

Dietary patterns of two herbivorous rodents: *Otomys unisulcatus* and *Parotomys brantsii* in the Karoo

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Received 5 June 1990; accepted 18 December 1990

Differences and overlap in the diets of two sympatric, herbivorous rodents *Otomys unisulcatus* and *Parotomys brantsii* were investigated. Frequency of occurrence of plant species in the diets were compared with availability of the plants in the rodents' habitats. Both rodents are generalist herbivores, eating plants species in proportion to the availability in their habitats. Dietary patterns, diversity of diet and degree of overlap between rodent's diets are a function of food availability in the different habitats. It is suggested that these rodents separate niches on a spatial rather than trophic basis. Differences in dietary patterns are therefore not critical for niche separation but are the result of habitat segregation.

Verskille en oorvleueling in die dieet van twee simpatriese herbivore knaagdier *Otomys unisulcatus* en *Parotomys brantsii* is ondersoek. Frekwensievoorkoms van plant spesies in die diëte is met beskikbaarheid van die plant spesies in die habitat vergelyk. Beide spesies is herbivore, en vreet plant spesies in verhouding met die beskikbaarheid van die plant. Voedselbeskikbaarheid in verskillende habitate bepaal die mate van oorvleueling in die knaagdiere se dieet, dieetdiversiteit en dieetpatrone. Daar word voorgestel dat die knaagdiere spesies nissekeiding handhaaf d.m.v. ruimtelike eerder dan trofiese skeiding. Verskille in dieetpatrone is derhalwe minder belangrik vir nissekeiding maar is eerder 'n gevolg van habitatsegregasie.

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The bush Karoo rat *Otomys unisulcatus* and Brants whistling rat *Parotomys brantsii* are largely sympatric, being limited to the drier regions of southern Africa. These closely related rodents are large (100–150 g), diurnal and herbivorous. They also exhibit similar foraging behaviour: they bite off lengths of vegetation and drag these to the entrances of their refuges where the foliage is consumed. These species differ, however, in their refuge strategies. *Otomys unisulcatus* builds shelters of sticks and twigs, whereas *P. brantsii* inhabits isolated burrow systems (De Graaff 1981; Nel & Rautenbach 1974; Smithers 1983; Kerley 1989; Du Plessis & Kerley 1991).

The combination of their diet, semi-arid environment and the potential for competition for food and space, lends these two rodents to the study of resource utilization and partitioning. In a comparable study on three syntopic species of wood rats *Neotoma* spp., Dial (1988) showed that clear trophic partitioning occurred, as well as interspecific competition for nest sites. The aim of this study is to describe the diet of these two species in the southern Karoo and to investigate any differences or overlap in the diets.

Methods

Sampling

The study area is located in the southern Karoo, South Africa, between 33°03' and 33°27'S and 19°44' and 24°12' E. Mean annual rainfall is approximately 200 mm. Sampling was conducted during winter (June 1987), spring (October 1987), summer (January 1988), and autumn (April 1988). Fresh (harvested within the previous 24 h) dietary items, recognized as characteristically bitten-off plant parts, were collected at entrances to nests of *O. unisulcatus* (219 samples) and warrens of *P. brantsii* (147 samples). Between 20 and 30 active refuges were sampled each season for each

species.

The frequency of occurrence of a plant species in the diet during each season was transformed to percentages for seasonal comparisons. Plant species with an occurrence < 4% during all seasons were grouped into 'other' material. The contribution of shrub, annual, tree, succulent and non-succulent plant species to diets for each rodent was noted.

The potential availability of perennial plant species in the rodent habitats was estimated (cover values of individual plant species) using the line-intercept method (Mueller-Dombois & Ellenberg 1974) during winter (Table 1). The availability of perennial plant species in winter is an indication of availability throughout the year, as non-significant differences in perennial shrub canopy cover between rainfall periods have been demonstrated (Novellie & Strydom 1987).

Data analysis

Diets were compared using (a) information theory measure of overlap (*Rho*; Horn 1966) for overlap in diet. This index is independent of sample size and ranges from 0 (no overlap) to 1 (complete overlap). (b) The Shannon-Wiener information theory diversity (H' , Zar 1984) was used for a sample obtained non-randomly from a population; *t* tests and variance of diversity (Zar 1984) were calculated. (c) Species richness

$$R = S - 1 / \ln N,$$

where *S* = number of plant species eaten and *N* = the frequency of occurrence for all plant species eaten (Margalef 1958).

Comparisons between plant species occurring in diets and their corresponding occurrence in the habitats of *O. unisulcatus* and *P. brantsii* were estimated, using rank-correlation methods (Zar 1984).

