Habitat utilization by the Cape porcupine *Hystrix africaeaustralis* in a savanna ecosystem

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(With 2 figures in the text)

Habitat utilization on three scales by Cape porcupines (*Hystrix africaeaustralis*) was investigated in a savanna ecosystem at Nylsvley Nature Reserve in the northern Transvaal, South Africa.

On the macroscale, radiotelemetry indicated that porcupines preferred broad-leaf *Burkea* savanna to *Acacia* savanna. The individual variation in macroscale habitat preferences indicates that porcupines may be constrained in their use of habitats by territoriality.

On the intermediate scale, no specific feeding areas within the home ranges of porcupines could be identified by using overlapping radiotelemetry circles.

On the microscale, observations of two leash-walked porcupines indicated that feeding patches are not randomly located but correspond to the distribution of certain plant species important in the diet of porcupines. Patches may be identified or protected by means of scent-marking.

Contents

Introduction

Cape porcupines (*Hystrix africaeaustralis*) are relatively large (12–18 kg; van Aarde, 1987), nocturnal hystricomorph rodents. They eat a wide variety of food items, digging for subterranean plant parts such as tree roots and tubers and also consuming above-ground plant parts such as the shoots of herbs and the stem tissue of trees (de Villiers, 1992). Porcupines appear to have a wide ecological tolerance, occurring throughout southern Africa in diverse habitats (Skinner & Smithers, 1990). In the present study, habitat utilization by these animals was investigated in a savanna ecosystem at Nylsvley Nature Reserve in the northern Transvaal, South Africa.

At this reserve, intensive pattern analysis revealed that the vegetation is highly responsive to nutrients at different levels of vegetation patterns—from a high level involving communities, to a low level involving single trees (Whittaker, Morris & Goodman, 1984). An equilibrium condition exists, with plant species diversity and structural complexity of the savanna community permitting the coexistence of a diverse animal community. This animal community contributes to the maintenance of the richness of the plant community by affecting plant dominance and increasing microsite heterogeneity (Whittaker et al., 1984).

Two scales of patches are evident from the pattern analysis of Whittaker et al. (1984). Macroscale patches correspond to plant communities or habitat types and utilization of these by porcupines was investigated by using radiotelemetry. Microscale patches may be as small as the area occupied by a single tree. Since radiotracking is not sensitive enough to gain information on this scale, microscale habitat utilization was investigated by observing tame, free-ranging porcupines. Telemetry also provided information on intermediate-scale habitat utilization of activity zones or areas of intensive use (Spitz, 1988).

Methods

Study area

Nylsvley Nature Reserve (24° 39′ S, 28° 42′ E) is situated in the northern Transvaal, South Africa, and research was conducted in a 745-ha study area on its south-eastern boundary (Fig. 1). Most of this area comprises a plateau at 1100 m above sea-level, gently sloping down to a floodplain at 1080 m above sea-level. The only prominent outcrop is Maroelakop, at an altitude of 1140 m (Huntley & Morris, 1982). Adjacent to the south-eastern border of the study area is a crop farm, Blindefontein. The remainder of the eastern border is flanked by abandoned farmland while the northern side of the study area borders on a privately-owned nature reserve. The Nyl River flows seasonally through the reserve. Two seasons are distinguishable in the area—a hot, wet season from October to March (summer) and a cool, dry season from April to September (winter). The mean annual temperature is 18·6 °C and the area receives a mean annual rainfall of 630 mm, 80% of which falls in the hot, wet months (Huntley & Morris, 1982).

The study area comprises 4 prominent plant communities, described in detail by Coetzee et al. (1976) (Fig. 2):

Burkea savanna (*Eragrostis pallens–Dombeya rotundifolia* variation). Sixty-five percent of the study area comprises a broadleaf deciduous woodland community, of which this is the dominant variation. The community occurs on deeper latosols which are relatively nutrient-poor and has a high plant species diversity.

