

## Short Communications

### Aspects of habitat disturbance by Cape porcupines in a savanna ecosystem

M.S. de Villiers and R.J. van Aarde\*

Mammal Research Institute, Department of Zoology,  
University of Pretoria, Pretoria, 0002 Republic of South Africa

Received 10 May 1993; accepted 1 November 1993

Habitat disturbances by Cape porcupines (*Hystrix africae-australis*) in a savanna ecosystem were investigated at Nylsvley Nature Reserve by using transect line surveys for signs of porcupine foraging activities. The density of foraging diggings was significantly higher in *Burkea* savanna than in *Acacia* savanna. A significantly higher proportion of trees was debarked in *Burkea* and rocky outcrop savanna than in *Acacia* savanna. The only two species which were preferentially debarked were dominant species in the former two habitat types. Significantly more trees had roots gnawed on by porcupines in *Burkea* savanna than elsewhere, and the species most affected (*Burkea africana*) was a dominant species in this habitat type. Concentrated feeding activities in *Burkea* and rocky outcrop savanna by porcupines may affect the structure of these plant communities.

Habitatversteurings deur die Kaapse ystervark (*Hystrix africae-australis*) in 'n savanna ekosisteem is op die Nylsvley Natuurreservaat ondersoek deur middel van transektlynopnames vir tekens van ystervark voedingsaktiwiteite. Die digtheid van ystervarkvoedingsgate was betekenisvol hoër in *Burkea* savanna as in *Acacia* savanna. Die proporsie bome waarvan die bas deur ystervarke gevreet was, was betekenisvol hoër in *Burkea* savanna en op koppies as in *Acacia* savanna. Die dominante spesies in eersgenoemde habitat-tipes was die enigste boomsoorte wat deur ystervarke verkies is. Ystervarke het die wortels van betekenisvol meer bome in *Burkea* savanna gevreet as in enige ander habitat-tipe. Die boomsoort wat die meeste op hierdie manier beïnvloed was, was die dominante boomsoort (*Burkea africana*) in die habitat-tipe. Deur voedingsaktiwiteite in *Burkea* savanna en op koppies te konsentreer, kan ystervarke die struktuur van hierdie plantgemeenskappe beïnvloed.

\* To whom correspondence should be addressed

Herbivorous mammals may affect their habitat by selective feeding on particular plant species and plant parts, and by disturbing the substrate in which these plants are rooted. When these activities are concentrated in specific plant communities, they can result in the restructuring of ecosystems. For example, pocket gophers (*Thomomys bottae*) slow down forest invasion and maintain the community composition of the meadows which they occupy through selective herbivory on aspens, *Populus tremuloides* (Cantor & Whitham 1989). Disturbances are an important cause of spatial and temporal heterogeneity in the structure and dynamics of biological communities.

Cape porcupines (*Hystrix africae-australis*) are widely distributed throughout southern Africa and occur in most habitats in the subregion. These relatively large, nocturnal

hystricomorph rodents are regarded as agricultural pests because of the extensive damage they cause to crops and plantations (Skinner & Smithers 1991). Cape porcupines are selective feeders (de Villiers unpub.) and create disturbances by digging for subterranean plant parts (Skinner & Smithers 1991) and by debarking trees (Yeaton 1988). In this paper, the selective use of habitats by porcupines for feeding activities is investigated and the effects of such use on these habitats are inferred.

Research was confined to a study area of 745 ha on the south-eastern boundary of the Nylsvley Nature Reserve (24°39'S; 28°42'E) in the northern Transvaal. Two seasons are distinguishable; 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 mean annual rainfall is 630 mm, 80% of which falls in the hot, wet months (Huntley & Morris 1982). The study area comprises three main habitats, described in detail by Coetzee, Van der Meulen, Zwanziger, Gonsalves & Weisser (1976). Sixty-five per cent comprises a broadleaf deciduous woodland community, *Burkea* savanna, on deep, relatively nutrient-poor latosols. Rocky outcrop savanna comprises 17% of the study area and occurs exclusively on rocky outcrops with lithosols without distinguishable soil horizons. Small patches of leptophyllous *Acacia* savanna occur on relatively nutrient-rich latosols and may owe their origin to pastoral settlements abandoned in 1925 (Huntley & Morris 1982).

The number of porcupine diggings (the result of foraging for below-ground plant parts), debarked trees and trees with roots gnawed on by porcupines, were counted along line transects surveyed in each habitat type. The number of transects and their dimensions in each habitat type are provided in Table 1. Transects for diggings and debarked trees in rocky outcrop savanna covered a smaller area than those in other habitat types.