Table 1 Seasonal diet of *Otomys unisulcatus* and *Parotomys brantsii* (of those species with a frequency of > 4% in any season), with availability of plants (expressed as per cent of total canopy cover). Frequency of occurrence in the diet is expressed in corresponding per cent for each plant species, where *n* = number of refuges sampled, * = dominant dietary species for that season, Wi = Winter (June), Sp = Spring (October), Su = Summer (January) and Au = Autumn (April)

Plant species	<i>O. unisulcatus</i>					<i>P. brantsii</i>				
	Cover (%)	Wi (n)38	Sp (n)64	Su (n)58	Au (n)59	Cover (%)	Wi (n)23	Sp (n)47	Su (n)35	Au (n)42
Succulent shrubs										
<i>Drosanthemum</i> sp.	7,82	10,7	*9,8	3,1	*11,8	5,92			1,5	
<i>Psilocaulon</i> sp.	13,38	10,7	4,3	*9,2	*8,0	6,72	7,5	*9,3	*9,4	*11,0
Mesembryanthemaceae*	0,04	2,4	6,8		6,0	1,00	0,8	10,7		
<i>Delosperma dijaguri</i>	0				8,0	0				
<i>Ruschia</i> sp.	0	6,0	2,5	1,2	1,3	9,77	*12,5	*12,9	*19,6	*20,4
<i>Eberlanzia</i> sp.	9,49	2,4	1,2	2,5		33,49	*9,2	*15,0	4,7	2,9
<i>Augea capensis</i>	0					9,52	5,0	5,0	8,4	6,6
<i>Aridaria</i> sp.	0	3,6	1,8		2,7	0	1,7		6,5	2,2
<i>Euphorbia maureitanica</i>	7,13	2,4	1,8	1,2	2,0	0				
<i>Sphalmanthus</i> sp.	0		1,8	1,8	2,0	0				
<i>Malephora</i> sp.	0,04		0,6		3,3	3,83	2,5	6,4		*7,3
<i>Lampranthus</i> sp.	0		0,6	4,3		0				
<i>Tylocodon</i> sp.	2,56	2,5	1,2			0				
Other					3,7				5,6	4,4
Non-succulent shrubs										
<i>Galenia africana</i>	12,31	*22,6	*20,3	*16,6	*9,3	3,40	4,2	*9,3	6,5	*7,3
<i>Lycium</i> sp.	25,00	*13,1		3,1	*10,0	1,46	6,7	2,9		1,5
<i>Atriplex</i> sp.	1,46	2,4	1,8	5,5	4,7	0,78	5,0	1,4	4,7	1,5
<i>Salsola</i> sp.	2,00	2,4	1,8	4,9	3,3	4,79	5,0	3,6	1,9	3,7
<i>Protasparagus</i> sp.	2,18	4,8	0,6	3,1	0,7	0,78	1,7			0,7
<i>Atriplex semibaccata</i>	2,37		1,2	3,1	1,3	0				
<i>Zygochloa</i> sp.	4,30	3,6		0,6	1,3	1,22	5,8	2,1	1,9	0,7
<i>Pentzia incana</i>	3,45	2,4	0,6	0,6	1,3	5,13	1,7	0,7		1,5
<i>Pteronia</i> sp.	0,09		1,8	2,5	0,7	6,17		4,3	2,8	
<i>Berkheya</i> sp.	0,63		0,6	1,8	1,3	0				
<i>Cotyledon orbicula</i>	0,14	2,4	1,2			0				
<i>Osteospermum sinuatum</i>	0					0	2,5	1,4	3,7	2,9
<i>Galenia fruticosa</i>	0					0	0,8			*7,3
<i>Eriocephalus ericoides</i>	3,47					0,30	2,5	1,4	0,9	
<i>Tetragonia</i> sp.	0,25					0,17	0,8			3,7
Other		1,2	0,6	2,5	8,0		4,2	1,4	1,9	1,5
Total for all shrubs		92,8	64,6	75,4	84,0		90,0	95,0	86,0	91,3
Annuals (Totals)		2,4	28,2	15,3	14,0		5,0	2,9	3,7	8,0
<i>Medicago sativa</i>	0		*12,3	3,1	0,7	0				
<i>Albica</i> sp.	0	6,1	4,3	2,0		0				
<i>Loranthus</i> sp.	0	1,2	4,3	2,5	1,3	0				
<i>Walafrida</i> sp.	0		1,2	1,8	2,0	0				
Liliaceae*	0				3,3	0				
<i>Sonchus</i> sp.	0		1,8		1,3	0				
<i>Pharnaceum</i> sp.	0					0			2,9	
Aizoaceae*	0					0	3,3			
Poaceae*	0		1,2	1,2	0,7	0			1,5	
Other		1,2	1,2	2,5	2,6		1,7	0,7	3,7	3,0
Trees (Totals)		2,4	4,9	6,8	2,0		0,7	2,8		
<i>Acacia karroo</i>	0,79	2,4	3,7	5,5	2,0	5,56			0,7	2,8
<i>Rhus undulata</i>	1,12		1,2	1,2		0				
Unidentified				2,5	2,5		5,0	3,5	7,5	1,4

* Unidentified items belonging to these families.