Rocky outcrop savanna (*Barleria bremekampii–Diplorhynchus* savanna). Seventeen percent of the study area comprises a second broadleaf tree savanna which occurs exclusively on rocky outcrops with lithosols without distinguishable soil horizons.

Floodplain (*Aristida bipartita–Setaria woodii* savanna). This community, which is mostly grassland, occupies a belt of self-mulching, black vertic soil.

Acacia savanna (*Acacia* spp.—*Eragrostis lehmanniana* savanna). Small patches of leptophyllous thorn savanna occur on relatively nutrient-rich latosols and may owe their origin to pastoral settlements abandoned in 1925 (Huntley & Morris, 1982).

Radiotelemetry

Eight adult porcupines trapped in the study area were immobilized by a combination of ketamine hydrochloride (Ketalar: Parke-Davis Laboratories (Pty) Ltd., Isando) and xylazine hydrochloride (Rompun: Bayer Pharmaceuticals (S.A.) (Pty) Ltd., Johannesburg) following van Aarde (1985a). Collars with Telonics
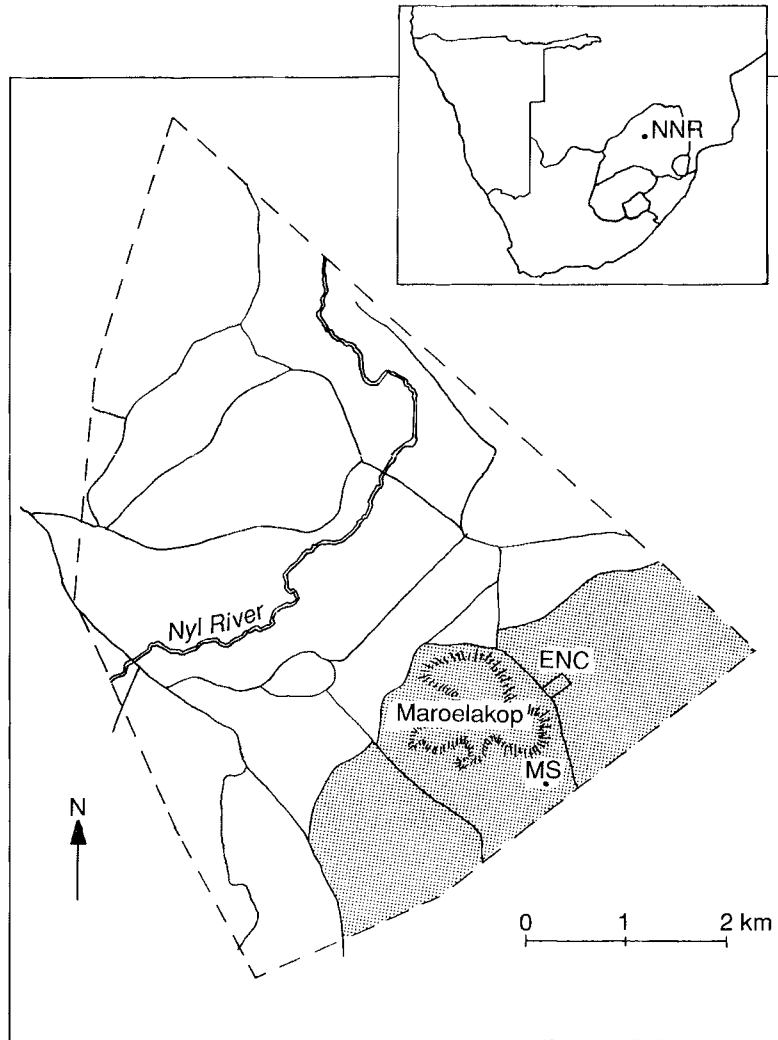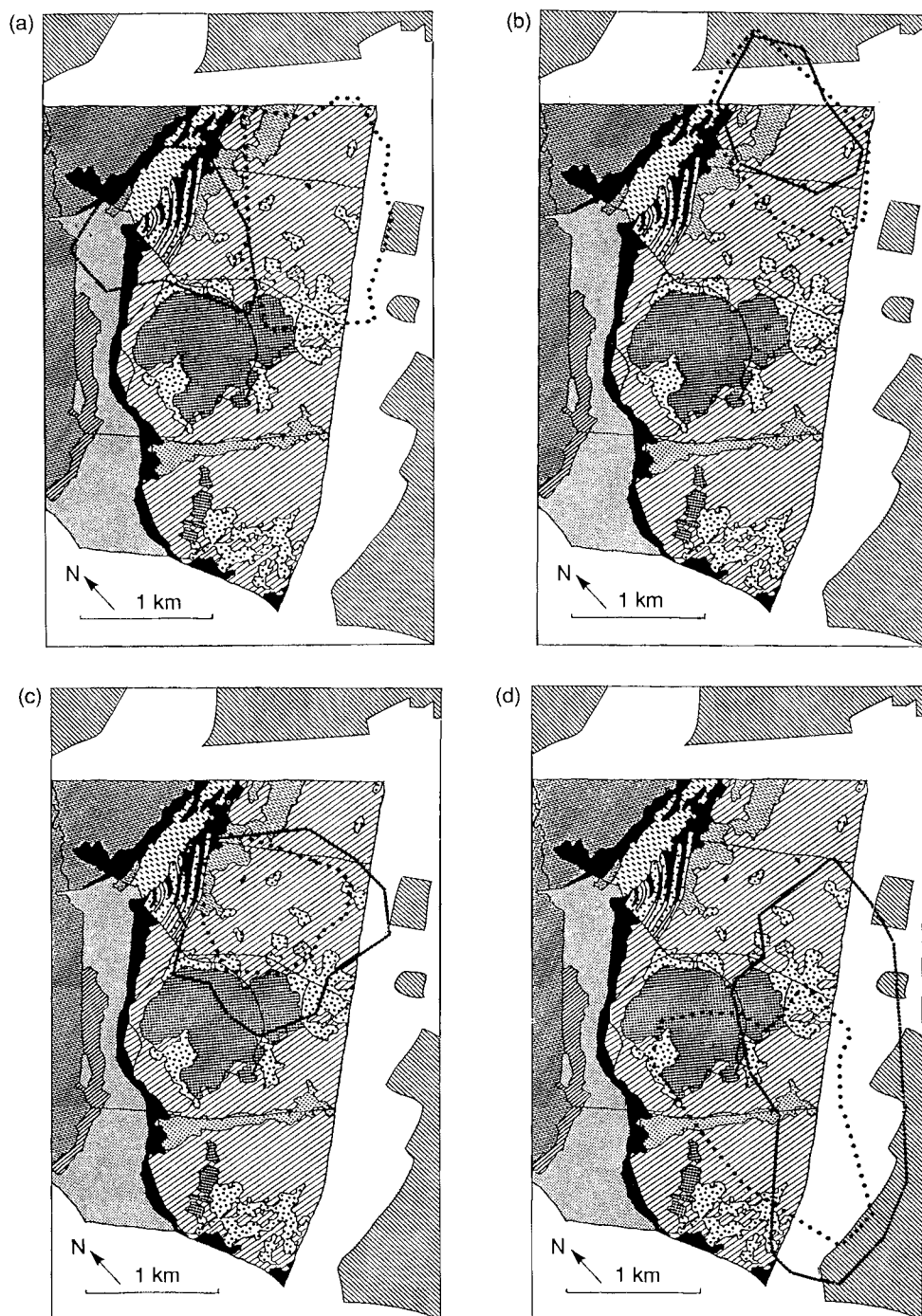
FIG. 1. Map of Nylsvley Nature Reserve (NNR) (adapted from Huntley & Morris, 1982), showing the location of the reserve and, within the reserve, the positions of the study area (▨), roads (———), meteorological station (MS) and the leash-walking enclosure (ENC).

MK5 transmitters (Telemetry-Electronics Consultants, Mesa, Arizona, USA) were fitted and the animals were sexed, weighed and aged according to van Aarde (1985*b*).

