Reproduction in the Cape porcupine *Hystrix africaeaustralis*: an ecological perspective

R.J. van Aarde

Mammal Research Institute, University of Pretoria, 0002 Pretoria, South Africa.

Cape porcupines, Hystrix africaeaustralis, *apparently have a wide ecological tolerance and are found extensively throughout Southern Africa. These fossorial hystricomorph rodents are monogamous, live in extended family groups, breed seasonally in summer rainfall areas, and adult pairs produce only a single litter each year. A litter interval of about one year is maintained through lactational anoestrus, lasting about 100 days followed by three to seven 'sterile' oestrous cycles, each lasting about 30 days. Changes in the age at first successful reproduction appear to be the most important result of a change in density, and regulation of numbers probably results from the effect(s) of social factors on reproductive output.*

Ystervarke, Hystrix africaeaustralis, *het oënskynlik 'n aansienlike ekologiese toleransie en is regoor Suider-Afrika versprei. Hierdie fossoriale histrikomorfe knaagdiersoort is monogamies, bly in uitgebreide familiegroepe, teel seisoenaal in die die somerreënvalstreke, en volgroeide pare produseer net een werpsel per jaar. 'n Werpselinterval van ongeveer 'n jaar word gekenmerk deur 'n laktasie-anestrus van ongeveer 100 dae, gevolg deur drie tot sewe 'steriele' estrussiklussè wat elk ongeveer 30 dae duur. Veranderings in die ouderdom waarop met welslae geteel word, blyk die belangrikste gevolg van veranderings in hul bevolkingsdigtheid te wees en die regulering van getalle kan waarskynlik toegeskryf word aan die invloed wat sosiale faktore op die voorplantingslewering het.*

Cape porcupines, *Hystrix africaeaustralis*, are catholic in their habitat requirements and are found commonly throughout Southern Africa, where crop-producing farmers often regard them as a nuisance and indigenous people favour their meat. They live in extended family groups and may attain an age of 20 years[1] in captivity. Males and females are similar in size, weigh 12 to 18 kg when adult[2] and attain sexual maturity during the first or second year of life.[3,4] Furthermore, porcupines are monogamous,[5] breed seasonally in summer rainfall areas,[3] and adult pairs produce only one litter per year.

Environmental and social factors are known to affect reproduction in mammals, and the reproductive performance, especially of rodents, is strongly influenced by social stimuli (see Bronson[6] for a review). The inhibition or stimulation of, for instance, sexual maturation and adult reproductive performance by social factors, which may operate in a density-dependent way, would not only affect recruitment but would conceivably also contribute to population regulation.

This paper describes some of the reproductive characteristics of the Cape porcupine in an attempt to illustrate how physiological and behavioural mechanisms that affect the reproductive output of groups of porcupines may contribute to the regulation of population size. This review is based on information obtained from groups of porcupines kept in captivity,[7] and from free-ranging porcupines killed every 2 months between February 1977 and January 1978 (n = 82) and from July 1981 to July i982 (n = 118). Information regarding social organization was obtained from captive animals, from porcupines trapped at their burrows at various localities in the Karoo and from animals observed foraging at night on the Tussen-die-Riviere game farm situated at the confluence of the Orange and Caledon rivers (30°25′S, 26°12′E).

The analyses of data and processing of collected material have been reported elsewhere[2–5,8,9] and will therefore not be repeated. Results are given as means ± one standard deviation of the mean.

Factors affecting reproductive output

Seasonality.

Free-ranging males are reproductively active throughout the year,[4] whereas females subjected to seasonal climatic changes in the Karoo reproduced seasonally, young being born during the relatively wet summer months from August to March.[10] Captive porcupines produce litters throughout the year, but most litters (78,7%, n = 165) are born between August and March.[3] Females are polyoestrous but do not experience oestrus during lactation, which lasts about 3,5 months ($\bar{x}$ = 101 ± 37,8 days, n = 9).[3]

Normal cyclic ovarian activity begins 2 to 42 days after the end of lactation,[3] but three to seven cycles elapse before conception,[10] each of these lasting about one month ($\bar{x}$ = 32,3 ± 4,6 days, n = 18).[3] The hormonal basis for these 'sterile' cycles is still not known, although progesterone concentrations during matings followed by conception ($\bar{x}$ = 3,2 ± 1,0 ng/ml, n = 3) were significantly higher (P<0,01) than values recorded on days of 'sterile' matings ($\bar{x}$ = 0,9 ± 0,5 ng/ml, n = 6).[11]

Litter interval

Females typically conceive only once a year and the interval between litters is approximately one year (gestation length = 93 days, lactational anoestrus = 101 ± 37,8 days, periods of 'sterile' cycles = 90 – 210 days).[3] Twenty-five intervals between litters recorded for parous females varied from 110 to 500 days, but young born after a litter interval of less than 200 days (n = 3) did not survive. The mean litter interval for surviving young was 345 ± 66 days (n = 22).

