

Differences in diet between two rodent species, *Mastomys natalensis* and *Gerbilliscus vicinus*, in fallow land habitats in central Tanzania[†]

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Received 10 April 2011. Accepted 5 October 2011.

Differences in the ecological niche requirements among rodent species competing in the same habitat may result from differences in the use of one to three resources: space, time and food or some combination of these. Alternatively, differences in resource use utilization among animal species may simply reflect availability of food, and when food is limited, different animal species compete. In this study, the diet of two rodent pest species, *Mastomys natalensis* and *Gerbilliscus vicinus*, coexisting in fallow land in central Tanzania were studied to assess the degree of diet differentiation among them. Dietary niche breadth of *G. vicinus* was greater than that of *M. natalensis* in all stages of the maize cropping seasons. The rodent species studied overlapped considerably in the food items consumed ranging from niche overlap (O_{jk}) of 0.77–0.89. Grains/seeds featured high in the diet of *M. natalensis* while plant material occurrence was high in *G. vicinus*. These two food categories may have contributed to differences in diet partitioning, which may, in turn, facilitate their coexistence in fallow land.

Key words: diet, fallow land, *Gerbilliscus vicinus*, *M. natalensis*, niche, resources.

INTRODUCTION

Biologists are interested in the way in which species differ in their utilization of resources (Krebs 1999). Theoretical and empirical studies have shown that partial separation of ecological niches in terms of diet or activity pattern or space is necessary to allow the coexistence of species (Giller 1984; Putman 1996). Resource partitioning among small mammal species has been the subject of numerous studies (Pianka 1973). However, competition is important when resources are limited (Bergalloand & Rocha 1994; Vrcibradic & Rocha 1996), but less important when resources are not limiting (Pianka 1973; Schoener 1974; Giller 1984). In this way, different species can overlap in habitat use and diet (Krebs 1999). For example, on

Mount Elgon, Clausnitzer *et al.* (2003) reported that *Crocidura montis* and *Lophuromys flavopunctatus* overlap in habitat occurrence, but *C. montis* ate a diversity of invertebrates while *L. flavopunctatus* ate some invertebrates in addition to plant materials. Therefore, information on overlapping of resource use is important for the understanding of species relationships.

In many countries in Africa, agricultural fields are surrounded by fallow land, which can provide suitable sites for shelter and breeding for rodents, while grasses and weeds may provide supplementary food (Mwanjabe 1993). Fallowland matrices thus serve as refuges for rodents that infest crop fields. Makundi *et al.* (1991) reported that in Tanzania, over 20 rodent genera and species are involved in crop damage in various parts of the country. *Mastomys natalensis* is the most destructive rodent pest in the country (Makundi *et al.*

[†]Paper presented at the 4th International Conference on Rodent Biology and Management (ICRBM), 12–16 April 2010, Bloemfontein, South Africa.

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1991). In different localities, however, other rodent pest species such as the African giant rat (*Cricetomys gambianus*), cane rat (*Thryonomys* spp.), gerbils (*Gerbilliscus* spp.), spiny mice (*Acomys* spp.), striped grass mouse (*Lemniscomys* spp.), crested porcupine (*Hystrix cristata*), ground squirrels (*Xerus* spp.) and mole rats (*Tachyoryctes* spp. and *Cryptomys* spp.) are found (Fiedler 1994; Makundi *et al.* 1991).

In central Tanzania, the major rodent pest species found in fallow land are *M. natalensis* and *G. vicinus*, both being nocturnal (Makundi *et al.* 2009). The mechanism by which these two rodent pest species partition and utilize their food has not been studied. Studies by Odhiambo *et al.* (2008) and Mulungu *et al.* (in press) reported that *M. natalensis* is opportunistic and consumes many types of food in frequencies reflecting the availability of food items in its habitat. Similarly, Odhiambo *et al.* (2005) reported that *Gerbilliscus vicinus* is omnivorous, but seeds were the most preferred diet category (mean contribution of 50.4%), followed by arthropods (25.7%), with other plant materials such as leaf, roots and stems being important during very dry periods.