A Yaesu (FT—290R II 2 m all mode) transceiver (Yaesu Musen Co., Ltd., Tokyo, Japan), a handheld Telonics H-antenna (Telemetry-Electronics Consultants, Mesa, Arizona, USA) and a Suunto hand-bearing compass (RL KB-77) with fluorescent dial (Wild & Leitz RSA (Pty) Ltd., Johannesburg, RSA) were used. Accuracy of technique and equipment in the study area was determined through the placement and subsequent relocation of transmitters at known locations. Mean error (Springer, 1979), calculated from bearings obtained when the distance between receiver and transmitter was between 200 and 1000 m, was −0·70° (±11·162°) with 95% confidence limits of −3·42 and 2·01. Signals obtained outside this distance

interval during tracking were ambiguous and were discarded. Locations obtained less than an hour after sunset or less than an hour before sunrise were also discarded, since 13 direct observations of porcupines revealed that times of emergence from burrows varied between 25 and 52 min after sunset. Porcupines were radiotracked from sunset to sunrise on 157 nights, from June 1989 to December 1990. One to 6 porcupines were tracked simultaneously per night, resulting in 620 nights of tracking data.

Unless otherwise stated, all computer programs were developed by H. M. Dott. Radiotracking data entered on the program 'Maps' enabled the 'Caddie' system (Vector Cad Cam (Pty) Ltd.) to calculate locations by triangulation and to store this information in a database. At a distance of 1000 m between transmitter and receiver, and a 90° angle between triangulation bearings and transmitter, an error arc (represented as the confidence limits of the mean error) results in an error polygon with a longest diagonal of 120 m (see Springer, 1979). Radiolocations and corresponding error circles were superimposed on a 1:17 953 vegetation map of the study area (adapted from Coetzee et al., 1976) by using a program, 'Habtat', linked to the Caddie system. The proportion which each habitat contributed to the 95% home ranges (Corbet, 1991) was measured by a program, 'Multarea', linked to a Quantimet 520 Image Analyser (Cambridge Instruments, Cambridge, UK).

Habitat preferences were determined from those radiolocations for which the entire error circle fell within one habitat type and also from areas of intensive use, defined as the area covered by intersecting error circles around locations obtained 1–2 h apart (Spitz, 1988). The maximum speed travelled in such a case is 240 m/h, which is less than the mean speed of 300 m/h calculated for radiotracked porcupines. Preferences were determined by means of Bonferroni confidence intervals according to the method of Neu, Byers & Peek (1974), as clarified by Byers & Steinhorst (1984). Bonferroni tables (Miller, 1966) were used to obtain the appropriate z values. The proportions that habitat types contributed to 95% home ranges were used to calculate the expected frequencies of locations in each habitat type. Habitat types were classified as preferred or rejected (if the proportion of expected locations fell outside the confidence interval calculated around the observed proportion of radiolocations), or tolerated (if this proportion fell within the confidence interval). Chi-square analysis was used to test for differences in summer and winter habitat preferences (Zar, 1984).

FIG. 2. Ninety-five percent home ranges of eight radiotracked porcupines superimposed on the vegetation map (from Coetzee et al., 1976) of the study area at Nylsvley Nature Reserve. (a) M1 (– – –) and M6 (• • • • •); (b) M5 (– – –) and F1 (• • • • •); (c) M2 (– – –) and F2 (• • • • •); (d) M4 (– – –) and M3 (• • • • •).