**Table 1** The number, width and total area or length of line transects surveyed for porcupine foraging diggings, debarked trees and trees with roots gnawed by porcupines, in three habitat types in the study area at Nylsvley Nature Reserve

Transect	Habitat type		
	<i>Acacia</i>	<i>Burkea</i>	Rocky outcrop
<b>Diggings</b>			
No. transects	7	9	5
Width (m)	7	5-8	5-7
Total area (m <sup>2</sup> )	36 000	31 000	22 000
<b>Debarked trees</b>			
No. transects	6	6	7
Width (m)	5	5	5
Total length (m)	2 000	2 300	1 000
<b>Gnawed roots</b>			
No. transects	4	4	4
Width (m)	6	6	6
Total length (m)	1 200	1 500	1 200

Fixed width (5–8 m) transects were surveyed on foot in each of the three habitats. Preliminary surveys allowed determination of the perpendicular distance from the transect line at which the soil surface was always visible in a given area, and transect widths were based on these estimates. The shape of the diggings made by feeding porcupines usually approximates a quarter-ellipsoid. Only such diggings, and not small scrapes or tunnels, were counted along transect lines.

To assess habitat preferences by comparing the densities of diggings, the lifespan of diggings (which depend on digging volumes and the rate at which diggings are filled in by soil and/or litter) for different habitat types had to be similar. To estimate filling-in rates, 20 artificial diggings were created in each habitat. Digging volume ( $u$ ) was calculated using the formula for half an ellipsoid (this being the shape of diggings excavated with a trowel), i.e.  $u = 2/3 \pi abc$ , where  $a$  = longest width/2,  $b$  = shortest width/2 and  $c$  = depth (Alkon & Olsvig-Whittaker 1989). Filling-in rates were calculated as the change in volume over time.

The volumes of 40 porcupine diggings ( $v$ ) in each habitat were calculated using the formula for quarter of an ellipsoid cylinder, i.e.  $v = 1/4 \pi Abc$ , where  $A$  = longest width. The mean lifespan ( $L$ ) of diggings in each habitat type was then calculated as  $L = \sum (v/R) / n$ , where  $R$  = mean filling-in rate and  $n$  = number of diggings. In habitats where differences in lifespans of diggings were not statistically significant (according to the Kruskal-Wallis and non-parametric multiple comparisons tests), densities were compared using the Mann-Whitney  $U$ -test (Zar 1984).

Fixed-width (5 m) strip transects were surveyed in each habitat type for debarked trees. A total of 2308 trees were investigated for the presence or absence of debarking resulting from gnawing by porcupines. Contingency table analysis was used to compare the proportion of debarked trees in each habitat type (Zar 1984). Nine common tree species were classified as preferred, tolerated or rejected. (These terms reflect whether species were used proportionately more, as much, or less than would be expected on the basis of availability.) Classification was accomplished using Bonferroni confidence intervals (Neu, Byers & Peck 1974, as clarified by Byers & Steinhorst 1984). Bonferroni tables (Miller 1966) were used to obtain the appropriate  $z$  values.

Fixed-width (6 m) transects were also surveyed to count trees with roots which had been gnawed by porcupines. One thousand and fifty-five trees belonging to 11 common species were investigated. Contingency table analysis was used to compare the proportion of affected trees in each habitat type.

Simultaneous comparisons of the lifespan of diggings in the three habitats revealed a significant difference (Kruskal-Wallis  $H_c = 403,57$ ;  $df = 2$ ;  $P < 0,001$ ), with lifespans in *Burkea* and *Acacia* savanna not being significantly different (non-parametric multiple comparisons  $q = 1,98$ ;  $P > 0,05$ ). Digging density (Table 2) was significantly higher in *Burkea* savanna than in *Acacia* savanna (Mann-Whitney  $U = 55$ ;  $n_1 = 7$ ;  $n_2 = 9$ ;  $P < 0,05$ ).

