Adaptations in three species of large mammals (*Antidorcas marsupialis, Hystrix africaeaustralis, Hyaena brunnea*) to arid environments

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Adaptations in the springbok *Antidorcas marsupialis*, porcupine *Hystrix africaeaustralis* and brown hyaena *Hyaena brunnea* to arid environments are discussed. Springbok evolved in the arid west of southern Africa. The proximate factor triggering the onset of oestrus is improved nutrition following rainfall and adaptations have evolved to ensure the success of year-round opportunistic breeding. The porcupine can also breed throughout the year but in the Karoo with its dry cold winters, young are only born in warmer wetter months. Following a gestation period of 93 days and lactation anoestrus lasting 120 days, the female porcupine has evolved a special adaptation whereby she will only conceive during the third to seventh oestrous cycle following the end of lactation. This period may be shortened or lengthened thereby enabling her to adjust to climatic conditions in an unpredictable arid environment. The brown hyaena is well adapted to living along the Namib coastal region where severe extremes in temperature occur and bitterly cold south-west winds sweep along the coastal strip. Long hair and pilo-erection probably assist brown hyaenas in adjusting to these adverse climatic conditions. The spotted hyaena, *Crocuta crocuta*, does not occur along the coast. Morphological differences between the two species are considered in the light of climatic differences between the coastal and interior desert regions.
S. Afr. J. Zool. 1984, 19: 82 – 86

Die aanpassings van die springbok *Antidorcas marsupialis*, ystervark *Hystrix africaeaustralis* en bruin hiëna *Hyaena brunnea* tot dorre streke word bespreek. Die springbok het in die dorre westelike gedeeltes van suidelike Afrika ontwikkel. Verbeterde voeding as gevolg van reënval dien as die onmiddellike faktor wat die aanvang van estrus bewerkstellig en 'n taktiek het ontwikkel om suksesvolle opportunistiese teling reg deur die jaar te verseker. Ystervarke teel ook reg deur die jaar maar in die Karoo waar die winters droog en koud is, word kleintjies net gedurende die warm, nat maande gebore. Die draagtydperk van 93 dae en laktasie-anestrus word gevolg deur 'n spesiale aanpassingstaktiek wat daartoe aanleiding gee dat wyfies slegs gedurende die derde tot sewende estrussiklus na laktasie bevrug word. Hierdie tydperk kan verkort of verleng word en stel die wyfie in staat om by heersende omgewingstoestande in die onvoorspelbare dorre omgewing aan te pas. Die bruin hiëna is goed aangepas om langs die kus van die Namib, waar uitermatige temperatuurverskille en baie koue winde heers, te oorleef. Lang hare en pilo-ereksie stel bruin hiënas waarskynlik in staat om by ongunstige weersomstandighede aan te pas. Die gevlekte hiëna, *Crocuta crocuta*, kom nie langs die kus voor nie. Morfologiese verskille tussen hierdie spesies met betrekking tot klimatologiese verskille tussen die kus en binnelandse gebiede van die woestyn word spekulatief bespreek.
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Fluctuations in primary production owing to low, seasonal, and often localized and unpredictable rainfall present constraints to organisms adapted to survive in semi-arid environments. Physiological and behavioural adaptations related to survival of mammals inhabiting African arid zones have received considerable attention (see Delany & Happold 1979; Maloiy 1979; Louw & Seely 1982) and we do not intend to review these. Instead, data related to reproductive patterns and climatological adaptations which we consider of importance to long-term survival of three southern African mammal species are presented.

Reproduction

One would expect that the timing of parturition in different species would have evolved to ensure neonate survival. This may be achieved through seasonal breeding where the climatic cycle is predictable. Baker (1938) suggested that the optimal conditions pertaining at birth and during lactation are the ultimate cause for the timing of breeding. Nevertheless, all phases of the reproductive cycle are subject to selective pressures and the final evolvement of the reproductive pattern will ensure the temporal placement of mating, gestation, parturition, lactation and weaning in such a way that these will be most beneficial to survival of the species.