It should thus be noted that despite the ideal conditions under which the porcupines were kept, only three of 25 intervals were less than 200 days. Females may therefore conceive while lactating or even during the first post-lactational oestrus. The deaths of the litters conceived during or just after lactation were not due to physiological limitations of the mother, but were the result of interference from members of the preceding litter, who actively prevented the newborn from sucking. To produce a litter with a high chance of survival, therefore, females must conceive at about yearly intervals. As free-ranging porcupines breed seasonally, one would expect selection to favour females that possess a mechanism that results in a litter interval of about one year. In porcupines this is achieved by lactational anoestrus followed by a variable number of 'sterile' cycles. The factors dictating seasonal breeding in free-ranging porcupines are still not known. However, seasonality, the relatively long interval between litters and small litter size ($\bar{x}$ = 1,5 ± 0,66, n = 165)[3], possibly limit annual and life-time reproductivity.

Group living

Cape porcupines maintained in captivity were observed to be monogamous.[5] Continual sexual activity, even during pregnancy, serves as a mechanism enhancing pair-bonding.[5] Only the adult pair in extended family groups reproduces and observations on eight pairs over a 5-year period indicated that each pair produced only one litter per year, its size varying from one to three.

Free-ranging porcupines usually forage alone, but 40 (29%) of the 138 animals encountered at night on the Tussen-die-Riviere game farm were active in groups of two or three. Seven of the 14 pairs encountered comprised an adult male and adult female. The occurrence of these pairs could not be ascribed to 'sexual attraction' for mating purposes as three of these females were pregnant, three in anoestrus (two of them lactating) and one in oestrus. These observations suggest that Cape porcupines live in pairs under natural conditions. This has been confirmed by observations on groups captured at their burrows.[12]

The other seven pairs encountered consisted of an adult male and a juvenile foraging together, the latter varying in age from two to five months. Juveniles start to forage on their own only when older than five months. All groups comprising three animals consisted of an adult male, adult female and a juvenile. An adult female has never been recorded as accompanying young in the absence of a male. It therefore appears that paired males contribute to some extent to the raising of their young, presumably not only when escorting them on foraging excursions, but also by attacking conspecific intruders (unpublished observation). Observations on captive groups support the conclusion that males and females contribute to the raising of their young.

Females housed in isolation from males do not experience cyclic ovarian activity even when continuously exposed to the odours of males (the latter kept in open pens next to the females). This suggests that physical contact between the sexes is required to initiate and maintain cycles of ovarian activity.

Females kept in their natal groups do display ovarian cycles but do not reproduce.[3] They will, however, breed when removed from these groups, and so dispersal appears to be a prerequisite for reproduction.

Regulation of numbers

Understanding the mechanisms responsible for the regulation of population numbers has been a major biological issue for decades.[13-15] In spite of this, it is accepted as axiomatic that populations reach the carrying capacity of their environmental conditions, and that reproductive rates are often negatively correlated with density. The discovery of compensatory mortality and changes in the quality of individuals with variations in density[16] renders the concept of density dependence less useful in explaining why populations do not increase in an unlimited fashion. Krebs[13] therefore suggested that the factors involved in maintaining stable populations can only be evaluated through the manipulation of numbers. For instance, by artificially reducing numbers (density) and quantifying the effect of this on demographic characteristics, insight may be gained into the mechanisms underlying population changes and regulation.

In the case of Cape porcupines, we recently had the opportunity to quantify the effect of an artificial reduction in numbers on factors such as age structure, age-specific survival and fecundity.[12] The opportunity arose through the decision to conduct a culling programme on the porcupine population of the Tussen-die-Riviere game farm.

The population probably originated from animals occupying the area when it was fenced off as a game farm. No large carnivores have been recorded there since its establishment in 1967; therefore, for a period of 10 years before the first culling operation (January 1977 to February 1978), porcupines were not subject to predation. The second culling operation was conducted from July 1981 to July 1982.

