Food preferences of the vlei rat (*Otomys irroratus*) and the four-striped mouse (*Rhabdomys pumilio*)

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The food preferences of *O. irroratus* and *R. pumilio* have been examined in laboratory tests. *O. irroratus* prefers green vegetation including herbs, shrubs and grasses whereas *R. pumilio* prefers fruits and seeds. Both species eat insects in the laboratory, but they are more important in the natural diet of *R. pumilio* than *O. irroratus*. *O. irroratus* readily eats grasses which are not consumed by *R. pumilio*. Partial dietary overlap occurs in the laboratory which suggests that some degree of competition for fruits and seeds will occur at certain seasons in natural populations.
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Die voedselvoorkeure van *O. irroratus* en *R. pumilio* is in laboratoriumtoetse ondersoek. *O. irroratus* verkies groen gewasse met inbegrip van kruidgewasse, struike en grassoorte terwyl *R. pumilio* vrugte en sade verkies. Albei spesies eet insekte in die laboratorium, maar insekte is belangriker in die dieet van *R. pumilio* as van *O. irroratus*. *O. irroratus* eet geredelik grassoorte wat nie deur *R. pumilio* geëet word nie. In die laboratorium kom die dieet van die twee gedeeltelik ooreen wat daarop dui dat in sekere seisoene daar by natuurlike bevolkings 'n mate van mededinging om vrugte en sade sal voorkom.
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Stomach content analyses of the two most common rodent species of the Fish River Valley Scrub community have revealed that the vlei rat, *Otomys irroratus*, is a strict herbivore with its trophic niche contained within that of an opportunistic omnivore, the four-striped mouse, *Rhabdomys pumilio*, (Perrin *In press*). Although there was a possible 30 − 50% dietary overlap in winter, it seemed unlikely that competition between the two species was great. The aim of this study was to demonstrate some particular food preferences in each species, and hence to provide more information on competition for food. Food preference tests were employed (Drozdz 1966; Zemanek 1972) to supplement previous information from stomach content analyses (Perrin *In press*). Such tests indicate food preference or selectivity rather than what was eaten out of necessity.

Methods

Rodents and food plants for the preference tests were collected from a study area located in the Andries Vosloo Kudu Reserve, 30 km north-east of Grahamstown in the eastern Cape (33°8′ S, 26°39′ E) during February and March. The reserve is situated in the Fish River Valley Scrub which, in its undamaged state is an extremely dense, semi-succulent, thorny veld type (Acocks 1975) but overgrazing has opened up the vegetation on some parts of the Reserve, which has been invaded by prickly pear, *Opuntia ficus-indica*, and *Euphorbia bothae*. As this study was designed to demonstrate the extent of dietary overlap between two rodent species rather than provide a comprehensive survey of all the foods eaten, a random representative sample of the most abundant plants occurring on the reserve was collected. Plants were identified by comparison with specimens in the Albany Museum Herbarium.

Collected food items were separated into categories based on their approximate nutrient content (or quality) (Perrin *In press*) and their size and position in the habitat (availability). The six categories recognized were (1) grass stems and leaves; (2) grass seeds; (3) herbs (excluding fruits or seeds); (4) shrubs (excluding fruits or seeds); (5) fruits and seeds (of herbs and shrubs); and (6) insects. During the presentation of results and in the discussion it was convenient to combine groups (1) & (2); and (3) & (4), which can be regarded as graze and browse respectively. Drupes consisting of a hard stone and soft flesh were analyzed as separate entities. Herbs were offered as whole plants, including leaves, stems and occasionally flowers. However, only the leaves of large shrubs were offered to the rodents. The consumption of grass seeds was determined separately from that of stems and leaves. A range of freshly killed insects was offered to the rodents when available. Owing to its larger size *O. irroratus* was given larger samples of food than *R. pumilio.* Water and laboratory rat pellets were available *ad libitum* during the feeding trials to eliminate eating of unpalatable foods due to excessive hunger.

Food preferences were determined using the cafeteria test method of Drozdz (1975). Several plant species within each category, but not between categories, were offered to each of ten animals of each species at the start of a three-day test period. After 24, 48 and 72 h the amount of the original food consumed was recorded using an arbitrary four-point scale and later converted to percentages (Drozdz 1975) (Table 1). The mean consumption of each food item was calculated daily and categorized or ranked as follows.

Class 1
Preferred: 50% or more consumed on the first day of the test. These species would be taken most readily in the wild.

Class 2
Palatable: 30 – 40% consumed on the first day or more than 50% taken in total after three days. These species are less palatable than those of Class 1, but would be likely to form a substantial part of the natural diet.