Baker (1938) distinguished ultimate causes operative in breeding seasons from proximate causes, the latter being the environmental cues which stimulate the parents to reproduce, so that phases in the reproductive cycle are ordered to make maximum use of optimal environmental conditions (ultimate causes). The timing of conception in certain species is initiated by daylength and regulated by the length of gestation to ensure that the young are born during favourable environmental conditions (Heape 1901).

Optimal conditions for breeding will differ in different environments and Sadleir (1969) distinguishes between:

(a) Temperate regions with a seasonal cycle where there is a fixed optimal season. The 'moist' eastern half of southern Africa with its pattern of summer rain would be an example.
(b) Deserts (and sub-deserts) with fickle climatic conditions and an unpredictable optimal season. The dry western half of southern Africa falls within this classification.
(c) Tropical and equatorial regions with a continual optimal season.

Springbok

In order to examine the manner in which proximate and ultimate factors influence reproduction in an arid environment, it is useful to compare the pattern of reproduction of a desert-dwelling antelope, the springbok *Antidorcas marsupialis*, with an antelope of similar size which has evolved in an area with a fixed optimal season, the impala *Aepyceros melampus*. The springbok, a water-independent species (Greenwald 1967), evolved on the drier western side of Africa, whereas the impala, a water-dependent species (Maloiy & Hopcroft 1971) evolved along the moister eastern half of Africa (Figure 1).