For all habitats combined, 16,9% of trees were debarked. A significantly higher proportion of trees was debarked in *Burkea* savanna than in *Acacia* savanna (contingency tables

**Table 2** The mean  $\pm$  sem percentage of trees debarked and with roots gnawed on by porcupines, and the mean  $\pm$  sem density of porcupine foraging diggings in three habitat types in the study area at Nylsvley Nature Reserve. Values in parentheses represent the number of transects surveyed

Habitat type	% debarked trees	% root-damaged trees	Digging density (no./km <sup>2</sup> )
<i>Acacia</i>	9,2 $\pm$ 2,52 (6)	0,0 (4)	1897 $\pm$ 577,5 (7)
<i>Burkea</i>	14,6 $\pm$ 1,75 (6)	3,6 $\pm$ 1,36 (4)	5270 $\pm$ 909,1 (9)
Rocky outcrop	21,9 $\pm$ 2,88 (7)	1,5 $\pm$ 0,50 (4)	2939 $\pm$ 488,9 (5)

$\chi^2 = 7,40$ ;  $df = 1$ ;  $P < 0,05$ ), while the proportion of trees debarked in rocky outcrop savanna was significantly higher than in *Burkea* savanna (contingency tables  $\chi^2 = 9,05$ ;  $df = 1$ ;  $P < 0,05$ ) (Table 2). *Diplorhynchus condylocarpon* and *Burkea africana* were preferentially debarked (Bonferroni confidence intervals, Table 3).

The proportion of trees with roots gnawed by porcupines was significantly different in the three habitats (contingency tables  $\chi^2 = 12,19$ ;  $df = 2$ ;  $P < 0,005$ ) (Table 1). This was due to a significantly higher ( $\sim 4$  times) proportion of trees with gnawed roots in *Burkea* savanna (contingency tables  $\chi^2 = 11,08$ ;  $df = 1$ ;  $P < 0,001$ ). The roots of five of the eleven species investigated were gnawed by porcupines, with *B. africana* being utilized most intensively (Table 4).

In the Negev Desert, up to 91% of seedling germination occurred in porcupine diggings and up to twice as many seedlings survived in diggings as out (Gutterman & Herr 1981). Similar patterns were observed in the Karoo, where seedling density was four times as high in diggings as out and significantly more seedlings germinated in diggings than on flat soil surfaces (Dean & Milton 1991). The concentration of digging activities by Cape porcupines in *Burkea* savanna may thus affect this community by enhancing the survival and germination of seedlings of particular species. Such effects should be relatively insignificant in *Acacia* savanna.

Crested porcupines (*Hystrix cristata*) remove the bark of saplings in winter (Santini 1980) and Indian crested porcupines (*Hystrix indica*) are responsible for heavy financial losses in agricultural areas where they debark mature trees and bite off seedlings and young saplings at ground level (Greaves & Aziz Khan 1978). Gaigher & Currie (1979) reported serious damage by Cape porcupines to certain indigenous tree species in two nature reserves in the Cape. Thomson (1974) reported damage to indigenous tree species in Zimbabwe. Yeaton (1988) proposed that at Nylsvley Nature Reserve, the combined effects of selective debarking by porcupines and of fire maintain the *Burkea* savanna as a mosaic of grassland and small woodland patches undergoing cyclical successions.

In this study, the proportion of debarked trees was higher in *Burkea* and rocky outcrop savanna than in *Acacia* savanna, probably because of the relative abundances of preferred tree species in the former habitat types. The preferred species, *B. africana* and *D. condylocarpon*, were dominant species in *Burkea* and rocky outcrop savanna

**Table 3** Proportional availability and debarking by porcupines of selected tree species in the study area at Nylsvley Nature Reserve.  $p_u$  and  $p_l$  are the upper and lower limits of the Bonferroni confidence. The codes, 'P', 'X' and 'R' indicate whether a tree species was debarked more than, as much as, or less than expected on the basis of availability. The  $\chi^2$  statistic, sample size ( $n$ ) and  $z$  value ( $Z_{(0,05/2k)}$ , where  $k$  = number of species compared and the  $z$  value is obtained in Bonferroni tables) are also presented

Tree species	Proportion of total number of trees (availability)	Observed number of debarked trees	Expected number of debarked trees	Confidence interval around observed proportion of debarked trees $p_l \leq p \leq p_u$	Availability $>p_u$ (R), $<p_l$ (P) or in interval (X)
<i>Burkea africana</i>	0,184	97	72	0,187 $\leq$ 0,294 $\leq$ 0,311	P
<i>Combretum molle</i>	0,016	10	6	0,003 $\leq$ 0,026 $\leq$ 0,049	X
<i>Combretum zeyheri</i>	0,032	17	12	0,015 $\leq$ 0,044 $\leq$ 0,073	X
<i>Dichrostachys cinerea</i>	0,107	14	42	0,009 $\leq$ 0,036 $\leq$ 0,063	R
<i>Diplorhynchus condylocarpon</i>	0,046	35	18	0,049 $\leq$ 0,090 $\leq$ 0,131	P
<i>Dombeya rotundifolia</i>	0,075	33	29	0,045 $\leq$ 0,085 $\leq$ 0,125	X
<i>Ochna pulchra</i>	0,095	41	37	0,061 $\leq$ 0,105 $\leq$ 0,149	X
<i>Peltophorum africanum</i>	0,026	11	10	0,005 $\leq$ 0,028 $\leq$ 0,051	X
<i>Terminalia sericea</i>	0,186	95	72	0,183 $\leq$ 0,244 $\leq$ 0,305	X
Other	0,233	36	91	0,052 $\leq$ 0,093 $\leq$ 0,134	X