Analyses of the age structures of the two sub-samples were based on the assumption that the standing age distribution (the number of animals in each age class relative to the number of newborn at the time of culling) represented a stable age distribution. The age-specific probability of survival, probability of dying, mortality rates and fecundity rates were calculated, as described by the present author.[12] Age determination was based on the age-specific sequence of tooth eruption and replacement.[8]

The standing age distribution changed significantly ($\chi^2_1 = 21{,}5$; $P < 0{,}001$) after the artificial reduction in density, with the contribution of the first year age class increasing from 32,2 to 46,2%. As climatic variables over the study period remained the same, it therefore seems as if the reduction in density resulted in the population becoming 'younger'. Because age-specific survival rates also did not change, this shift in age distribution can only be ascribed to a difference in age-specific fecundity rates; a notion confirmed by observation.[12]

Females in the first-year age class did not reproduce before the reduction in density, but thereafter, 100 females in this age group produced 56 surviving female offspring.[12] The fecundity of the other age groups was also higher after the reduction in density,[12] this conceivably affecting population growth rate and thus population stability.

Since it appears that the most important response of the porcupine population to the reduction in density was a change in age-specific fecundity, the question that arises is how this was effected. Reproductive output is limited by monogamy and seasonality and animals do not reproduce in their natal groups, so it can only mean that the observed reduction in age at first breeding resulted from a shortened period of social inhibition of reproduction, mainly due to increased opportunities for dispersal.

Porcupine numbers therefore appear to be regulated through social factors affecting reproduction. A decrease in density probably permits offspring to leave their natal warrens sooner, resulting in a reduced age at first reproduction and an increase in the population growth rate. It also appears that the age at which the animals first produce offspring and juvenile survival are the most important demographic factors responsible for population changes, implying that the regulation of their numbers under the conditions of the present experiment, or in the absence of predators, is density dependent and brought about by social factors that provide a 'self-regulating mechanism'.

Financial support was provided by the University of Pretoria, the CSIR Foundation for Research Development, and the Transvaal Branch of the Wildlife Society of Southern Africa. Assistance and hospitality received from the Nature Conservation and Management Branch of the Provincial Administration of the Orange Free State is gratefully acknowledged. Mr Denvin Majola was responsible for the maintenance of the captive porcupine colony.

1. Kingdon J. (1974). *East African Mammals: An Atlas of Evolution in Africa*, vol. 2, part B. Academic Press, London.
2. Van Aarde R.J. (1987). Pre- and postnatal growth of the porcupine *Hystrix africaeaustralis*. *J. Zool. (Lond.* **211**, 25 – 33.
3. Van Aarde R.J. (1985). Reproduction in captive female Cape porcupines (*Hystrix africaeaustralis*). *J. Reprod. Fert.* **75**, 577 – 582.
4. Van Aarde R.J. and Skinner J.D. (1986). Reproductive biology of the male Cape porcupine, *Hystrix africaeaustralis*. *J. Reprod. Fert.* **76**, 545 – 552.
5. Morris D. and Van Aarde R.J. (1985). Sexual behaviour of the female porcupine *Hystrix africaeaustralis*. *Horm. Behav.* **19**, 400 – 412.
6. Bronson F.H. (1985). Mammalian reproduction: an ecological perspective. *Biol. Reprod.* **32**, 1 – 26.
7. Van Aarde R.J. (1985). Husbandry and immobilization of captive porcupines (*Hystrix africaeaustralis*). *S. Afr. J. Wildl. Res.* **15**, 77 – 79.
8. Van Aarde R.J. (1985). Age determination of Cape porcupines *Hystrix africaeaustralis*. *S. Afr. J. Zool.* **20**, 232 – 236.
9. Van Aarde R.J. (1985). Circulating progesterone and oestradiol-17β concentrations in cyclic Cape porcupine, *Hystrix africaeaustralis*. *J. Reprod. Fert.* **75**, 583 – 591.

10. Skinner J.D., Van Aarde R.J. and Van Jaarsveld A.S. (1984). Adaptations in three species of large mammals (*Antidorcas marsupialis, Hystrix africaeaustralis, Hyaena brunnea*) to arid environments. *S. Afr. J. Zool.* **19**, 82–86.
11. Van Aarde R.J. and Potgieter H.C. (1986). Circulating progesterone, progesteron-binding proteins and oestradiol-17 in the pregnant Cape porcupine, *Hystrix africaeaustralis*. *J. Reprod. Fert.* **76**, 561–567.
12. Van Aarde R.J. (in press). Demography of a Cape porcupine *Hystrix africaeaustralis* population. *J. Zool.* (*Lond.*).
13. Krebs C.J. (1978). A review of the Chitty hypothesis of population regulation. *Can. J. Zool.* **12**, 2463–2480.
14. Stickel L.F. (1979). Population ecology of house mice in unstable habitats. *J. Anim. Ecol.* **48**, 871–887.
15. Elseth G.D. and Baumgardner K.D. (1981). *Population Biology*. Van Nostrand, London.
16. Chitty D. (1960). Population processes in the vole and their relevance to general theory. *Can. J. Zool.* **38**, 99–113.