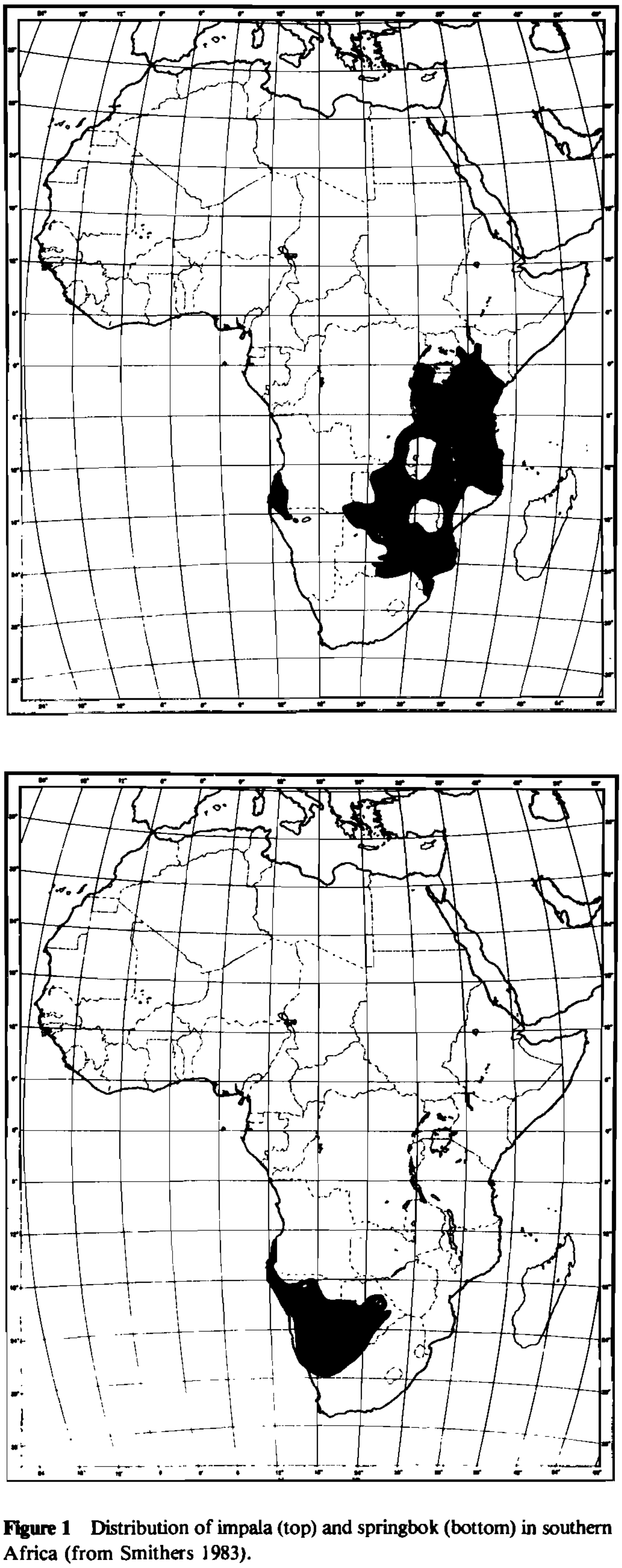

Figure 1 Distribution of impala (top) and springbok (bottom) in southern Africa (from Smithers 1983).

Impala migrations are of only a minor nature and usually along or between water courses. They are able to utilize a wide variety of plants including monocotyledons following the flush of spring growth. During the winter dicotyledons make up the bulk of their diet (Skinner, Monro & Zimmermann 1984). Their woodland savanna habitat in southern Africa is heavily influenced by a climatic cycle of dry winters and wet summers (October – March). Following the advent of summer rainfall, conditions for the nutrition (via lactation and later, development of the rumen) and growth of neonates are optimal.

In order to capitalize on this fixed climatic cycle, impala respond to the only unvariable, proximate, environmental cue namely daylength. They mate in autumn (early May in southern Africa) and this mating period is only marginally affected by severe changes in climatic conditions such as drought when the duration of the mating season is slightly extended (Fairall 1983). Moreover, an important observation by Fairall (1983) was that they have only two oestrous cycles each season. Following a gestation period of 28 weeks (Fairall 1968) lambs are born from November to January after the onset of the summer rains (Figure 2).

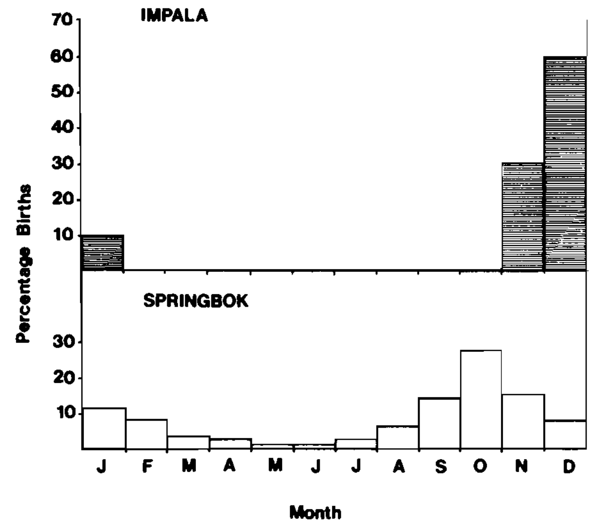

Figure 2 Annual distribution of births for springbok and impala in southern Africa. Compiled from 3 000 springbok births from different areas in the summer rainfall region, the masking effect of the rainfall pattern can be noted; and more than 3 000 impala births from different areas (adapted from Skinner, Nel & Millar 1977).

In the arid plains where springbok evolved there is no fixed optimal season and the reproductive patterns they employ differ from those of impala. Springbok are nomadic and treks have been documented where they have migrated in hundreds of thousands over arid plains in the Cape Province particularly following droughts (Sparrmann 1886). Many of these treks occurred in the north-west where precipitation occurs in summer in the east and in winter in the west, with a transitional area between. Springbok can apparently detect (presumably by smell or sight) the occurrence of rainfall over hundreds of kilometres of flat plains. Following rainfall, short succulent grasses such as *Enneapogon desvauxii* have a rapid growth response. The springbok show a predilection for these grass-shoots (Liversidge 1968), always selecting succulent forage and turning to forbs as grasses become lignified.