$\chi^2 = 89,826$ ;  $v = 9$ ;  $P < 0,01$ ;  $n = 389$ ;  $z = 2,807$

**Table 4** The percentage of trees of 11 species with roots gnawed by porcupines

Species	Sample size	% root-damaged trees
<i>Burkea africana</i>	406	11,3
<i>Dombeya rotundifolia</i>	53	3,8
<i>Combretum molle</i>	51	2,0
<i>Combretum zeyheri</i>	82	1,2
<i>Terminalia sericea</i>	152	0,7
<i>Acacia nilotica</i>	50	0,0
<i>Acacia tortilis</i>	92	0,0
<i>Dichrostachys cinerea</i>	71	0,0
<i>Ochna pulchra</i>	323	0,0
<i>Peltophorum africanum</i>	73	0,0
<i>Sirynchos pungens</i>	42	0,0

respectively, and were relatively scarce in *Acacia* savanna (Whittaker, Morris & Goodman 1984). In *Acacia* savanna, the proportion of debarked trees was far lower. Furthermore, the dominant species in this habitat type were rarely debarked (the proportion of debarked trees belonging to the genus *Acacia* was so low that the genus could not be included in the Bonferroni confidence interval analysis). Porcupines are thus unlikely to prevent the development of a mature woodland in *Acacia* savanna. The effect of selective debarking in selected habitats by porcupines may thus ultimately be to enhance the encroachment of *Acacia* patches into the broadleaf woodland of Nylsvley — a process which was probably initiated over a century ago by human settlement in the area (Huntley & Morris 1982).

The proportion of trees with roots damaged by the gnawing of porcupines was low in all habitat types but highest in *Burkea* savanna, where a relatively high proportion of *B. africana* trees was affected. No information was obtained on

mortality related to root-damage, although a few trees which had fallen over were seen to have roots that were severely damaged as a result of gnawing by porcupines (pers. obs.). If root-damage does affect tree survival, then the effect of debarking by porcupines on *Burkea* savanna may be exacerbated by the concentration of root-gnawing activities on the dominant species in this habitat type.

#### Acknowledgements

Financial assistance, provided by the University of Pretoria, the Foundation for Research and Development and the Bob Blundell Memorial Scholarship, is gratefully acknowledged.

#### References

- ALKON, P.U. & OLSVIG-WHITTAKER, L. 1989. Crested porcupine digs in the Negev desert highlands: Patterns of density, size and longevity. *J. Arid Env.* 17: 83–95.
- BYERS, C.R. & STEINHORST, R.K. 1984. Clarification of a technique for analysis of utilization-availability data. *J. Wildl. Mgmt* 48: 1050–1053.
- CANTOR, L.F. & WHITHAM, T.G. 1989. Importance of below-ground herbivory: Pocket gophers may limit aspen to rock outcrop refugia. *Ecology* 70: 962–970.
- COETZEE, B.J., VAN DER MEULEN, F., ZWANZIGER, S., GONSALVES, P. & WEISSER, P.J. 1976. A phytosociological classification of the Nylsvley Nature Reserve. *Bothalia* 12: 137–160.
- DEAN, W.R.J. & MILTON, S.J. 1991. Disturbances in semi-arid shrubland and arid grassland in the Karoo, South Africa: Mammal diggings as germination sites. *Afr. J. Ecol.* 29: 11–16.
- GAIGHER, I.G. & CURRIE, M.H. 1979. Preliminary studies on the ecology of the South African porcupine, *Hystrix africae-australis*. Research Report: Mammals, Cape Dept. of Nature and Environmental Conservation, pp. 55–69.