Key to habitat types: (abbreviations in parentheses correspond to abbreviations used in Table I)
Communities of elevated sandstone and felsite regions
Eragrostis pallens–Burkea savanna
Eragrostis pallens–Dombeya rotundifolia variation (Burkea savanna—B: ▨)
Eragrostis pallens–Trachypogon spicatus variation (ET: ▦)
Eragrostis pallens–Setaria perennis variation (ES: ▨)
Barleria bremekampii–Diplorhynchus savanna (rocky outcrop savanna—R: ▦)
Eragrostis racemosa–Schizachyrium jeffreysii savanna and grassland
Tristachya rehmannii–Digitaria monodactyla variation (TD: ■)
Communities of alluvial flats
Sporobolus ioclados–Acacia tortilis and Euclea undulata–Acacia tortilis savanna (AF: ▨)
Communities of self-mulching vertic soils
Savanna variation ▨
Grassland variation (floodplain—SG: ▨)
Disturbed areas
Disturbed areas within the reserve (Acacia savanna—A: ▨)
Areas outside the reserve, excluding farmland (O: ☐)
Farmland (F: ▨)

Leash-walking of tame porcupines

Two captive-bred porcupines (1 male and 1 female) were tamed and leash-walked in a 30 496 m² enclosure in an area of *Burkea* savanna in the study area. The animals ranged freely, except for being prevented from leaving the enclosure. Continuous observations were made over a period of about 3 h per night for 65 nights. The enclosure was divided into a grid with perimeter cells of ≈ 100 m² and the other cells of ≈ 200 m². Time spent in each cell was recorded. Grid cells were categorized according to the presence or absence of 9 plant species (see Table II) on which one or both porcupines spent most time feeding (de Villiers, 1992). Time spent in each of these categories of cells was then compared by using the Mann–Whitney U test (Zar, 1984).

Time spent in grid cells was divided into 23 10-min time intervals and the number of cells in each interval was calculated. Since 72% of cells fell within the first 3 intervals (up to 29 min per cell), cells in which more than 30 min were spent were recategorized as feeding patches, and all other cells excluding perimeter cells as non-feeding patches. The number and rate of scent-marking in grid cells were recorded and rates for the 2 animals were compared by the Mann–Whitney U test. The total frequency and rate (total no. of scent-marks in cell/total time in cell) of scent-marking by the male in feeding, non-feeding and perimeter cells were compared by using the Mann–Whitney U test.

Results

Habitat utilization as determined from radiotelemetry data

The 95% home ranges of the eight radio-tracked porcupines, superimposed on the vegetation map of the study area, are illustrated in Fig. 2. Classifications of habitat types as preferred, tolerated or rejected, are presented in Table I. Preferences determined from radiolocations which

TABLE I

Yearly classification of habitat types as preferred (P), rejected (R) or tolerated (X), using (a) locations for which error circles did not overlap more than one habitat type (code in bold type) and (b) areas of intensive use

| | Habitat types[a] | | | | | | | | | | | | | | | | | | | |
| | B | | A | | R | | O | | F | | ET | | TD | | ES | | SG | | AF | |
Porcupine	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
M1	X	X		P									R	R		X	P	X	X	X
M2	P	P	R	R	X	X									X	P				
M3	P	P	R	R	R	R	R		X			X								
M4	P	P	X	P	X		R	R	R											
M5	R	R					P	X							P	P				
M6	P	P	R	X			R	R												
F1	R	R					P	P	R						P	P				
F2	P	X		X											R	X				

[a] Codes for habitat types (from Coetzee *et al.*, 1976):

    B: *Eragrostis pallens–Dombeya rotundifolia* variation (*Burkea* savanna)
    A: Disturbed areas within the reserve (*Acacia* savanna)
    R: *Barleria bremekampii–Diplorhynchus* savanna (rocky outcrop savanna)
    O: Areas outside the reserve, excluding farmland
    F: Farmland
    ET: *Eragrostis pallens–Trachypogon spicatus* variation
    TD: *Tristachya rehmannii–Digitaria monodactyla* variation
    ES: *Eragrostis pallens–Setaria perennis* variation
    SG: Grassland variation (floodplain)
    AF: *Sporobolus ioclados–Acacia tortilis* and *Euclea undulata–Acacia tortilis* savanna

fell entirely within one habitat type and from areas of intensive use were compared. In five of 30 comparisons, sample size for areas of intensive use was too small to permit classification of habitat types. In 18 of the remaining 25 cases, results of the analyses were identical and in the remaining seven cases, the difference lay in the expected proportion of locations falling in or out of the confidence interval.