Springbok breed throughout the year (Skinner, von La Chevallerie & van Zyl 1971) and therefore respond to proximate climatic cues in an unpredictable environment. They obviously cannot predict what conditions will be when the lambs are born, and the lack of selection for specific timing at birth allows for indeterminate breeding (Figure 2). Nutrition, the overriding factor in the desert, is influenced by rainfall. Rain may fall in a particular area once in a decade and springbok have the mobility to reach areas where rains occurs. The flush of green forage is well known as a proximate factor influencing reproduction in ungulates (Laing 1957). Those springbok capable of responding (post-pubertal and not lactating) to the sprouting green forage will exhibit oestrus and be mated. Springbok rams, unlike impala (Skinner 1971), are capable of breeding throughout the year (Skinner & van Zyl 1970a). The springbok gestation period of 24 weeks (Skinner & van Zyl 1970b) results in lambs being born not necessarily at a favourable time but the ability of the ewes to migrate over great distances minimizes the risk and ensures a more consistent supply of preferred food.

Puberty in impala ewes is reached at 16 months but, if not achieved by that particular mating season, may be delayed for a year. In contrast, springbok ewes under optimal conditions reach puberty by six months of age independently of seasonal changes. Populations of springbok may crash at unfavourable times but through opportunistic breeding and migration, herds have the ability to recover rapidly.

Porcupines

The second example is also related to reproduction and refers to the Cape porcupine *Hystrix africaeaustralis*, Africa's largest rodent. It apparently has a wide ecological tolerance, occurring in most habitat types including the extreme, arid zones of southern Africa. Porcupines are predominantly nocturnal and avoid the high diurnal temperatures typical of most arid zones by sheltering in subterranean burrows, rock crevices and caves.

Porcupines in the Tussen-die-Riviere Game Farm (30°25′S/26°12′E) situated in the Karoo, between the Orange and Caledon Rivers, are strictly seasonal in their breeding. Litters are produced during the hot, wet months between August and March when most (81,7%) of the annual rainfall (440 mm) is recorded. The length of their gestation period is 93 to 94 days with the mating season extending over a period of eight months from May to December. As in most large mammals the sequence of reproductive events (ovulation, mating, conception and pregnancy) commences when environmental conditions are different to those when the young are born.

Captive porcupines exposed to natural illumination and a constant food supply, breed throughout the year with females conceiving only once per annum (mean litter interval = 405,8 ± 86,2 days; n = 5). Furthermore females are polyoestrous but do not cycle while lactating and only conceive during the third to seventh 30-day cycle following the end of lactation (n = 8); this probably enables the female to adjust to unpredictable environmental conditions.

In considering the time interval of events from one conception to the next in a specific female (pregnancy = 93 days + lactation = 120 (90 – 148) days + five oestrous cycles = 150 days) it is clear why females will conceive only once in a year (Figure 3). Lactation probably results in a reduction in energy reserves to below the threshold necessary for conception and implantation to occur. The flexibility provided by three to seven cycles elapsing between the end of lactation and conception provides the female with the opportunity to replenish energy reserves. The sum total of all reproductive events between conceptions culminates in seasonality in reproduction. The extended suckling period, during which females do not conceive, and the small litter size, result in a relatively high reproductive input to a specific litter. Considering that porcupines attain sexual maturity during the second year of life, a relatively high rate of intrinsic increase can be maintained. Therefore, although having elements of a K-selected species (see Pianka 1970) the observed pattern of reproduction may explain how porcupine populations cope with survival in an unstable environment.