- GREAVES, J.H. & AZIZ KHAN, A. 1978. The status and control of porcupines, genus *Hystrix* as forest pests. *Commonw. For. Rev.* 57: 25–32.
- GUTTERMAN, Y. & HERR, N. 1981. Influences of porcupine (*Hystrix indica*) activity on the slopes of the northern Negev mountains — germination and vegetation renewal in different geomorphological types and slope directions. *Oecologia* 51: 332–334.
- HUNTLEY, B.J. & MORRIS, J.W. 1982. Structure of the Nylsvley savanna. In: *Ecology of Tropical Savannas*, (eds B.J. Huntley & J.W. Morris, pp. 433–455. Springer-Verlag, Berlin.
- MILLER, R.G. 1966. *Simultaneous Statistical Inference*. McGraw-Hill, Inc., USA.
- NEU, C.W., BYERS, C.R. & PEEK, J.M. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Mgmt* 38: 541–545.
- SANTINI, L. 1980. The habits and influence on the environment of the Old World porcupine *Hystrix cristata* L. in the northernmost part of its range. *Proceedings: Ninth Vertebrate Pest Conference; March 1980, Fresno, California*, pp. 149–153.
- SKINNER, J.D. & SMITHERS, R.H.N. 1990. *The Mammals of the Southern African Subregion*. University of Pretoria, Pretoria.
- THOMSON, W.R. 1974. Tree damage by porcupine in south-east Rhodesia. *J. south. Afr. Wildl. Manage. Assoc.* 4: 123–127.
- WHITTAKER, R.H., MORRIS, J.W. & GOODMAN, D. 1984. Pattern analysis in savanna woodlands at Nylsvley, South Africa. *Mem. Bot. Surv. S. Afr.* No. 49. Botanical Research Institute, Department of Agriculture, R.S.A.
- YEATON, R.I. 1988. Porcupines, fires and the dynamics of the tree layer of the *Burkea africana* savanna. *J. Ecol.* 76: 1017–1029.
- ZAR, J.H. 1984. *Biostatistical Analysis*, 2nd edn. Prentice-Hall, New Jersey.

## Schizamniogenesis in the rusty bat, *Pipistrellus rusticus*

M. van der Merwe

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

Received 20 September 1993; accepted 3 May 1994

Rusty bats are seasonally monoestrous, carrying a single foetus in each of the two uterine horns. Implantation is superficial with amniogenesis initiated very early during embryogenesis. Contrary to most other bat species where the amnion is formed by folding, it is formed by cavitation in the rusty bat.

Roeskleurvlermuis is seisoenaal monestrus en dra 'n enkele fetus in elk van die twee uterushorings. Inplanting is oppervlakkig en amniogenese neem reeds baie vroeg 'n aanvang tydens embriogenese. In teenstelling met die meeste ander vlermuis-spesies waar die amnion deur vouing gevorm word, geskied dit in die roeskleurvlermuis deur middel van uitholling.

The rusty bat (*Pipistrellus rusticus*) is one of the smaller vespertilionids, with a body mass of between 3 and 4 g (Skinner & Smithers 1990). In the Southern African subregion it occurs in the northern and eastern Transvaal, Zimbabwe, northern Botswana and north-eastern and central Namibia (Meester, Rautenbach, Dippenaar & Baker 1986). Rusty bats are seasonally monoestrous giving birth to twins in November. The uterus is bicornuate, the uterine horns being of equal size and each carrying a single foetus during pregnancy (Van der Merwe & Rautenbach 1990).

Mossman (1937) recognized two distinct methods of amnion formation: formation by folding and formation by cavitation, with the latter being considered more specialized. He reported that the type of amniogenesis is correlated with the method of implantation so that the pleuramnion, which is formed by folding, is associated with superficial implantation and the schizamnion, formed by cavitation, with interstitial implantation.

Ten female rusty bats were collected during September 1988 in the Transvaal, 30 km NE of Vaalwater, South Africa (24°08'S; 28°18'E). All ten individuals were in early stages of pregnancy.

The genital tracts, complete with intact embryos were dissected out, fixed in Bouin's fluid, embedded in paraffin wax, serially sectioned (5 µm), mounted and stained with Ehrlich's haematoxylin and counterstained with eosin.

Implantation in the rusty bat was superficial, but the inner cell mass developed a cavity which persisted as the true or definitive amniotic cavity (Figure 1a). The roof of the amniotic cavity did not rupture at any stage and eventually formed the ectodermal part of the amnion (Figure 1a & b), while the floor of the amniotic cavity formed the embryonic disc (Figure 1a–c). The basal layer of the trophoblast (cytotrophoblast), underlying the syncytiotrophoblast (Figure 1c & d) formed the ectodermal component of the chorion throughout development. The inner surface of the chorion eventually became covered with extra-embryonic mesoderm.