

tests may have resembled these berries in shape more closely than they did the wild olives. Thus, it is possible that the thrushes perceived the pear pieces as more similar to *P. angastifolia* fruit, and for this reason, ate the orange pear pieces first; *P. angastifolia* berries are black when rotten, and would therefore probably be unpalatable.

Davison (1962) offered frugivorous birds several species of fruit of different colours, and observed that they ate similar quantities of different coloured fruits of different species. Davison concluded that colour was of little significance in fruit choice in birds. However, Davison did not consider that colour preferences by birds could vary according to the species of fruit offered, as has been demonstrated by McPherson (1988) and the present study. Similarly, Willson *et al.* (1990) found that colour was important in fruit selection in frugivorous birds, and that colour preferences varied according to the circumstances under which fruit were offered.

Two conclusions can be reached in the present study: (i) colour is important in fruit selection in olive thrushes; and (ii) colour preferences vary depending on the type of fruit offered.

Acknowledgements

We wish to thank the following: the staff, particularly Mr Quinton Coetzee, of the Johannesburg Zoological Gardens, Mr Barrie Sanders for technical assistance, and Dr Jackie Galpin for assistance with the statistical analysis.

References

- BURKHARDT, D. 1982. Birds, berries and UV. *Naturwissenschaften* 69: 153–157.
- DAVISON, V.E. 1962. Taste, not colour, draws birds to berries and seeds. *Audubon* 64: 346–350.
- FOSTER, M.S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* 58: 73–85.
- HERRERA, C.M. 1987. Vertebrate-dispersed plants of the Iberian peninsula: a study of fruit characteristics. *Ecol. Monog.* 57: 305–331.
- KANTAK, G.E. 1979. Observations on some fruit-eating birds in Mexico. *Auk* 96: 183–186.
- KNIGHT, R.S. & SIEGFRIED, W.R. 1983. Inter-relationships between type, size and colour of fruits and dispersal in southern African trees. *Oecologia* 56: 405–412.
- LEVEY, D.J. 1987a. Seed size and fruit handling techniques of avian frugivores. *Am. Nat.* 129: 471–485.
- LEVEY, D.J. 1987b. Sugar-tasting ability and fruit selection in tropical fruit-eating birds. *Auk* 104: 173–179.
- McPHERSON, J.M. 1988. Preferences of cedar waxwings in the laboratory for fruit species, colour and size: a comparison with field observations. *Anim. Behav.* 36: 961–969.
- MOERMOND, T.C. & DENSLOW, J.S. 1985. Neotropical avian frugivores: patterns of behaviour, morphology, and nutrition, with consequences for fruit selection. *Am. Ornithol. Union Monogr.* 36: 865–897.
- MOERMOND, T.C., DENSLOW, J.S., LEVEY, D.J. & SANTANA, E.C. 1987. The influence of context on choice behaviour: fruit selection by tropical birds. In: Quantitative analysis of Behaviour VI: foraging. (Eds) M. Commons, S. Shettleworth & A. Kacelnik. Lawrence Erlbaum Publ. pp. 229–254.
- RIDLEY, H.N. 1930. The dispersal of plants throughout the world. L. Reeve. Kent, England. 176pp.
- SALLABANKS, R. 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology* 74: 1326–1336.
- SORENSEN, A.E. 1983. Taste aversion and frugivore preference. *Oecologia* 36: 117–120.
- SNOW, D.W. 1971. Evolutionary aspects of fruit-eating by birds. *Ibis* 113: 194–202.
- STILES, E.W. 1982. Fruit-flags: two hypotheses. *Am. Nat.* 120: 500–509.
- WHEELWRIGHT, N.T. 1988. Fruit-eating birds and bird-dispersed plants in the tropics and temperate zone. *Trends Evol. Ecol.* 3: 270–274.
- WHEELWRIGHT, N.T. & JANSON, C.H. 1985. Colours of fruit displays of bird-dispersed plants in two tropical forests. *Am. Nat.* 126: 777–799.
- WILLSON, M.F., GRAFF, D.A. & WHELAN, C.J. 1990. Colour preferences of frugivorous birds in relation to the colours of fleshy fruits. *Condor* 92: 545–555.
- ZAR, J.H. 1984. Biostatistical analysis, 2nd Edition. Prentice-Hall Inc., New York.