Class 3
Unpalatable: 10 – 20% taken on the first day or 30 – 50% taken in total over the three day period. This food would only be eaten if species of the above two categories were not available.

Class 4
Inedible: None eaten on the first day and less than 30% taken in total after three days, or 10% taken on the first day, but thereafter not touched. These species are not likely to be consumed in the wild and would only be selected in cases of extreme food shortage. They may contain unpalatable toxins or physical defence mechanisms such as spines or numerous silica bodies.

The preferences of both rodent species were ranked linearly for all food items tested within a dietary category, in order to employ Mann–Whitney U tests (Sokal & Rohlf 1969: p. 391 – 4). These tests are based on the sequence or ordering of observations, in this case dietary preferences; they are semigraphical and nonparametric. Due to the small sample sizes, categories (1) and (2) were combined for ranking and analysis.

Table 1 An example of individual variation in food preference in four-striped field mice *(Rhabdomys pumilio)* in 10 separate tests. Food consumption was determined, using the cafeteria test and a four-point scale. Mean values and percentage consumption has been determined

	Rhabdomys pumilio											
Plant species	1	2	3	4	5	6	7	8	9	10	$\bar{X}$	%
Acacia karoo	1	0	1	1	1	0	1	1	1	1	0,8	20
Grewia robusta F	2	3	3	2	1	3	1	1	3	3	2,2	60
Grewia robusta S	1	2	3	1	1	1	1	0	1	2	1,4	40
Maytenus capitata	2	3	3	2	2	3	2	3	2	3	2,5	70
Ruschia sp.	1	3	3	1	3	3	3	3	1	3	2,5	70
Diospyros dichrophylla	0	0	0	3	0	0	0	0	0	0	0,3	10
Maytenus heterophylla	1	0	2	1	1	3	1	1	3	1	1,5	40
Lantana camara	3	3	3	3	3	3	3	3	3	3	3	90
Phyllanthus verrucosus	3	3	3	3	3	3	3	3	3	3	3	90
Cyphostemma quinata	0	0	0	1	0	0	2	0	0	1	0,4	10
Putterlickia pyracantha	3	1	0	2	0	1	1	2	1	0	1,1	30
Rhigozum obovatum	2	2	1	3	2	2	1	1	1	0	1,6	50

S = Stone. F = Flesh.

Results

The individual results of the food preference tests are presented in Tables 2 and 3, and demonstrate the potential food of each rodent species. Figure 1 shows the percentage of food consumed in each dietary category after one day of the feeding trials. It can be seen that there was an inverse relationship between the preferences of *O. irroratus* and *R. pumilio. O. irroratus* had a marked preference for grass seeds, stems and leaves, herbs and shrubs, but also ate insects, seeds and fruits. *R. pumilio* showed greatest preference for insects, seeds and fruits, with a lower preference for grass seeds, herbs and shrubs. Grass leaves and stems were not eaten by *R. pumilio.* The results of Mann-Whitney U-tests (Table 4) substantiate these findings but fail to demonstrate the preference shown by *R. pumilio* for insects over *O. irroratus.*

Seeds and fruits

Most of these foods were classified as either preferred or palatable to both *O. irroratus* and *R. pumilio. O. irroratus* showed a strong preference for the fleshy fruit of drupes over their stones. This preference was not so marked for *R. pumilio* which had an equally high preference for the stones and flesh of *Jasminum angulare* and *Pappea capensis.* The high preference of both rodents for *Lycium campulatum, Maytenus capitata, Lantana camara, Rhigozum obovatum, Asparagus africanus* and the flesh of *Jasminum angulare, Pappea capensis* and *Grewia robusta* suggest that there is overlap between the two rodent species for preferred fruits and seeds. Only two species, *Opuntia ficus-indica* and *Diospyros dichrophylla,* were classed as unpalatable foods of *O. irroratus,* and only *Zizyphus mucronata* stones and *Cyphostemma quinata* were inedible. *O. ficus-indica* was a preferred fruit of *R. pumilio,* but *D. dichrophylla* was unpalatable; *Ziyphus* stones and *Cyphostemma* were inedible.