Results

Otomys unisulcatus and *P. brantsii* consumed the foliage and succulent stems of 60 and 47 plant species, respectively (see Table 1 for those species with a frequency of > 4% in any season). Shrubs, rather than annuals or trees, were dominant in their diets during each season (Table 1). The diet of *P. brantsii* was dominated by succulents (Figure 1, Table 1), which had the lowest frequency in winter (49,2% of diet). Succulents were less important in *O. unisulcatus* diet (Figure 1), and several non-succulent perennials dominated (Table 1). Annuals were more frequent in the diet of *O. unisulcatus* than in that of *P. brantsii*, especially in spring and summer (Figure 1).

Generally plants occurred in the rats' diets in proportion to their occurrence in the rats' habitats, as indicated by the

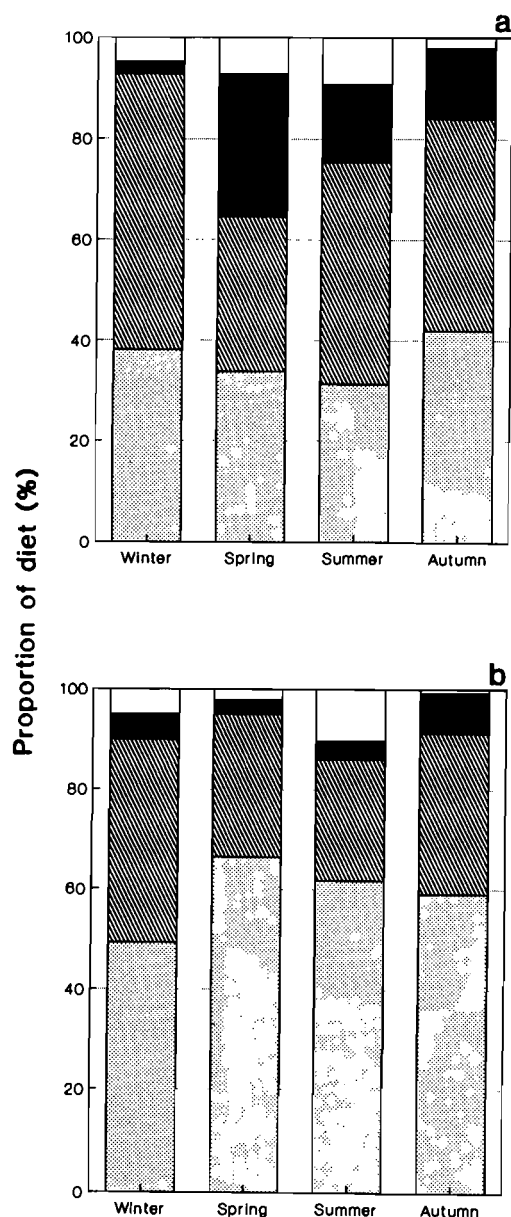


Figure 1 Contribution of succulents (stippled), non-succulents (lines), annuals (solid) and 'other material' (open) to the diets of (a) *Otomys unisulcatus* and (b) *Parotomys brantsii*. Frequency of occurrence in the diet expressed as percentage. See text for definition of seasons and food categories.

Table 2 Seasonal diversity ($H' \pm$ variance) and species richness (R) for *Otomys unisulcatus* and *Parotomys brantsii* diets

Season	<i>O. unisulcatus</i>		<i>P. brantsii</i>	
	Diversity	Richness	Diversity	Richness
Winter	2,23 (\pm 0,01)	4,08	2,52 (\pm 0,01)	4,69
Spring	2,59 (\pm 0,01)	5,72	2,43 (\pm 0,01)	4,05
Summer	2,86 (\pm 0,01)	6,91	2,39 (\pm 0,01)	4,58
Autumn	2,90 (\pm 0,01)	7,98	2,60 (\pm 0,01)	6,32

Table 3 Intraspecific seasonal comparisons of diets of *Otomys unisulcatus* and *Parotomys brantsii*, based on Student's t tests for significant differences between the information theory diversity measure

Seasons	<i>O. unisulcatus</i>				<i>P. brantsii</i>			
	t	$d.f.$	p	Rho	t	$d.f.$	p	Rho
Winter : spring	-2,85	188	**	0,68	0,95	240	n.s.	0,81
Winter : summer	-5,16	169	**	0,68	1,23	192	n.s.	0,77
Winter : autumn	-5,46	173	**	0,72	-0,67	239	n.s.	0,73
Spring : summer	-2,44	313	*	0,76	0,44	195	n.s.	0,69
Spring : autumn	-2,80	308	**	0,68	-1,50	248	n.s.	0,72
Summer : autumn	-0,43	308	n.s.	0,65	-1,71	229	n.s.	0,71

* $p < 0,05$; ** $p < 0,001$

n.s. — not significant at $p < 0,05$.

high correlation between diet and habitat (for *O. unisulcatus* $r = 0,73$; $p = 0,016$; and for *P. brantsii* $r = 0,73$; $p = 0,001$).

