AN ECOLOGICAL PERSPECTIVE OF REPRODUCTION IN THE CAPE PORCUPINE

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SUMMARY

Cape porcupines *Hystrix africaeaustralis* occur throughout southern Africa and their resistance and resilience to disturbances is ascribed to the response of reproductive mechanisms to perturbations. In the Cape porcupine physical contact between the sexes maintains cyclic ovarian activity and pair-bonding. Group formation and maintenance are a prerequisite for conception, and only one female in a group reproduces. However, porcupine females do have the ability to compensate for the loss of litters by conceiving within a few days of such loss. Dispersal of young from their natal colonies is a prerequisite for reproduction. Such dispersal, stimulated by the artificial reduction in density, may give rise to a decrease in the age of first reproduction and thus an increase in population growth rate in response to disturbance.

INTRODUCTION

Cape porcupines *Hystrix africaeaustralis* are common in tropical forests, woodlands, savannas, grasslands, semi-arid and deserts throughout the southern African Subregion. The high densities (up to 25 individuals km^{-2} on riverine plains in the Karoo; Van Aarde, 1984) at which porcupines can occur suggests that they may play an important role in the structure and function of their natural environment. They mainly feed on subterranean tubers and bulbs (De Villiers, 1992), and surface disturbances brought about by their foraging activities benefit plant rejuvenation and seed germination (Gutterman & Herr, 1981; Dean & Milton, 1991). Their habit of ringbarking selected trees apparently assists in the maintenance of savannas as mosaics of grasslands and woodland patches undergoing cyclical succession (Yeaton, 1988).

The damage porcupines cause to crops, and their value as a source of meat to indigenous people, leave them vulnerable to hunting, trapping and snaring in agricultural areas throughout southern Africa. The ability of porcupine populations to withstand these onslaughts, as well as that caused by natural predation (often lion and leopard) under a wide range of environmental conditions, may be explained in terms of their reproductive biology. The present review therefore centres on the consequences of sociality and population disruptions for the reproductive biology of the Cape porcupine. This review is based on my own published research and those of several postgraduate students supervised by me over a period of 12 years.

MATERIALS AND METHODS

Data on the population biology and reproduction of free-ranging porcupines were collected as described by Van Aarde (1984, 1985a,b, 1987a). De Villiers (1992) and De Villiers *et al.* (1994) described our studies on habitat utilisation and diet, while information on social organisation

and home range use were obtained as described by Corbet (1991) and Corbet & Van Aarde (1996). Captive colonies were maintained at the University of Pretoria's animal experimental facility and all experimental procedures have been sanctioned by the ethical committee of the university. The maintenance of these colonies and the experimental procedures relevant to the present review have been reported on in several papers (Morris & Van Aarde, 1985; Van Aarde, 1985c, 1987a,b,c; Van Wyk, 1991; Van Wyk & Van Aarde, 1991; Van Aarde & Van Wyk, 1991; Van Wyk *et al.*, 1994; White, 1994).

RESULTS AND DISCUSSION

Space use

Local movement is affected by season, but the home ranges of adult pairs of porcupines studied in the Nylsvley Nature Reserve extended over the same general location throughout the year (Corbet & Van Aarde, 1996). Most activity occurred in a relatively small portion of the large home range. Home ranges of adjacent groups overlapped little and neighbours rarely encountered one another in the areas of overlap. This pattern of space use suggests territoriality, with territories being shared by adult pairs and probably maintained through scent marking (Corbet & Van Aarde, 1996). Males are known to scent-mark more in frequently visited feeding patches than in other areas (De Villiers *et al.*, 1994). Mature offspring may stay in the natal group when dispersion opportunities are limited (Van Aarde, 1987c; Corbet & Van Aarde, 1996), thereby giving rise to the development of extended family units.

Home range areas do not always occupy exactly the same position from month to month, and territorial boundaries do not appear to be permanent or rigidly defined (Corbet, 1991). The large, non-exclusive areas surrounding a smaller exclusive core area may serve as a buffer zone between neighbouring territories. It also may allow individuals to shift their centres of activity in response to short-term changes in local resource availability without incurring territorial disputes.