The feeding ecology of *M. natalensis* and *G. vicinus* might be sufficiently different to allow their coexistence in fallow land (Dunham 1983; M'Closkey & Baia 1987). However, their diets are more similar in habitats with limited resources, at least in some seasons (Odhiambo *et al.* 2005, 2008). Because of the sympatric distribution of *M. natalensis* and *G. vicinus* in central Tanzania, the question of how these species interact is important for management strategies. In order to understand the factors allowing the coexistence between these species, we determined the dietary niche differences and resource utilization by these two species at one site only.

MATERIALS & METHODS

Location and trapping

The study was carried out at Berega village (06°10'S, 37°5'E, 840 m. a.s.l.), Kilosa district, Morogoro region, Tanzania between March 2008 and February 2009. The study area is dominated by cultivated fields and fallow land, with maize being the main crop. Trapping sessions were thus timed to coincide with the cropping (February to May), harvesting (June to July), and non-cropping (August to November) seasons for maize.

We conducted monthly trapping of rodents in

one mosaic fallow field using Sherman LFA Live Traps (7.5 by 9.0 by 23.0 cm; H.B. Sherman Traps, Inc., Tallahassee, FL) and snap (kill) traps (1.0 × 8.5 × 16.5 cm). Twenty-five snap traps and 25 Sherman live traps were placed at alternate stations along a trap line at a distance of 10 m apart for three consecutive nights per month. Five trap lines were set per field.

The traps were baited with a mixture of peanut butter and maize bran; they were set in the afternoon and checked early the morning. Trapped animals were collected and identified to species level following the established taxonomic nomenclature (Kingdon 1997). Only individuals with full stomachs (pylorus and cardium) collected from snap traps were removed, placed in labelled small bottles and preserved in 70% alcohol for food category analyses (micro-histological examination of undigested potential bias, digested food preferred fragments).

Data collection

The preserved stomach contents were opened and spread out in a Petri dish and sorted under ×25 or ×50 magnifications using a binocular microscope. Seven food categories were examined in each stomach, *viz.* seed/grain, plant materials (roots, stem, and leaves), invertebrates (beetles, worms, etc.), pods, fruits, hairs, and other unidentified materials. If necessary, a lugol solution was used to determine the presence of starch to indicate the presence of seeds/grain.

Data analysis

As described by Smith *et al.* (2002), percentage contribution of each food category to the volume of the particular stomach's contents (PV) was estimated to the nearest 10% (crude) percent, with an additional category of 5% where an item was present but contributed <10% to stomach-content by volume. Percentage occurrence (PC) of a particular food item in a sampling period was calculated from the number of stomachs it was found within, divided by the number of stomachs examined. Diet variety was taken to be the number of diet food categories recorded in the sampling period, and diet diversity was calculated following Ebersole & Wilson (1980) using Levins' index (Levins 1968).

$$\frac{1}{\sum p_i^2},$$

where P (= PV) is the percentage value of each of

Table 1. Percentage occurrence of the most important food categories in the diets of *Mastomys natalensis* and *Gerbilliscus vicinus* in fallow land during the different seasons of the maize cropping calendar.

Food type	Rodent species and crop season					
	<i>M. natalensis</i>			<i>G. vicinus</i>		
	Maize cropping period (n = 21)	Maize harvesting period (n = 15)	Non maize cropping period (n = 9)	Maize cropping period (n = 8)	Maize harvesting period (n = 6)	Non maize cropping period (n = 12)
Seeds/grains	100.00	100.00	100.00	87.46	100.00	100.00
Plant material	85.71	83.33	88.89	100.00	100.00	100.00
Pods	38.10	33.33	55.56	24.96	100.00	0.00
Invertebrates	90.48	83.33	88.89	100.00	33.33	89.56
Hairs	80.95	53.00	33.33	74.96	33.33	100.00
Others	100.00	100.00	100.00	100.00	100.00	100.00

the diet categories. Levins' index ranges from 1 to n (n = total number of food categories) and was used to calculate diversity indices for different seasonal samples of *M. natalensis* and *G. vicinus*. Diversity was standardized to a scale of 0.0 to 1.0 by using Hurlbert's method (Krebs 1989).

$$B_s = \frac{(B - 1)}{(n - 1)},$$

where B_s is Levins's standardized niche breadth, B is Levins's measure of niche breadth, and n is the number of possible resource states. An importance value ($IV = PV \times PC/100$) was also calculated for each diet item (Cooper & Skinner 1978). The relative importance value of a particular item was taken as the importance value of that item expressed as a percentage of the sum of the importance values for all items ($100 \times IV/\Sigma IV$).