Herbs and shrubs

Most of the herbs and shrubs were preferred by *O. irroratus* with only *Kalanchoë rotundifolia, Tecomaria capensis* and *Portulacaria afra* being classed as palatable rather than preferred. There were no unpalatable or inedible species for *O. irroratus.* The only preferred species of *R. pumilio* was *Hermania althacoides,* 14 were palatable, five unpalatable and only *K. rotundifolia* was inedible. These results show that all of the green plant material offered, with the excep-

Table 2 Food preference of *Otomys irroratus* and *Rhabdomys pumilio.* Each test was conducted over a three-day period and the percentage of each food species consumed per day was recorded. Preference categories (Column 4 for each species) are as described in the text

	Otomys irroratus					*Rhabdomys pumilio*				
Food species	One day	Two days	Three days	Prefer-ence	Rank-ing	One day	Two days	Three days	Prefer-ence	Rank-ing
Fruits and seeds										
Lycium campanulatum	90	–	–	1	2	90	–	–	1	1
Maytenus capitata	80	10	–	1	6	70	10	10	1	12
Jasminum angulare F	80	10	–	1	8	80	10	10	1	9
Jasminum angulare S	40	20	20	2	26	60	10	10	1	21
Ehretia rigida	80	–	–	1	10	–	–	–	–	49
Lantana camara	80	–	–	1	11	90	–	–	1	3
Maytenus heterophylla	70	10	10	1	13	40	20	10	2	28
Rhigozum obovatum	70	10	–	1	16	50	–	10	1	24
Asparagus africanus	70	–	10	1	17	70	–	–	1	18
Pappea capensis F	60	30	–	1	19	80	10	–	1	7
Pappea capensis S	20	30	10	2	39	80	10	–	1	5
Grewia robusta F	60	10	10	1	22	60	20	–	1	20
Grewia robusta S	30	20	10	2	35	40	10	10	2	30
Acacia karoo	50	10	10	1	23	20	10	30	2	40
Putterlickia pyracantha	40	20	20	2	27	30	30	20	2	33
Zizyphus mucronata F	40	20	10	2	29	30	10	20	2	36
Zizyphus mucronata S	–	10	10	4	47	10	10	–	3	43
Ruschia sp. 1	40	10	10	2	31	70	10	–	1	14
Passiflora coerulea	40	10	–	2	32	70	10	–	1	15
Phyllanthus verrucosus	30	30	10	2	34	90	–	–	1	4
Combretum caffrum	30	10	20	2	37	30	10	10	2	38
Scutia myrtina	20	10	20	2	41	–	–	–	–	50
Opuntia ficus-indica	–	20	10	3	44	50	–	–	1	25
Diospyros dichrophylla	–	10	20	3	45	10	–	–	4	46
Cyphostemma quinata	–	–	20	4	48	10	10	10	3	42
Herbs										
Cyperus teneriffae	90	–	–	1	1	40	20	–	2	15
Crassula tetragona	90	–	–	1	2	10	20	10	3	24
Anthospermum sp.	90	–	–	1	3	40	20	–	2	16
Stachys kuntzei	90	–	–	1	4	40	10	10	2	17
Crassula lycopodioides	80	10	–	1	5	30	10	10	2	20
Delosperma sp.	80	10	–	1	6	20	20	10	2	22
Commelina africana	80	10	–	1	7	40	–	10	2	18
Pentzia incana	70	–	20	1	8	20	30	–	2	21
Mohria caffrorum	70	–	–	1	9	10	10	–	3	25
Ruschia sp. 2	60	20	10	1	10	30	20	10	2	19
Helichrysum rosum	60	10	10	1	11	20	10	10	3	23
Crassula trachysantha	50	20	10	1	12	40	30	10	2	13
Kalanchoë rotundifolia	40	20	20	2	14	–	–	10	4	26
Shrubs										
Rhigozum obovatum	90	–	–	1	1	30	10	20	2	12
Asparagus suaveolus	80	–	10	1	2	20	10	10	3	15
Grewia robusta	80	–	–	1	3	20	10	–	3	16
Hermania althaeoides	70	10	10	1	4	50	–	10	1	7
Phyllanthus verrucosus	70	–	20	1	5	20	20	20	2	14
Hypoesta verticillata	50	10	10	1	6	40	–	10	2	10
Tecomaria capensis	40	20	–	2	9	20	30	10	2	13
Portulacaria afra	30	20	20	2	11	40	20	10	2	8
Moss	70	–	–	1	–	40	20	–	2	–
Grewia stems	50	10	–	1	–	20	20	–	2	–
Delosperma stems	80	10	–	1	–	40	20	10	2	–

Table 3 Food preference of *Otomys irroratus* and *Rhabdomys pumilio*. Tests were conducted over a period of one day for insects and two days for grasses. Figures indicate the percentage of each food eaten per day. Preference categories are as described in the text