Group living for porcupines probably provides opportunity for the cooperative maintenance of territories. An incident in which a burrow was taken over immediately following the death of one pair member suggests that the pair-bond may provide an extra incentive to maintain a territory, even if both pair members are not directly engaged in territorial maintenance (Corbet & Van Aarde, 1996).

The social system

Family groups appear to be typical of the social organisation of the Cape porcupine (Shortridge, 1934; Van Aarde, 1987c; Corbet & Van Aarde, 1996). Both Shortridge (1934) and Van Aarde (1987c) observed up to 14 individuals sharing a burrow. Van Aarde (1987c) recorded two extended family groups in the semi-arid Karoo region of South Africa, each consisting of an adult pair, two subadults and two juveniles. Thus a family group may develop as a result of immature offspring remaining with the parental pair.

Group members share a burrow, and it is thought that the primary advantage for this group living is energy conservation from huddling (Haim *et al.*, 1990; Haim *et al.*, 1992). This is most important for newborn offspring as they do not leave the burrow for the first 9 weeks – they thus may be able to allocate more energy, otherwise spent on thermoregulation, to growth (Haim *et al.*, 1992). The sharing of burrows also reduces vulnerability of the offspring and encourages cooperative rearing.

Cape porcupines, like crested porcupines (*H. cristata*) and Indian porcupines (*H. indica*),

are monogamous ((Morris & Van Aarde, 1985; Sever & Mendelssohn, 1988; Pigozzi, 1987). Male and female Cape porcupines are similar in body size and their monogamous pair-bond breeding system favours a lack of sexual dimorphism imposed through sexual selection (Van Aarde, 1987b). Few mammalian species (3%) are monogamous and monogamy is expected to evolve only in situations where males are unable to secure relatively exclusive access to more than one female, perhaps due to the pattern of female dispersion coupled with either synchronised oestrus or polyoestrus (Macdonald, 1983; Mock & Fujioka, 1990). However, once monogamous the only way a male can increase his reproductive success, apart from extra-pair matings, is to invest in parental care.

The significance of the pair bond

Like many other monogamous males, male porcupines do care for their offspring by accompanying them on foraging trips, grooming and providing thermoregulatory benefits through huddling (Van Aarde, 1987c; Haim et al., 1992). Experimental trials in captivity also showed that males actively protect the young from intruders.

Cape porcupines housed in pairs in captivity indulge in sexual activity (lordosis, mounting and occasional ejaculation) throughout the oestrous cycle, pregnancy and lactation, but copulation occurs only during oestrus (Morris & Van Aarde, 1985). Copulation during other stages of the cycle is hindered by the presence of a vaginal closure membrane, which usually perforates in synchrony with peak levels in ovarian oestradiol secretion (Van Aarde, 1985d).

The apparent maintenance of the pair-bond through frequent sexual activity (Morris & Van Aarde, 1985), the active participation of males in the raising of offspring (Van Aarde, 1987c) and cohabitation of burrows and territories by the pair (Corbet, 1991; Corbet & Van Aarde, 1996), all indicate that females are almost continuously exposed to sexually mature male porcupines. Considering the potential influence of social factors on ovarian function, possible stress evoked by the absence of a male may be responsible for the impairment in ovarian function in captive females isolated from males (White, 1994). Although the mean length of the ovarian cycles, based on the perforation of the vaginal closure membrane of females kept individually and isolated from males, was similar to those of females that had contact with males, oestrous cycle lengths tend to vary more in females isolated from males than in females housed with males. From this it would appear that the absence of a male does not suppress ovarian activity, but results in greater variability in cycle lengths. However, based on patterns in plasma progesterone levels it is clear that contact between males and females does influence ovarian activity through decreased luteal activity. The lack of distinct luteal phases in the cycles of females isolated from males also implies that ovulation may be affected by the presence of the male. Thus it appears that actual physical contact with males is necessary to sustain regular follicular and luteal activities in females and might be necessary for the ripening of the follicles (White, 1994).

