

Demography of a Cape porcupine, *Hystrix africaeaustralis*, population

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(Accepted 17 February 1987)

(With 2 figures in the text)

The Cape porcupine is a large (12.0 kg), nocturnal hystricomorph rodent and widely distributed throughout southern Africa. The present paper examines age-specific survival, mortality and fecundity rates in a population, evaluates the roles of possible density-dependent changes of population parameters in the regulation of porcupine numbers, and describes the life history strategy of the species. The study is based on data sets obtained from animals collected during 1977/78 and during 1981/82. Changes in demographic characteristics are ascribed to an artificial reduction in density, resulting in the relaxation of social factors inhibiting reproduction in young adults.

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Introduction

Cape porcupines, *Hystrix africaeaustralis*, appear to have a wide ecological tolerance since they occur in most habitats throughout southern Africa. Porcupines are large (12 kg; van Aarde, 1987) hystricomorph rodents, attain sexual maturity during their second year of life (van Aarde, 1985a; van Aarde & Skinner, 1986), are monogamous (Morris & van Aarde, 1985), breed seasonally in summer rainfall areas (van Aarde, 1985a), live in extended family groups, and can live for up to 20 years in captivity (Kingdon, 1974). Litter size varies from 1–3, and adult pairs produce only a single litter per year (van Aarde, 1985a). No information has as yet been published on their population biology.

The artificial reduction of the numbers of porcupines on the Tussen-die-Riviere Game Farm (30°25'S, 26°12'E), as part of a management programme, provided the material required for defining demographic characteristics of the population. The present paper reports on age-specific

survival, mortality and fecundity rates, and seasonal changes of the age structure of the population. Furthermore, it attempts to evaluate the role of possible density-dependent changes of population parameters in the regulation of population size, and describes the life history strategy of the species.

Study area

The Tussen-die-Riviere Game Farm, is situated at the confluence of the Orange and Caledon rivers in the False Upper Karoo Veld Type of South Africa. The area is subjected to seasonal climatic conditions and is defined as arid, with the summer rainy season extending from November to April. The average annual rainfall has been recorded at 440 mm (Werger, 1980). The average daily minimum temperature is 0.1°C for the coldest month (July) and the average maximum daily temperature for the hottest month (January) is 31.2 °C (Werger, 1973).

The porcupine population living there probably originated from porcupines present within the area when it was fenced (22,000 ha) as a Game Farm. No large carnivores lived on the Game Farm since its inception during 1967 and thus, for about 20 years before the study, porcupines were not exposed to predation or culling operations.

Material and methods

As part of a management programme, all porcupines encountered at night in the beam of a spotlight were killed at bimonthly intervals between February 1977 and January 1978 ($n=82$) and from July 1981 to July 1982 ($n=118$). Dead porcupines were weighed, sexed, and female reproductive tracts were inspected macroscopically for implantations and placental scars. Foetal ages were determined as described by van Aarde (1987), and conception and birth dates for each litter were calculated as the sampling date minus foetal age and the conception date plus 93 days (gestation period), respectively.

Examination of maxillar tooththrows provided an opportunity to assign each specimen to 1 of 9 dental age classes. Chronological age was assigned to 6 of these on the basis of the age-specific sequence of tooth eruption and replacement recorded in known-age specimens ($n=23$; see van Aarde, 1985*b*).

Analyses of the age structures of the 2 subsamples were based on the assumption that the standing age distribution (the number of animals relative to the number of new-born in each age class at the time of culling) represented a stable age distribution. Age-specific probability of surviving (l_x), probability of dying (d_x), mortality rates (q_x) and fecundity rates (m_x) were calculated following Caughley (1977). The calculation of net reproductive rates (R_0) (Elseth & Baumgardner, 1981) was based on the assumption that the probability of survival of adults (l_3-l_{10}) decreases constantly with age (x) (see Silver, 1979), that longevity in the wild is 10 years and that fecundity rate (m_x) for porcupines older than 24 months of age (m_3-m_{10}) remained constant. It is believed that the interval between sampling (3 years) was enough to allow the age distribution to converge to stability.

Information on social organization was obtained from captive animals (see Morris & van Aarde, 1985; van Aarde, 1985*c*), from porcupines trapped at their burrows at various localities in the Karoo, and from porcupines observed foraging at night on the Tussen-die-Riviere Game Farm.

All means are followed by one standard deviation (\pm S.D.) of the mean, unless otherwise indicated.