	Otomys irroratus				*Rhabdomys pumilio*			
Food species	One day	Two days	Prefer-ence	Rank-ing	One day	Two days	Prefer-ence	Rank-ing
Insects								
Grasshoppers (Acrididae)	90	–	1	3	90	–	1	1
Termites (*Hodotermes mossambicus*)	50	–	1	6	90	–	1	1
Cockroaches (*Periplaneta americana*)	30	–	2	7	30	–	2	8
Mealworms (*Tenebrio molitor*)	30	–	2	9	90	–	1	4
Toktokkies (*Psammodes* sp.)	20	–	3	10	–	–	4	11
Crickets (Gryllidae)	–	–	–	12	90	–	1	5
Grass seeds								
Panicum sp. cf. *coloratum*	70	–	1	8	30	10	2	12
Eragrostis obtusa	80	–	1	4	30	20	2	11
Digitaria sp.	70	10	1	6	40	20	2	9
Setaria sp.	80	–	1	5	40	20	2	10
Grass stems and leaves								
Panicum sp. cf. *coloratum*	70	10	1	7	–	–	4	13
Panicum denstum	90	–	1	1	–	–	4	14
Sporobolus sp.	90	–	1	2	–	–	4	15
Cynodon dactylon	90	–	1	3	–	–	4	16

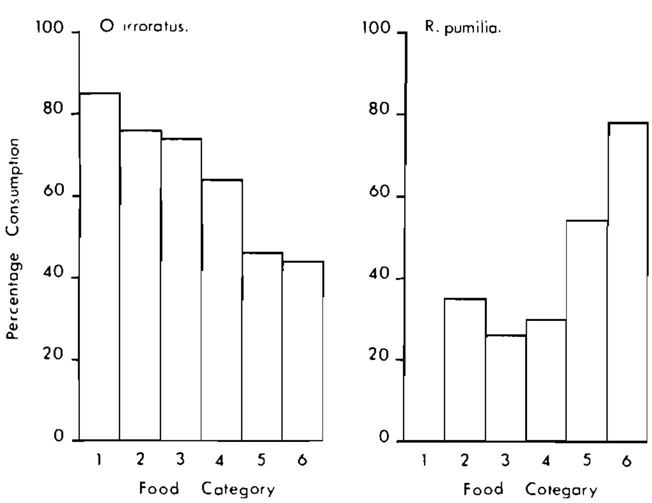

Fig. 1 Food preferences of *O. irroratus* and *R. pumilio*. Histograms indicate mean consumption of food after 24 h of testing. Food category 1 = grass stems and leaves, 2 = grass seeds, 3 = herbs, 4 = shrubs, 5 = fruits and seeds, 6 = insects.

tion of *K. rotundifolia*, is a potential food source for both rodents. However, *O. irroratus* shows a significant preference for herbage over *R. pumilio* (Table 4).

The stems of two shrub species were offered as food; both were readily eaten by *O. irroratus* but not by *R. pumilio*. Both rodents tended to strip bark from stems rather than eat the whole stem. The soft succulent stems of *Delosperma* sp. were consumed more extensively than the woody *Grewia robusta* stems. When herbs were offered as whole plants, *O. irroratus* ate the flowers and stems as well as the leaves, while *R. pumilio* ate only leaves. It appears therefore that the smaller rodent species is a more selective feeder within this food category. Moss was offered on one occasion and was readily eaten by *O. irroratus* but not by *R. pumilio*.

Table 4 Results of Mann-Whitney U-tests for the food preferences shown by *Otomys irroratus* and *Rhabdomys pumilio*

Food category	Preferred by	Mann-Whitney statistics	Signi-ficance
Fruits and seeds	*R. pumilio*	331	$p < 0{,}002$
Herbs	*O. irroratus*	168	$p < 0{,}001$
Shrubs	*O. irroratus*	59	$p < 0{,}005$
Insects	Neither	26	—
Grasses	*O. irroratus*	64	$p < 0{,}001$

Insects

The values indicated in Table 3 for insect preferences may be misleadingly high because insects were offered with only rat pellets as an alternative food. Since insects were usually offered dead, no prey capture was necessary. When offered live cockroaches and beetles, neither rodent would catch or kill them. Live grasshoppers and crickets were readily caught and eaten by *R. pumilio* but were rejected by *O. irroratus*. Both rodents preferred grasshoppers and termites as insect food, possibly because they are abundant in the study area. Insects were more readily eaten by *R. pumilio* than *O. irroratus*.

Grasses

All grass stems, leaves and seeds offered to *O. irroratus* were consumed, but only grass seeds were eaten by *R. pumilio*. This represents a marked difference in the feeding habits of these two coexisting rodents.