Frequent sexual activity thus may be important to maintain effective ovarian activity and hence successful conception. In captivity, isolation from a partner did not affect pregnancy and all females kept isolated from males did produce offspring (Van Aarde & Potgieter, 1986). The adaptive advantage of the impairment of ovarian function may be considered in terms of the advantage accrued to the female through the presence of the male, not only in territorial defence but also in direct care afforded to the offspring of the pair (Corbet & Van Aarde, 1996)

During a study on the Nylsvley Nature Reserve pairs spent over 50% of their night-time activities within 200 metres from each other. The few interactions recorded between neighbours suggest that extra-pair matings may occur but that these are uncommon and opportunistic as would be expected in a monogamous species. Sever & Mendelssohn (1991) also recorded that

pair members always foraged in close proximity to one another. Such close contact may serve a mate-guarding function since there is no evidence that porcupines cooperate in anti-predator defence or foraging.

The reproductive cycle

The yearly reproductive cycle of the Cape porcupine is characterised by pregnancy (93 days) followed by lactational anoestrus (110 days) and 3–7 "sterile" cycles when oestrus and mating do not result in pregnancy (Van Aarde, 1985c; Skinner *et al.*, 1984) The general pattern of steroid secretion during the 30-day oestrous cycle of females housed with an adult male is that of a surge in plasma oestradiol-17ß concentrations at the time of perforation of the vaginal closure membrane, followed by an increase in plasma progesterone values to peak levels 14 days after the onset of oestrus. The luteal phase characterised by elevated plasma progesterone concentrations (>1ng/ml) represents 22–35 days (93%) of the cycle length of these females (Van Aarde, 1985c).

Atypical of New World hystricomorph rodents, the relatively long gestation period in the Cape porcupine is associated with relatively fast prenatal development and growth (Van Aarde, 1987b) . In pregnant females plasma progesterone concentrations peak 50–60 days after mating and are an order of magnitude higher than those recorded in most mammals other than hystricomorph rodents (Van Aarde & Potgieter, 1986). These high progesterone levels probably result from the protection afforded to it by the high concentrations of progesterone binding globulins being produced by the porcupine (Louw *et al.*, 1992; Van Wyk *et al.*, 1994; Van Wyk *et al.*, 1995).

Captive females do breed throughout most of the year, but in South Africa most litters (78.8%; n=165) are produced between August and March. Free-ranging porcupines reproduce seasonally in summer rainfall areas (Van Aarde, 1985b) and this may maximise neonatal survival, especially in arid regions experiencing cold, dry winters (Skinner *et al.*, 1984). Litter size at birth varies from 1–3 (1.5±0.66; n=165), with most litters (59%) comprising a single offspring (Van Aarde, 1985b).

Reproductive suppression

In the Cape porcupine only the adult pair reproduces (Van Aarde & Van Wyk, 1991). Subordinate females (daughters of the breeding pair) experience cyclic ovarian activity and though incestuous copulations have been recorded, only the dominant female (mother) conceives (Van Aarde, 1985b). The mechanism of reproductive suppression in subordinate porcupines is not fully understood, but their progesterone concentrations, in spite of cyclical changes, apparently remain insufficient for implantation, and thus pregnancy (Van Aarde & Van Wyk, 1991). When comparing progesterone profiles for breeding (dominant) females between the end of lactation and conception with those for non-breeding (subdominant) females, one obvious difference becomes apparent – baseline levels of progesterone in breeding females never drop below 1–2 ng/ml while those in subdominant females always drop to zero at the end of the follicular phase (Van Aarde & Van Wyk, 1991). We still do not know the physiological basis for this difference, but it may be due to differences in the luteotrophic complex, and possibly in prolactin levels. Prolactanaemia may thus be the cause of reproductive suppression, and consequently in the down regulation of progesterone receptors, resulting in the uterus not being prepared to receive the conceptus.