The observed and expected frequencies of utilization of habitat types were significantly different ($P < 0.01$) for all animals except F2. For this individual, the analysis using areas of intensive use indicated that habitat types were used in proportion to their occurrence ($\chi^2 = 1.26$, $v = 2$, $P > 0.05$). Table I illustrates that five of the eight porcupines preferred *Burkea* savanna (B) and three of these rejected *Acacia* savanna (A), while two porcupines rejected *Burkea* savanna. No animals preferred rocky outcrop savanna (R) and M3 rejected this habitat type. Three of the five animals which spent time outside the reserve (O) rejected such areas, while F1 and M5 preferred these areas. None of the porcupines preferred farmland (F) and such areas were rejected by M4. Only M1 made ₋ubstantial use of *Tristachya rehmanii–Digitaria monodactyla* variation (TD) and the floodplain (SG), rejecting the former and preferring the latter habitat type. F1 and M5 preferred *Eragrostis pallens–Setaria perennis* variation (ES, henceforth referred to as *Setaria* savanna) while F2 rejected this habitat type.

Insufficient data were available to compare seasonal habitat preferences of F2. For all other animals except M6, there was a significant difference in summer and winter habitat preferences (M1: $\chi^2 = 47.00$, $v = 6$, $P < 0.001$; M2: $\chi^2 = 17.93$, $v = 4$, $P < 0.005$; M3: $\chi^2 = 39.41$, $v = 5$, $P < 0.001$; M4: $\chi^2 = 20.53$, $v = 5$, $P < 0.001$; M5: $\chi^2 = 33.36$, $v = 2$, $P < 0.001$; M6: $\chi^2 = 7.58$, $v = 4$, $P > 0.1$; F1: $\chi^2 = 37.17$, $v = 2$, $P < 0.001$).

Habitat utilization as determined by leash-walking of tame porcupines

The nine plant species for which grid cells were investigated are listed in Table II. Of these, two (*Strychnos pungens* and *Ozoroa paniculosa*) were too rare and one (*Commelina* spp.) too widespread to allow statistical comparison of cells where the species were present and absent. The

TABLE II

Comparison of time spent by two leash-walked porcupines in grid cells (of an enclosure in the study area) classified according to the presence or absence of each of nine plant species. **Z** *values (normal approximation to the Mann–Whitney* **U** *test) are presented*

Plant species	Z values	
	Female	Male
Burkea africana (tree)	1·059	1·882*
Combretum zeyheri (tree)	−0·982	−0·618
Commelina spp. (herb)	—	—
Dichapetalum cymosum (herb)	−0·492	0·717
Dombeya rotundifolia (tree)	2·635*	2·972*
Euphorbia trichadenia (herb)	2·077*	−0·211
Mariscus saxiflorus (herb)	0·140	2·730*
Ozoroa paniculosa (tree)	—	—
Strychnos pungens (tree)	—	—

* $P < 0.05$

male porcupine spent significantly more time in grid cells containing three of the remaining six species, namely *B. africana*, *D. rotundifolia* and *Mariscus saxiflorus* (Table II). The female's activities also corresponded to the distribution of *D. rotundifolia*, and to the distribution of *Euphorbia trichadenia* (Table II).

There was a significant difference ($U = 93$, $n_1 = 11$, $n_2 = 10$, $P < 0.01$) in the mean rate of scent-marking by the male (14·9 marks/h) and the female (1·8 marks/h). The male scent-marked significantly more in feeding patches than in non-feeding patches ($Z = 5.06$, $P < 0.001$). There was no significant difference in the number of scent-marks in feeding and perimeter cells ($Z = -1.87$, $P > 0.05$). The rate of scent-marking in feeding and non-feeding patches was, however, not significantly different ($Z = -1.89$, $P > 0.05$) but was significantly higher in perimeter cells than elsewhere ($Z = -5.79$, $P < 0.001$).