Results

Fecundity

Extrapolation of birth dates based on the estimated ages of foetuses on the date of collection suggests that all births occurred from August to March, with a peak in January. The mean date of

TABLE I

Age-specific fecundity schedules for the porcupine population on the Tussen-die-Riviere Game Farm, based on the assumption that litter size at birth equals litter size in captivity. (Sample sizes included in parenthesis)

Age (months)	Percentage reproductively active during breeding season		Female births per female per season (m_x)	
	1977/78	1981/82	1977/78	1981/82
< 6	0.0 (5)	0.0 (18)	0.00	0.00
> 6 ≤ 12	0.0 (5)	75.0 (4)	0.00	0.56
> 12 ≤ 24	63.6 (11)	88.9 (9)	0.48	0.67
> 24	88.2 (17)	95.7 (22)	0.66	0.72

birth for 19 litters was 21 December \pm 18.6 (S.E.) days. Litter size at birth for free-ranging females is unknown, but their prenatal litter size was similar to that in captive females ($\bar{x} = 1.5 \pm 0.66$; $n = 165$). Moreover, placental scars recorded in 28 free-ranging lactating females averaged 1.4 ± 0.5 . Sex ratio at birth did not deviate from unity ($\chi^2 = 0.55$; $n = 23$) and the average annual incidence of pregnancy (Caughley, 1977) was 1.2, suggesting that free-ranging females produced one litter per year.

Age-specific fecundity schedules (m_x) based on the information given above and the frequency of occurrence of reproductively active females is provided in Table I. None of the females > 6 months and ≤ 12 months collected during 1977/78 were reproductively active, while three of four females in this age class reproduced during 1981/82 (Table I). Age-specific fecundity for other age classes were also higher during 1981/82 than during 1977/78 (see Table I). The average annual production of female offspring per female older than six months was 0.49 in 1977/78 and 0.69 in 1981/82.

Age structure

Age composition of both the 1977/78 and 1981/82 populations changed seasonally, and differed considerably from each other (Fig. 1). The biphasic pattern in the presence of porcupines ≤ 12 months of age during 1977/78 was not evident during 1981/82 (Fig. 1). The monthly contribution of the first year age class to the total subsample varied from 14.3–15.5% ($\bar{x} = 32 \pm 16.9\%$; $n = 6$) during 1977/78 and from 42.0–55.5% ($\bar{x} = 46.2 \pm 8.5\%$; $n = 6$) in 1981/82. Standing age distribution of male and female cohorts was similar during both sampling periods ($\chi^2 = 0.74$ and 1.51, respectively; $d.f. = 3$). Pooled data for the sexes indicate a significant difference ($\chi^2 = 21.5$; $P < 0.001$; $d.f. = 7$) in the age structures of the two subsamples. This difference was also significant ($\chi^2 = 10.8$; $P < 0.05$; $d.f. = 3$) when reducing the nine dental age classes to four chronological age classes (< 6 months, 6–12 months, > 12–24 months, and > 24 months).

Survival and mortality rates

Data on age-specific probability of survival (l_x), probability of dying (d_x) and mortality rate (q_x) are provided in Table II. Life table statistics suggest a low mortality rate during the first two months of life, which increased to 0.445 and 0.669 during the first year of life (Table II). The

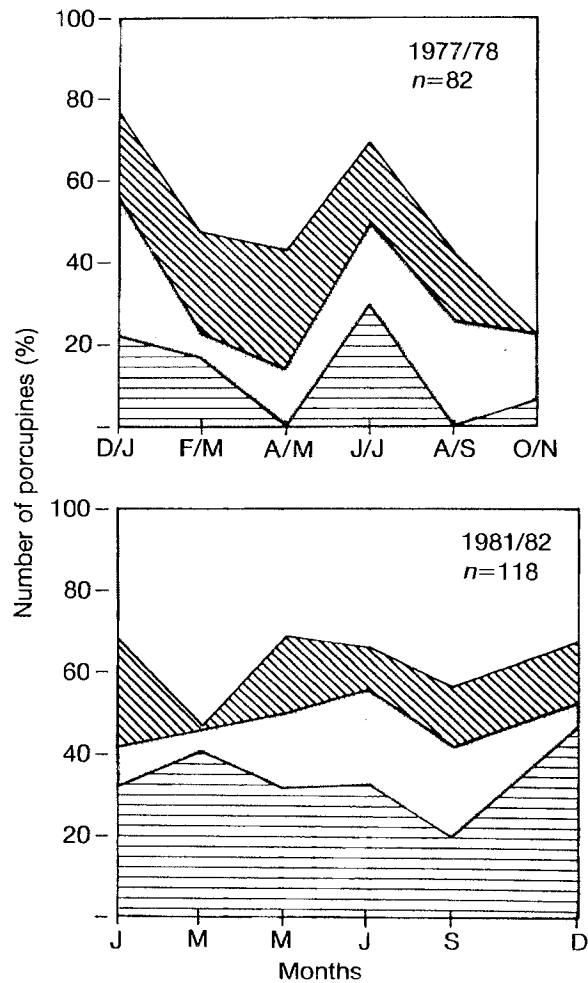


FIG. 1. Seasonal changes in the age structures of the porcupine population on the Tussen-die-Riviere Game Farm as reflected by subsamples collected between February 1977 and January 1978 ($n=82$) and between September 1981 and July 1982 ($n=118$). \square = < 6 months; \square = > 6 \leq 12 months; \square = > 12 \leq 24 months; \square = > 24 months.

probability of surviving to an age of 18 months was 0.464 and 0.331 during 1977/78 and 1981/82, respectively.

