovarian follicular activity from non-pregnant females also seemed to be supported although too few specimens were available to enable conclusive deductions.

Conclusions

The examples discussed indicate that where photoperiod is the proximate cue initiating reproduction the pattern may also be confounded in males by factors such as social status. It is much more difficult however, to identify cues other than photoperiod particularly when one of these may confound the effects of another and where their cummulative effects may provide the optimum situation. Despite the widespread occurrence of seasonal breeding in African mammals, our knowledge concerning the factors that influence or affect seasonality is scant. The development of techniques for the assesment of endocrinological parameters in anaesthetised animals must be regarded as a high prority, if we hope to unravel the multitude of factors that influence and initiate seasonal breeding in African mammals.