Discussion

Habitat utilization can be investigated on at least three levels, or scales. First, Fretwell & Luca (1970) described a habitat as an area which is homogeneous with regard to factors important to its inhabitants. Determining the relevant factors may be difficult since one is constrained to define habitats according to features which can be recognized and measured. Habitat types are, however, usually taken to correspond to vegetation communities. Secondly, utilization of smaller patches differing only in relative productivity may be investigated (Arditi & Dacorogna, 1988). Habitat utilization on both these scales is rarely investigated in a single study (for exceptions, see Owen-Smith & Novellie, 1982; Brown, 1988). Thirdly, activity zones within an animal's home range may be identified and may provide information on feeding and/or social activities (Spitz, 1988).

Macroscale habitat utilization

Unless an entire error circle around a radiolocation falls within a habitat type, one cannot be certain of the habitat type in which a radiotracked animal was located. In the present paper, therefore, habitat preferences are discussed in terms of classifications made on the basis of those radiolocations for which the entire error circle fell within one habitat type.

The density of diggings for subterranean food items and the proportion of debarked trees and trees with roots damaged by gnawing by porcupines are all higher in *Burkea* savanna than in *Acacia* savanna (de Villiers, 1992). The preference of five of the eight radiotracked porcupines for *Burkea* savanna and their lack of preference for *Acacia* savanna is thus probably due to their feeding habits. Six of seven porcupines showed seasonal differences in habitat preferences, indicating the possible influence of food availability on habitat utilization.

Despite the above preference for *Burkea* savanna, there was considerable individual variation in yearly habitat preferences. In terms of optimal foraging behaviour (Emlen, 1966; MacArthur & Pianka, 1966), the reproductive fitness of those individuals which make the best use of the range of available habitats will be enhanced. Several constraints affect an individual, however, including phylogeny, pathways of development, general architecture (S. J. Gould & Lewontin, 1979) and social organization. The foraging pattern of an individual may thus reflect the best possible solution under the circumstances rather than the perfect solution. Furthermore, optimal foraging models are usually subject to a number of assumptions which may not hold true under real-life conditions, e.g. constant encounter rates, handling times and yields, all independent of previous events (Heth, Golenberg & Nevo, 1989).

Porcupines may, for instance, be limited in their use of different habitats by territoriality. Corbet

(1991) suggested that, although there is some overlap between total home ranges of pairs of porcupines, the pair has almost exclusive access to a smaller area within the home range, and this area may be defended as a territory. The ideal free distribution model of Fretwell & Lucas (1970) proposes that the proportion of animals in a population in various habitats is a function of the proportion of resources in those habitats. Messier, Virgl & Marinelli (1990) showed that, for muskrats, the predictions of this model are rejected. They proposed an alternative, the ideal despotic distribution model, which predicts that animals inhabiting prime habitats will monopolize such resources. If such a model is applicable to porcupines, then some habitat types which are classified as preferred might have been used more than would be predicted on the basis of availability only because animals were forced into them by more dominant neighbours. This would explain why, for example, F1 and M5 apparently rejected *Burkea* savanna, and why these animals preferred *Setaria* savanna while F2 rejected the latter habitat type.

Utilization of several other habitat types may be influenced by factors other than food availability. Despite the high incidence of debarked trees in rocky outcrop savanna (de Villiers, 1992), this habitat type was never preferred by the study animals. Other uncollared porcupines may have monopolized this area, or this habitat type may be unsuitable for feeding on important subterranean food items such as tubers and tree roots, because of the rocky substratum. F1 and M5 both made extensive use of a burrow outside the reserve, which may explain why only they showed a preference for such areas. No study animals preferred farmland. Although this habitat must yield a high reward in terms of food, there are considerable risks associated with utilizing it. Successive radiolocations were never obtained on farmland, indicating that farm visits were not prolonged—porcupines probably make use of a 'smash-and-grab' technique, as was indicated by the presence of maize cobs around the entrances to their burrows.