Apparent differences in net reproductive rates between the two subsamples, using the equation $R_0 = \sum l_x m_x$ (see Elseth & Baumgardner, 1981), mainly result from an earlier age at first reproduction during 1981/82 rather than during 1977/78 (Fig. 2).

Social organization

Most (89.3%) porcupines encountered foraging ($n=118$) at night were solitary. Groups comprising two individuals were seen on seven occasions, while three individuals foraging together were seen twice only. Three of the seven pairs comprised one adult male and one adult female (all females pregnant), while other pairs ($n=4$) comprised an adult male and a juvenile, 2.5–5.5

TABLE II

Age-specific probability of surviving (l_x) and dying (d_x) for the 1977/78 and 1981/82 porcupine populations based on the assumption that the standing age distribution equals temporal age distribution. (See Caughley for definitions)

Age (months) (x)	Median age (months) (x+x+1/2)	Frequency* (f_x)		Probability of surviving (l_x)		Probability of dying (d_x)		Mortality rate (q_x)	
		1977/78	81/82	1977/78	81/82	1977/78	81/82	1977/78	81/82
0-2	1	32.3**	51.4**	1.000	1.000****	0.164	0.000	0.164	0.000
> 2 ≤ 12	7	27.0	53.0***	0.836	1.000	0.372	0.669	0.445	0.669
> 12 ≤ 24	18	15.0	17.0	0.464	0.331	—	—	—	—
> 24		38.0	48.0	—	—	—	—	—	—

* Age-specific sex ratios did not differ significantly and data for males and females were therefore combined

** Estimated from age-specific fecundity schedules and presents the expected number of new-born females within the subsamples

*** 13.64% of females in this class were reproductively active and m_x thus 0.102

**** f_x at $x+1$ larger than at x and l_x thus 1.000

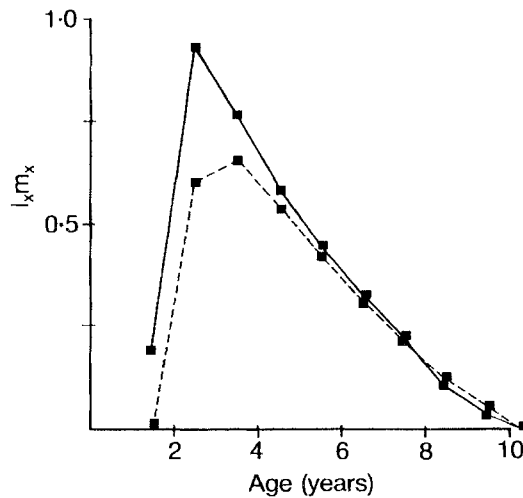


FIG. 2. Age-specific changes in $l_x m_x$ values for the porcupine population on the Tussen-die-Riviere Game Farm, illustrating that differences in net reproductive rates between the two subsamples resulted from an earlier age at first reproduction during 1981/82 (■---■) than during 1977/78 (■----■).

months of age. Both groups of three comprised an adult male, an adult female and a juvenile. All adult males encountered in groups were more than 24 months of age.

Groups trapped at the same burrows comprised an adult male and an adult female ($n=4$), an adult male and a juvenile ($n=3$), juveniles only ($n=2$), an adult male, adult female and a juvenile ($n=2$) and an adult male, adult female, two subadults and two juveniles ($n=2$). It is not known if all animals in each group were caught.

The number of reproducing females in captive groups corresponded to the number of adult males present within the group. Only one of two females housed with a male ($n=4$ groups) reproduced over a two-year-period. This was also the case when three females were housed with one adult male ($n=2$ groups). In two cases where two adult females were housed with two adult males, both females reproduced.

None of the three females kept in natal groups up to the age of three years reproduced, in spite of regular cyclic ovarian activity and the presence of unrelated males. They, however, reproduced within six months after being separated from their natal groups. Incest was never recorded.

Discussion

Harvesting has become an important measure in the management of confined mammal populations. In spite of several shortcomings in data obtained during such operations (i.e. non-random sampling, and insufficient sample sizes), scientists studying population dynamics have little other material on which to rely. Moreover, relatively little is known about the dynamics and regulation of African mammal populations.