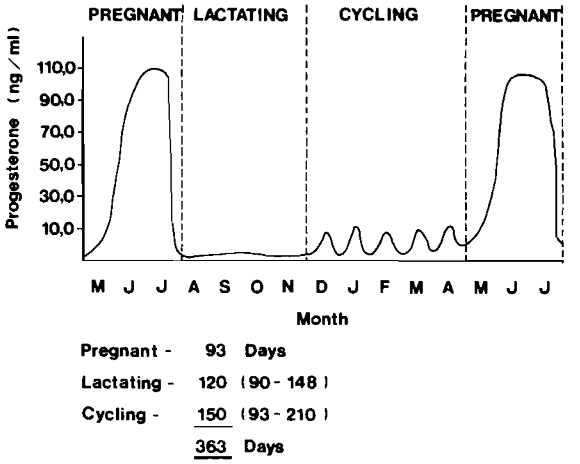

Figure 3 Annual reproductive cycle of adult female porcupines.

Climatology

Hyaenas

The third example we wish to discuss concerns a carnivore and is related to thermoregulation under the unusual climatic conditions pertaining along the west coast of the Namib desert. Brown hyaenas, *Hyaena brunnea*, are widespread over most of southern Africa but tend to predominate in the arid, western parts of the subregion. In some protected areas they are sympatric with the social and larger spotted hyaenas *Crocuta crocuta* which may compete with them, placing them at a disadvantage (Mills & Mills 1982).

The pattern of distribution of these two species in South-West Africa has been reviewed by Skinner & van Aarde (1981). Spotted hyaenas do not occur along the coast of the central Namib Desert where brown hyaenas are common (Figure 4), the latter living off seal colonies and other vertebrate material which has been washed up. Initial attempts to explain this geographical separation centred on differences in prey availability, the occurrence of fresh water and differences which have evolved in the social structures of the two species (Skinner & van Aarde 1981).

The Namib Desert has a steep climatic gradient attributed to the presence of the Benguela Current and its associated upwelling (Ward, Seely & Lancaster 1983). In an attempt to relate the observed pattern of distribution to climatological differences between the coastal and the interior regions, meteorological data, obtained from the Weather Bureau (1980, 1983) and an unpublished report (Lancaster, Lancaster & Seely 1983), were processed and related to hyaena distribution.

Hill's 'cooling factor' (Lamb 1977) was calculated for each of the 12 stations for which meteorological data were available (Figure 5) using the equation $H = (0{,}14 + 0{,}47\sqrt{V})(36{,}5 - T)$ where V = median annual windspeed (m s^{-1}), T = mean