Discussion

Dietary overlap occurs for certain of the natural foods eaten by *O. irroratus* and *R. pumilio,* but their relative proportions differ. *O. irroratus* is predominantly herbivorous and selects large quantities of grasses and herbs in preference to fruits and seeds. Although insects were eaten during laboratory tests they do not form a substantial part of the natural diet (Davis 1973; Perrin *In press*). *R. pumilio* has a high preference for insects, seeds, and fruits but not for herbage. When eating herbage it has a greater preference for shrub leaves than herbs and shows considerable selectivity. *O. irroratus* is catholic in eating many types of green vegetation but unlike *R. pumilio* has a higher preference for herbs than shrubs, possibly because the whole herbaceous plant is edible. Grass, which forms a significant part (45%) of the natural diet of *O. irroratus* (Perrin *In press*) and is readily eaten in laboratory tests, is not consumed by *R. pumilio.*

One cause of food unpalatability may be due to toxins. For example, *Kalanchoë rotundifolia* is known to contain picrotoxins which attack the mammalian central nervous system causing paralysis (Steyn 1949). The leaves of this species, which are less toxic than the flowers and seeds, were avoided by *R. pumilio* but were palatable to *O. irroratus.* This might indicate some degree of adaptation to plant toxicity by the herbivorous *O. irroratus.*

Although food selection tests indicate food preferences they cannot demonstrate the composition of a natural diet. However, it is most valuable to compare food preferences with the results of stomach content analyses. Often the two approaches correlate well (Drozdz 1966, 1967; Zemanek 1972). Stomach content analyses (Perrin *In press*) from the study area revealed a mean abundance of 90 – 100% of green plant material throughout the year, but only negligible amounts of seeds and essentially no insects. Thus, *O. irroratus* will eat seeds and insects, as demonstrated by laboratory tests, but these items do not form a large or important part of the natural diet. Both approaches show that *O. irroratus* eats a substantial amount of woody material. Grass was a prominent dietary item in stomach analyses and in food tests. Sections of grass stems were found in *O. irroratus* runways, from which *Panicum* sp. and *Digitaria* sp. were identified, confirming that these grases are eaten in the wild.

Davis (1973) mentioned that *O. irroratus* ate nearly all plant species common to its distribution on a grid in the Transvaal. Although not all species from our study area were offered to *O. irroratus* in this study, those shrubs and herbs offered were readily eaten. *O. irroratus* does not appear to be a selective feeder within the category of green plant material. Perrin (*In press*) noted from numerous stomach content analyses that when leaves formed a large part of the diet the diversity of leaves eaten was low, suggesting selective feeding.

The results presented here indicate that *R. pumilio* selects fruits and seeds preferentially but readily eats insects and the leaves of some shrubs. The preference for herbage is low and grasses are not eaten. These findings correspond well with those from stomach content analyses from the same locality and time of year (Perrin *In press*). Marked changes in the composition and quality of the diet occur seasonally (Perrin *In press*) and *R. pumilio* appears to be an opportunistic feeder. In summer when insects and seeds are abundant these are taken in large quantities but during winter *R. pumilio* is compelled to eat less preferred herbs and shrubs. Regional as well as seasonal changes in diet are known to exist. In the Transvaal, *R. pumilio*'s diet consists of predominantly of seeds throughout the year, but in February and March much of the diet consists of white vegetable matter and few insects (Brooks 1974). In Uganda, grass probably forms an important component of the diet of *R. pumilio* (Delany 1975), and in Malawi, large quantities of green vegetation are taken (Hanney 1965), which contrasts strongly with the current results.

Seasonal changes in the composition and nutritive values of the diet are believed to be very important in the timing of breeding, reproductive tactics and the dynamics of these two coexisting rodents (Perrin *In press*), and in other rodent communities (Field 1975). The seasonality and intensity of breeding in opportunistic feeders appears to be correlated with the availability of insects or seeds in the diet (Perrin *In press;* Field 1975). Changes in the availability of nutrient foods (insects and seeds) are likely to influence foraging behaviour, diet quality, maternal nutrition and hence juvenile recruitment and population dynamics. In a herbivorous species such as *O. irroratus* which has morphological specializations to herbivory (Curtis 1978) and where green vegetation forms the major part of the diet, seasonal or year round breeding is likely. However, the low energy content of the diet might affect the lengths of gestation and weaning, litter size and hence reproductive success and rates of increase. Obviously differences in food preferences and availability can have very profound affects upon the coexistence and abundance of *O. irroratus* and *R. pumilio.*

Food preference tests at other seasons would demonstrate whether seasonal changes in stomach contents (Perrin *In press*) are due to changes in food availability and/or palatability. Studies on the nutritive values, toxicology and digestability of natural foods would be of great value in determining food selectivity by these two coexisting rodents.

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