Intermediate-scale habitat utilization

Spitz (1988) proposed that animals utilize certain areas within their home ranges more intensively than others, and that these areas can be identified by means of overlapping error circles. When moving through such areas, animals are expected to travel more slowly than elsewhere. For radiotracked porcupines, the maximum speed travelled within an area of intensive use was less than the mean speed of movement, indicating that areas of intensive use might be useful for identifying activity zones. If these zones correspond to specific feeding areas within the home range, habitat preference classifications by means of all radiolocations and by means of areas of intensive use may be substantially different.

Most classifications of habitat types made from radiolocations for which the entire error circle fell within one habitat type, and from areas of intensive use, were identical. The only differences obtained were those where the expected proportion of frequencies fell in or out of the Bonferroni confidence intervals. There are three possible explanations for this. First, feeding and non-feeding activities may occur in the same habitat types. Secondly, porcupines may not use certain areas within the home range for intensive feeding activities, but feed opportunistically throughout their range. Areas subject to intensive use might have been correctly identified, but activities other than feeding would occur there. Thirdly, the method used to identify activity zones may not have been sensitive enough. By definition, these zones are based on radiotracking inaccuracy (being identified by overlapping error circles). If feeding areas are substantially smaller than the maximum area covered by an area of intensive use (in this study, the area covered by two error circles of 120 m diameter), they will not be identifiable.

Microscale habitat utilization

In discussing microscale habitat utilization, it should be remembered that observations were made on captive-born, tame porcupines. J. L. Gould & Marler (1987) proposed that the process of learning may be guided by information which is genetically determined for an animal and specialized for tasks which the animal is likely to encounter. The animal may thus be innately equipped to recognize when to learn, what cues to attend to, how to store the learnt information and how to refer to it in the future (J. L. Gould & Marler, 1987). Captive-born porcupines introduced to their natural environment may thus possess the basic innate information needed to survive. A tame animal's foraging behaviour may, however, be influenced by its morphology and physiology (maintenance diets can affect gut size and nutritional plane) and by its altered experiences (e.g. through allelomimicry and the influence of experience on the abilities of generalization and discrimination) (Olson-Rutz & Urness, 1987).

Utilization of grid cells or microscale food patches by the leash-walked porcupines was no. random, but coincided with the distribution of certain important dietary items. The porcupines' activities may only have corresponded with the distribution of certain of the food items because the animals only used a few of the patches in which some items occurred.

The male porcupine scent-marked more in feeding patches than in non-feeding patches. This may be due to more time spent in such patches rather than to the presence of food items. Two observations support this explanation: the number of scent-marks in feeding patches was no higher than in perimeter cells along paths where feeding opportunities were limited; and the rate of scent-marking in feeding and non-feeding patches was not significantly different. Scent-marking may have a number of effects, including deterrence of aggression, sexual attraction, orientation, individual identification and alarm (Moran & Sorensen, 1986). Although the male apparently made no specific effort to scent-mark feeding patches, the high number of scent-marks in such areas could warn competitors away from feeding patches, or identify these areas for the scent-marking individual or for members of that individual's group. The rate of scent-marking was significantly higher in perimeter cells than elsewhere. This may be because the leash-walked porcupine regarded such paths as territory boundaries.

Summary

Habitat utilization on three scales by Cape porcupines was investigated. Habitat preferences determined from areas of intensive use did not differ from those determined from radiolocations for which the entire error circle fell within one habitat type. This may be because feeding and non-feeding activities occur in the same habitat types, because porcupines feed opportunistically throughout their ranges or because the technique used was too insensitive to identify activity zones. There was considerable individual variation in macroscale habitat preference, suggesting that porcupines may be constrained in their utilization of habitat types by territoriality, with animals inhabiting prime habitat types monopolizing such areas. Porcupines apparently prefer *Burkea* savanna to *Acacia* savanna and this is probably due to a concentration of preferred food items in the former habitat type. Leash-walked porcupines used microscale feeding patches and the location of these coincided with the distribution of certain plant species which were important in their diets. The male scent-marked in feeding patches more frequently than he did in other areas, perhaps protecting or identifying the patches in this way.

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