Reproductive suppression should result in mature offspring dispersing from their natal group as soon as possible, thus enabling them to maximise their reproductive opportunities. Extended porcupine family groups thus should only develop where opportunities for dispersal are

restricted. Barriers to dispersal may include a lack of vacant territories as a result of high population densities (Van Aarde, 1987a,b) or limited resources, e.g. food or burrows (Corbet, 1991). Females are dependent on dispersal opportunities before they can start producing their own offspring and, in captivity, conception occurs 70–120 days after separation from a dominant female (Van Aarde & Van Wyk, 1991). Thus, subordinate females do have the potential to reproduce, suggesting that socially induced reproductive suppression in porcupines should be viewed as reproductive delay in response to social environment. Reproductive inhibition can thus be seen as the result of individual selection, with conception only occurring when there is reasonable certainty of reproductive success. Support for this suggestion is provided by our observation that, when young porcupines of different ages are kept in the same enclosure, the youngest always dies due to losing the "battle for the teat". It thus follows that, when more than one litter is produced in a group of porcupines during a breeding season, the youngest litter probably will not survive. It would, therefore, not be to the advantage of a female to breed while living in a group in which another female is reproducing. By delaying her reproductive output until the opportunity arises to disperse from her natal colony, a female will improve her own lifetime reproductive value. But what are the consequences of reproductive suppression for the group?

By modelling group size as a factor of age-specific mortality rates, based on data collected from a free-ranging population (Van Aarde, 1987a), life long reproductive rate, longevity, set at fixed intervals from 14 to 24 years, we could illustrate that reproductive suppression can result in the regulation of group size and thus of the population.

Compensation for pre-weaning mortality

Litter intervals in porcupine mothers suckling their young to the cessation of lactation are governed by the extended period of gestation (93 days), lactation (110 days) and the occurrence of three to seven 30 day long sterile oestrous cycles, resulting in them usually conceiving only once annually. The inability to conceive soon after having suckled surviving young may be ascribed to relatively poor body condition of females nursing their young to weaning age (Van Aarde, 1995).

However, porcupines losing their young prior to weaning have the ability to compensate for such loss by conceiving more than once during a given breeding season (Van Aarde, 1995). This provides the group an opportunity to optimize annual reproductive output by compensating for postnatal and pre-weaning mortality. Conception intervals in porcupines rearing their young to weaning ranged from 210 to 500 days (mean = 340±64.8 days; n=25) and were considerably longer than those for females losing their young before weaning (mean = 148±36.5 days; range = 110–216 days; n=14).The suckling stimulus is known to influence ovarian activity, and the shortening of the conception intervals of females losing their young prior to weaning may result from the sudden interruption of milk flow causing endocrinological changes which initiate ovulation and conception (Van Aarde, 1995).

An ecological perspective

A study on the consequences of a reduction in density for age-specific survival and reproductive rates showed that such a disturbance resulted in little change in survival probabilities but in a major reduction in the age at sexual maturity. As a consequence the estimated intrinsic rate of population increase, based on age structures, survival probabilities and fecundity schedules, nearly doubled (Van Aarde, 1984; Van Aarde, 1987a,c). Based on the reproductive biology of the porcupine we deduced that this doubling in population growth rate in response to the artificial reduction in density resulted from vacancies in space availability, providing non-breed-

ing porcupines opportunities to disperse and thus in the relaxation of reproductive suppression (Van Aarde, 1987a,c). Disturbances in population numbers thus interfere with reproductive suppression as a mechanism which may regulate population size.

The porcupine's resistance and resilience to man-induced disturbances and to predation may be explained in terms of reproductive plasticity, where changes in the social environment induce a response on the reproductive axis. The socially induced delay in reproduction limits population growth, while a relaxation of reproductive suppression, through the creation of dipersal opportunities, enhances population growth rate. Porcupine populations may thus be self regulatory.

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