The diet of *P. brantsii* varied less seasonally than that of *O. unisulcatus* (Tables 2 & 3), which differed significantly between seasons. The highest overlap in diet between the two species occurred in winter ($Rho = 0,72$). The overlap in plant species between the rodent's diets was higher than the overlap in availability of these plant species ($Rho = 0,52$).

Discussion

This study supports the suggestions (Nel & Rautenbach 1974; Smithers 1983) that *Otomys unisulcatus* and *P. brantsii* are generalist herbivores. The diet of both rodents consists of a broad range of plant species. This generalist approach is to be expected in an environment with low predictability of annual precipitation and plant growth (Smith & Folmer 1971) with perennials forming a stable dietary base.

The higher contribution of succulents to the diet of *P. brantsii* than to that of *O. unisulcatus* (Figure 1), may be due to the much higher availability of succulents in their habitat (Table 1). In winter, succulents comprised 66,4% of the total plant cover in *P. brantsii* habitats, in contrast with 35,0% in *O. unisulcatus* habitats.

Seasonal shifts occurred in the diets of both species, with more herbaceous items (annuals and succulents) being consumed in spring and summer, and more non-succulent

perennial shrubs in winter (Figure 1). These seasonal shifts can probably be attributed to the combined effects of changes in availability of plants within the habitats of these species, as well as higher water requirements experienced during the hot season (Du Plessis, Erasmus & Kerley 1989). In the absence of free water in their habitats, food functions as the primary water source. The rodents would then be expected to select for the higher water-content of succulents and annuals. In contrast, higher energy requirements are experienced by the rats during the cold winter, thus the preference for perennials, as reported for *Thomomys bottae* (Gettinger 1984).

The diet of *O. unisulcatus* was more varied than that of *P. brantsii* over all seasons, except in winter (diversity and richness, Table 2). This difference between the diets is a result of their different habitats. Of the 28 plant species (15 listed in Table 1) eaten by *O. unisulcatus* but not by *P. brantsii*, none were recorded in *P. brantsii* habitat. Of the 13 plant species (seven listed in Table 1) unique to *P. brantsii*'s diet, four occur in *O. unisulcatus*'s habitat, but with a low availability (in winter, < 4% of total plant cover). Also, the lower diversity of plants eaten by *O. unisulcatus* in winter (Table 2) was a function of the significantly lower plant diversity in their habitat compared with that of *P. brantsii* ($t = 49.78$; $d.f. = 46868$; $p < 0.001$). In spring, summer and autumn the greater contribution of annuals to the *O. unisulcatus* diet may explain the higher diversity, compared with that of *P. brantsii*.

Limited overlap occurred between the diets of *O. unisulcatus* and *P. brantsii* in winter, when low temperatures limit plant production. The dietary overlap observed here contrasts with that of the North American woodrats *Neotoma* spp.), which are ecologically convergent with these two species (Du Plessis 1989). Dial (1988) demonstrated marked trophic resource partitioning between three *Neotoma* species. These differences in resource partitioning may be a consequence of the fact that these *Neotoma* species are syntopic, while *P. brantsii* and *O. unisulcatus* were not in the study area (Du Plessis & Kerley 1991), thus there would be no selective pressure to partition trophic resources.

Dietary overlap and similarities between *O. unisulcatus* and *P. brantsii* are thus a reflection of availability in their habitats. Competition between *O. unisulcatus* and *P. brantsii* for food resources is unlikely during critical periods. In their natural environment, partitioning of food resources does occur, owing to a spatial separation rather than a food habit separation. It was demonstrated that habitat segregation does occur between *O. unisulcatus* and *P. brantsii*, as the result of the constraints of their different refuge strategies (Du Plessis 1989). Therefore niche separation occurs by habitat specialization rather than by food specialization.

Acknowledgements

We thank Messrs C. van Rensburg, J.A. van de Vyver, P. Marincowitz, C. Marincowitz, L. Fouché and R.B. Kirkman for permission to work on their properties, and their kind hospitality; An de Ruyck, Dawn Flegg and Hendrik Jerling for assistance in the field; Sue Milton for identification of plant specimens, and Prof. T. Erasmus and two anonymous referees for comments on earlier drafts. The project was funded by the Foundation for Research Development as part of the Karoo Biome Project. Delta Motor Corporation assisted with transport.

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