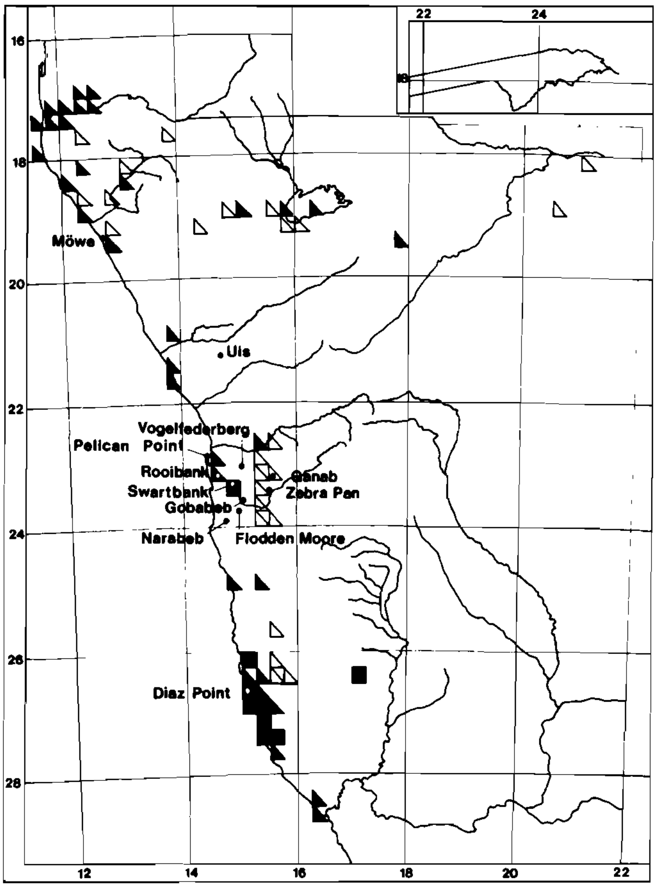

Figure 4 Distribution of brown hyaenas (◣) and spotted hyaenas (◺) in the central Namib Desert. Also indicating the 12 weather stations for which meteorological data were available (named).

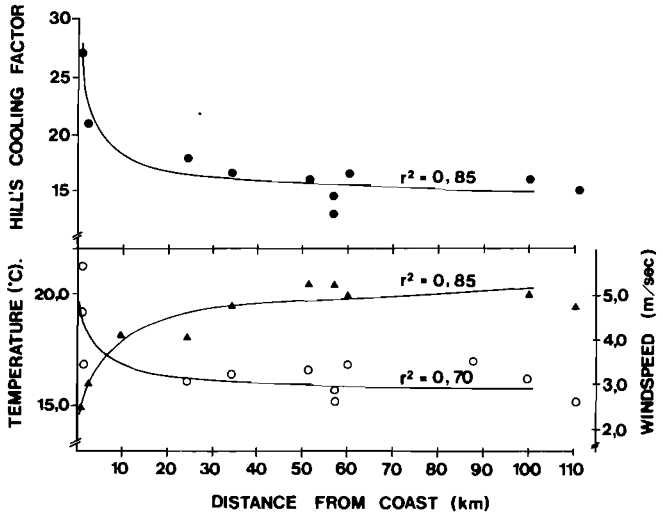

Figure 5 The relationship between distance from the coast (km), mean annual temperature (▲), median annual windspeed (o) and Hill's cooling factor (●). Curves were fitted through non-linear regression analysis.

annual air temperature in °C and H = thousands of calories lost per cm^2 skin per second. Because of inadequate data on wet bulb temperatures, non-sweating conditions were assumed.

The altitude (m) of the meteorological stations included in our analyses increased linearly and significantly ($r^2 = 0{,}90$; $P < 0{,}001$) with increasing distance (km) from the coast. Mean annual temperature (°C) increases with an increase in distance from the coast but stabilizes after approximately 40 km. The median annual windspeed (m s^{-1}) recorded at each station decreases with an increase in distance from the coast up to approximately 20 km after which few changes occur (Figure 5). Hill's cooling factor, based on these variables, decreases with an increase in distance up to approximately 40 km from the coast after which it stabilizes (Figure 5). This factor, expressing the cooling power of air and therefore the amount of thermal comfort experienced by an organism, suggests that hyaenas living on the coast are experiencing extremely cold environmental conditions ($H > 20$ regarded as extremely cold; see Lamb 1977). Considering that spotted hyaenas do not occur on the coast in spite of a relatively abundant food supply, this may well be one of the factors responsible for their absence and therefore for the observed geographical separation between the two species.

Thermal insulation provided by fur is of value to mammals during cold exposure. Fur depth, furthermore, seems to be one of the most important factors determining heat loss in mammals (McClure & Porter 1983) and can be increased in most mammals through the development of long hair and/or piloerection. The long hair of brown hyaenas, when compared to that of spotted hyaenas (112 ± 60 mm *cf* 33,4 ± 10,4 mm, Keogh 1979), will conceivably provide more efficient thermal insulation during cold exposure.

In conclusion we would like to emphasize that adaptations in mammals to arid environments are complex and involve a multitude of factors. Rarely does one outstanding feature predominate in this regard and one should examine the interaction between ecological, physiological and ethological characteristics of each species in determining how it has adapted.

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