Stomach contents of 19 species of small mammals from Swaziland

A. Monadjem

Department of Biological Sciences, University of Swaziland, Private Bag 4, Kwaluseni, Swaziland

Received 20 August 1996; accepted 12 November 1996

The stomach contents of 14 species of Rodentia and five species of Insectivora are reported from Swaziland. The importance of different food types in the diet of these species was estimated using two methods. The results of the frequency of occurrence method closely mirror those of the proportional contribution method. The rodents exhibited a wide range of diets. *Otomys* species were strictly herbivorous, while only three species (*Mus minutoides*, *Tatera leucogaster* and *Dendromus mystacalis*) were observed to have high proportions of all food types in their stomachs. All other rodents fed on green plant matter and seeds, in varying proportions. Shrews were predominantly insectivorous.

The diets of most southern African small mammals have been recorded as anecdotal observations (e.g. Rautenbach 1982; Skinner & Smithers 1990). More detailed studies have been conducted in the Karoo (Kerley 1989, 1992), KwaZulu-Natal Drakensberg (Rowe-Rowe 1986) and KwaZulu-Natal midlands forest (Wirminghaus & Perrin 1992). However, no detailed studies have been undertaken on small mammal diets in the extensive moist savannas of southern Africa. Furthermore, no previously published research has been conducted on any aspect of small mammal communities of Swaziland.

This study was conducted at eight localities (Table 1) in all four geographical regions of Swaziland. Sites varied greatly in climate, geology, altitude and plant community composition (Table 1). Rainfall is highest, and daily maximum and minimum temperatures are lowest, at the highveld sites. In contrast, the lowveld sites experience higher temperatures and a lower annual rainfall. The vegetation of the middleveld,

Table 1 Gazetteer of localities at which small mammals were caught. Also shown are each site's altitude, dominant vegetation type and geographical region within Swaziland

Area	Locality	Vegetation	Altitude (m)	Region
Malolotja Reserve	26°08'S 31°08'E	Sour grassveld	1460	Highveld
Malolotja Reserve	26°10'S 31°05'E	Montane forest	1440	Highveld
Ekundizeni farm	26°33'S 31°16'E	Open bushveld	700	Middleveld
Phophonyane	25°53'S 31°17'E	Thickets	600	Middleveld
Mutimuti Reserve	26°29'S 31°58'E	Forest/thickets	760	Lubombo
Mhlosinga Reserve	26°46'S 31°54'E	Acacia savanna	160	Lowveld
Tshaneni Dam	25°58'S 31°43'E	Broadleaved savanna	300	Lowveld
Mlawula Reserve	26°12'S 32°01'E	Acacia savanna	160	Lowveld

lowveld and Lubombo sites is typical bushveld (Acocks 1988), but can be further differentiated into more specific vegetation categories (Table 1). The one highveld site was located in sour grassveld while the other was in north-east mountain sourveld forest (Acocks 1988).

At least 30 Longworth live traps and 50 break-back mouse traps, baited with peanut butter and oats, were set at 10–15 m intervals for five consecutive nights at each site (for a minimum of 400 trap nights per site). Trapping was carried out between June and August 1994 in the austral winter. Small mammals caught in live traps were killed with chloroform in the field. The stomach contents of all specimens were immediately removed and preserved in 70% alcohol.

Where possible, five specimens of each species from each site were arbitrarily chosen for stomach analysis. The following four dietary categories were recognized: foliage (green plant material), seeds, insects and unidentified material (the latter category included bait and was removed from all subsequent analyses).

The importance of each food type was expressed in two ways: a) frequency of occurrence; and b) proportional contribution expressed as a percentage. Frequency of occurrence was calculated as the number of stomachs in which a particular food type was observed. Percentage contribution was determined as follows: the contents of each stomach were mixed gently and examined under a dissection microscope (Hansson 1970; Kerley 1989). An estimate of the relative cover of each food category in the microscope field was made for five randomly placed fields. The relative cover of each food type was then averaged over the five fields and expressed as a percentage. Since unidentified material was excluded from these analyses, the combined contribution of all food types adds up to 100%. The percentage contribution of each food type is presented together with standard errors (SE).

The stomachs of 100 rodents and 20 shrews were examined, of which three rodent and seven shrew stomachs were

empty (and have been omitted from all subsequent analyses). Insects were found in all shrew stomachs, but only in a relatively few rodent stomachs (Table 2). No seeds were found in shrew stomachs. In contrast, seeds and foliage were found in almost all rodent stomachs. Both *Otomys* species appeared to be strictly herbivorous, judging by the lack of seeds and insects in their stomachs. A high proportion (62.1%) of all stomach material comprised bait or could not be identified. Kerley (1989) also quoted a high percentage of unidentified material, which he attributed to the fact that the stomach contents had not been washed and sieved. The stomach contents were not cleaned in this study, which may also explain the high proportion of unidentified material. Since only relative proportions of food types, and not exact quantities, are required to compare and classify the diets of the different species (Kerley 1989), the high proportions of unidentified material should not detract from the value of this study.