Mechanisms of population regulation have been widely discussed for decades (see Krebs, 1978 for references), and it is accepted, as a general axiom, that populations reach equilibrium under particular environmental conditions, with rates of reproduction and mortality being affected by density (Krebs, 1985). Krebs (1978) suggested that the factors involved in maintaining stability in populations can best be evaluated through the manipulation of numbers. By artificially reducing numbers (density), and by quantifying the effect(s) of this manipulation on demographic characteristics, as attempted in the present analysis, insight may be gained into the mechanisms underlying the regulation of numbers and thus the long-term stability in density.

In spite of the inability to assign annual age classes to porcupines older than 24 months (see van Aarde, 1985*b*), which precluded the derivation of full life tables, and limited sample sizes, the present investigation suggests important differences in certain demographic characteristics between the 1977/78 and 1981/82 subsample. Changes in age-specific fecundity and first year survival may be attributed to environmental changes but rainfall figures for the sampling periods, and presumably therefore primary productivity, do not support such a hypothesis. Forces responsible for the observed differences may be explained in terms of changes in population densities, induced by the first culling operation, as follows:

Porcupines live in extended family groups where each group comprises at least an adult male, one adult reproducing female and a varying number of siblings. Both parents take care of the young, and males, actively protecting young against intruders (van Aarde, unpubl. obs.), accompany them during foraging excursions for the first few months of life. This may contribute to high juvenile survival rates during the early stages of life (see Table II).

Age-specific fecundity rates (Table I) during 1981/82 (after reduction in density) were higher than during 1977/78. Reproductive activity also commenced at an earlier age during 1981/82 than during 1977/78. Considering that reproduction is limited by monogamy, is seasonal and that dispersal of young may be reduced as a result of high density, population reduction could have resulted in an earlier age at first reproduction and thus the increase in age-specific fecundity. Unfortunately, sample size for females 6–12 months of age are insufficient to show statistically significant change in age-specific fecundity rates. The observed trend is nevertheless of interest and the conclusion that age-specific fecundity is a factor of density should be considered cautiously.

It thus appears that the most important response of the studied population to the reduction in density was a change in age-specific productivity, which would conceivably affect population growth rate. The present analysis thus suggests that porcupine numbers are, at least partly, regulated through social factors affecting reproductive activity. It appears that age at first reproduction is the most important demographic mechanism responsible for population changes, implying that the regulation of their numbers under the conditions of the present examination, i.e. in the absence of predators, is density-dependent.

The relationship between habitat, ecological strategies and population parameters can be explained in terms of r- and K-selection and this approach features prominently in the analysis of life-history tactics (Stearns, 1976). K-selection is geared towards the efficient use of environmental resources and favours interparity, an extended life-span, delayed sexual maturity, small litters, large body size and intensive parental care (Pianka, 1970).

The porcupine, a relatively large rodent with a long gestation period (93 days), small litter size and a long life-span (van Aarde, 1985*a, b*), may be considered a K-strategist. This is supported by the analysis of the demographic characteristics of the free-ranging population studied during the present investigation, which suggests that density is regulated by the dependence of reproductive activity on social factors. Other reproductive attributes, such as the extended lactation period, low offspring:adult weight ratio and intensive parental care, support a reproductive strategy that involves a large parental investment in a small number of offspring. This predicts a high chance of survival for each offspring as shown during this investigation.

Summary

Cape porcupines *Hystrix africaeaustralis* apparently have a wide ecological tolerance and occur commonly in most habitat types throughout the southern African subregion. The present paper describes demographic characteristics of a population inhabiting the Tussen-die-Riviere Game Farm situated in the False Upper Karoo (South Africa). This analysis is based on two independent subsamples collected at bimonthly intervals during 1977/78 and 1981/82, the first representing a population not exposed to natural or artificial predation for 20 years, and the second a population 3-5 years after a reduction in density.

A comparison of statistics derived from the two subsamples revealed a change in age structure and age-specific fecundity rates. The increase in the age-specific fecundity rates is ascribed to a reduction in age at sexual maturity which would affect net reproductive rate and population growth rate.

A decrease in density conceivably permitted offspring to disperse from their family groups and, considering that reproduction within a group is limited to parents, dispersal due to 'vacancies' created by the first culling operation may explain the earlier age at first reproduction thereafter. It thus appears that age at first reproduction is the most important mechanism responsible for changes in population growth rates, suggesting that regulation of numbers results from the effect(s) of social factors on reproductive output.

Financial support was provided by the University of Pretoria, and the Council for Scientific and Industrial Research. Assistance and hospitality received from the Nature Conservation and Management Branch of the Provincial Administration of the Orange Free State is gratefully acknowledged. Messrs M. Haupt, D. Majola and W. Nel provided technical assistance. This formed part of a wider study for a doctoral thesis for which I was the recipient of the Maberly Memorial Scholarship of the Transvaal Branch of the Wildlife Society of Southern Africa.

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