The proportions of different foods in the stomachs of the small mammals corresponded closely to the frequency of occurrence of these foods (Table 2). Four feeding categories are apparent: herbivory, mixed granivory-herbivory, omnivory and insectivory. Both *Otomys* species contained only grass remains in their stomachs, an observation that concurs with other studies (Perrin 1980; Rowe-Rowe 1986; Kerley 1989). *Mus minutoides*, *Tatera leucogaster* and *Dendromus mystacalis* had high proportions or frequencies of all three food categories in their stomach contents suggesting omnivory, a conclusion reached by other studies (Hanney 1965; Perrin & Curtis 1980; Kerley 1989). Shrews are essentially insectivorous (Churchfield 1985; Rowe-Rowe 1986; Skinner & Smithers 1990), and all five species in this study had predominantly insect remains in their stomachs.

The majority of the rodent species fell under the category of mixed granivory-herbivory. *Lemniscomys rosalia*, *Rhabdomys pumilio*, *Aethomys namaquensis* and *Steatomys pratensis* had a greater proportion or frequency of foliage than seeds in their stomach contents; while *Mastomys natalensis*, *Saccostomus campestris*, *Rattus rattus*, *Dendromus mesomelas* and *Aethomys chrysophilus* had more seeds.

Aethomys chrysophilus, *A. namaquensis*, *L. rosalia* and *R. pumilio* are considered to be omnivorous, tending towards herbivory (Perrin & Curtis 1980, Rautenbach 1982; Churchfield 1985) or granivory (Rowe-Rowe 1986; Skinner & Smithers 1990). This study suggests that *A. namaquensis*, *R. pumilio* and *L. rosalia* show a tendency towards herbivory while *A. chrysophilus* shows a tendency towards granivory. *Steatomys pratensis* is described as granivorous (Perrin & Curtis 1980), while this study suggests that it is a mixed granivore-herbivore.

Mastomys natalensis is generally regarded as an omnivore (Perrin 1980; Swanepoel 1980; Rautenbach 1982; Skinner & Smithers 1990). Although *M. natalensis* was predominantly granivorous in this study, foliage also appeared to be an important food category. Arthropods, perhaps owing to a seasonal effect, comprised an insignificant proportion of the stomach contents. *Saccostomus campestris* has been classified as a granivore (Jacobsen 1977; DeGraaff 1981), an insectivorous granivore (Perrin & Curtis 1980) and an omnivore

Table 2 Proportional contribution ($\pm SE$) and frequency of occurrence (in brackets) of food types (both figures expressed as percentages) found in the stomachs of 19 species of small mammals, caught in Swaziland

Species	n	Foliage	Seeds	Arthropods	Dietary class
Rodentia					
<i>Otomys angoniensis</i>	1	100 (100)	0 (0)	0 (0)	Herbivore
<i>Otomys irroratus</i>	5	100 \pm 0 (100)	0 (0)	0 (0)	Herbivore
<i>Lemniscomys rosalia</i>	9	84.6 \pm 9.2 (100)	15.4 \pm 9.2 (55.6)	0 (0)	Herbivore-granivore
<i>Rhabdomys pumilio</i>	8	63.7 \pm 8.8 (100)	32.5 \pm 8.8 (100)	3.8 \pm 1.5 (25)	Herbivore-granivore
<i>Aethomys namaquensis</i>	6	59.8 \pm 11 (100)	40.2 \pm 11 (100)	0 (0)	Herbivore-granivore
<i>Steatomys pratensis</i>	2	61.2 (100)	38.8 (100)	0 (0)	Herbivore-granivore
<i>Mastomys natalensis</i>	19	20.3 \pm 5.4 (73.7)	78.6 \pm 5.9 (100)	1.1 \pm 1.0 (5)	Granivore-herbivore
<i>Saccostomus campestris</i>	1	33.3 (100)	66.7 (100)	0 (0)	Granivore-herbivore
<i>Rattus rattus</i>	3	38.4 \pm 7.5 (100)	61.2 \pm 7.5 (100)	0.4 \pm 0.4 (33.3)	Granivore-herbivore
<i>Dendromus mesomelas</i>	5	11.7 \pm 8 (60)	87 \pm 7.8 (100)	1.3 \pm 1.3 (20)	Granivore-herbivore
<i>Aethomys chrysophilus</i>	10	37.5 \pm 9.9 (80)	58.3 \pm 10 (100)	0 (0)	Granivore-herbivore
<i>Mus minutoides</i>	17	52.4 \pm 8.3 (82.3)	33.3 \pm 6.4 (82.3)	14.3 \pm 6.9 (29.4)	Omnivore
<i>Tatera leucogaster</i>	5	49.6 \pm 15 (100)	25.5 \pm 8.9 (100)	24.9 \pm 10.8 (80)	Omnivore
<i>Dendromus mystacalis</i>	6	44.1 \pm 15 (83.3)	39.7 \pm 14 (83.3)	16.2 \pm 8 (66.6)	Omnivore
Insectivora					
<i>Myosorex cafer</i>	2	25.2 (100)	0 (0)	74.8 (100)	Insectivore
<i>Myosorex varius</i>	4	2.9 \pm 2.8 (25)	0 (0)	97.1 \pm 2.99 (100)	Insectivore
<i>Crocidura mariquensis</i>	1	0 (0)	0 (0)	100 (100)	Insectivore
<i>Crocidura cyanea</i>	5	0 (0)	0 (0)	100 \pm 0 (100)	Insectivore
<i>Crocidura flavescens</i>	1	6.7 (100)	0 (0)	93.3 (100)	Insectivore

(Neal 1984; Kerley 1989). Results from the single stomach examined during this study suggest that *S. campestris* is a granivore.

The findings of this study generally agree with those of other similar studies. It must, however, be stressed that the data presented in this study were collected over a single winter season, and thus do not take into account seasonal variations in diet. Further research is required on both the effect of seasonality and habitat type on the diet of small mammals in Swaziland.

Acknowledgements

Gary Bronner, Graham Kerley and an anonymous reviewer are thanked for commenting on earlier drafts. Identifications were confirmed by the Transvaal Museum and voucher specimens are deposited there. Numerous landowners and farm managers allowed me free access to their property and helped with various logistical aspects of the study. Dr. H. Mwageni, the Director of Parks of Swaziland, and R.C. Boycott, Senior Warden of Malolotja Nature Reserve, arranged the relevant permits and allowed me access to the reserves of Swaziland.

Finally, thanks to Themba Nkambule and Qondile Mdziniso for assistance in the field, and to Qondile Mdziniso for analysis of the stomach contents.

References

- ACOCKS, J.A. 1988. Veld types of South Africa. *Mem. Bot. Surv. S. Afr.* 57: 1–146.
- CHURCHFIELD, S. 1985. Diets of two syntopic small mammals in the Inyanga National Park, Zimbabwe. *S. Afr. J. Zool.* 20: 65–67.
- DE GRAAFF, G. 1981. The rodents of Southern Africa. Butterworths, Durban.
- HANNEY, P. 1965. The Muridae of Malawi (Africa: Nyasaland). *J. Zool., Lond.* 146: 577–633.
- HANSSON, L. 1970. Methods of morphological diet microanalysis in rodents. *Oikos* 21: 255–266.
- JACOBSEN, N.H.G. 1977. An annotated checklist of the amphibians, reptiles and mammals of the Nylsvley Nature Reserve. *S. Afr. Nat. Sci. Prog. Rpt.* 21: 1–65.
- KERLEY, G.I.H. 1989. Diet of small mammals from the Karoo, South Africa. *S. Afr. J. Wildl. Res.* 19: 67–72.
- KERLEY, G.I.H. 1992. Trophic status of small mammals in the semi-arid Karoo, South Africa. *J. Zool., Lond.* 226: 563–572.
- NEAL, B.R. 1984. Seasonal feeding habits of small mammals in Kenya. *Z. Saugetierkunde* 49: 226–234.
- PERRIN, M.R. 1980. The feeding habits of two coexisting rodents, *Rhabdomys pumilio* and *Otomys angoniensis* in relation to rainfall and reproduction. *Acta Oecologica Oecol. Gener.* 1: 71–89.
- PERRIN, M.R. & CURTIS, B.A. 1980. Comparative morphology of the digestive system of 19 species of Southern African myomorph rodents in relation to diet and evolution. *S. Afr. J. Zool.* 15: 22–33.
- RAUTENBACH, I.L. 1982. Mammals of the Transvaal. *Ecoplan Monogr.* 1: 1–211.
- ROWE-ROWE, D.T. 1986. Stomach contents of small mammals from the Drakensberg, South Africa. *S. Afr. J. Wildl. Res.* 16: 32–35.
- SKINNER, J.D. & SMITHERS, R.H.N. 1990. The mammals of the Southern African Subregion. University of Pretoria, Pretoria.
- SWANEPOEL, C.M. 1980. Some factors influencing the breeding season of *Praomys natalensis*. *S. Afr. J. Zool.* 15: 95–98.
- WIRMINGHAUS, J.O. & PERRIN, M.R. 1992. Diets of small mammals in a southern African temperate forest. *Israel J. Zool.* 38: 353–361.