Niche overlap measure was computed using the following symmetric formula (Pianka 1973, 1974):

$$o_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}},$$

where, O_{jk} = Pianka's measure of niche overlap between species j and k , p_{ij} and p_{ik} = are proportions of the i th resource used by the j th and k th species, respectively. Overlap values obtained from this equation vary from zero (no overlap) to one (total overlap).

Statistical evaluation of the diet categories across different seasons and species were done using a two-way analysis of variance (ANOVA) by the statistical package SAS (1990). Analyses based on percent food categories were arcsine transformed in order to normalize.

RESULTS

A total of 45 and 26 stomachs of *M. natalensis* and *G. vicinus*, respectively, were analysed with respect to percentage food occurrence in relation to maize cropping calendars (Table 1). Significant difference ($F_{1,2} = 75.8, P = 0.01$) was observed between species on plant materials occurrence. Plant material occur more in *Gerbilliscus vicinus* stomachs (100%) than in *M. natalensis* (85.9%). However, no significant ($P > 0.05$) differences in plant materials occurrence between seasons were observed. Similarly, no significant differences were observed of other food categories both for rodent pest species and across the seasons.

Seeds/grains contributed more to the diet of both rodent species during the maize cropping and harvesting periods (Table 2). In general, seeds/grains predominated in the diets of individuals of both rodent pest species (Table 2) and a significant difference ($F_{1,2} = 27.78, P = 0.03$) was observed between the species. *Mastomys natalensis* consumed more seeds/grains (54%) than *G. vicinus* (37.5%). However, no significant ($F_{2,2} = 11.4; P = 0.08$) differences between seasons were observed. Similarly, no significant differences were observed for contribution of other food categories both for rodent pest species and seasons.

The two rodent species differed significantly in niche breadth ($F_{1,2} = 0.09, P = 0.02$) but this did not vary with season ($F_{2,2} = 0.003, P = 0.72$). However, food diversity of *M. natalensis* was relatively lower during the maize harvesting period (Table 3). The food diversity of *G. vicinus* was relatively high in all three maize cropping seasons (Table 3).

Niche overlap between *M. natalensis* and *G. vicinus*, which varied from 0.77–0.89, was generally

Table 2. Percentage contribution of the most important food categories in diet of *Mastomys natalensis* and *Gerbilliscus vicinus* in fallow land and different seasons of maize cropping calendar.

Food type	Rodent species and crop season					
	<i>M. natalensis</i>			<i>G. vicinus</i>		
	Maize cropping period (n = 21)	Maize harvesting period (n = 15)	Non maize cropping period (n = 9)	Maize cropping period (n = 8)	Maize harvesting period (n = 6)	Non maize cropping period (n = 12)
Seeds/grains	59.52	61.67	41.11	37.50	45.00	30.00
Plant material	4.76	5.00	23.33	23.13	8.33	12.50
Pods	1.90	1.67	3.89	1.25	36.17	0.00
Invertebrates	14.52	20.00	15.00	13.75	1.67	20.00
Hairs	5.00	2.50	2.22	3.75	1.67	5.00
Others	13.57	9.17	14.44	20.63	6.67	32.50

Table 3. Niche breadth (\pm S.E.) and niche overlap for dietary partitioning between *Mastomys natalensis* and *Gerbilliscus vicinus* in fallow land and different seasons of maize cropping calendar.

Cropping calendar	Rodent pest species		Niche overlap (Q_{jk})
	<i>M. natalensis</i> (n = 45)	<i>G. vicina</i> (n = 26)	
Maize cropping period	0.24 \pm 0.05	0.49 \pm 0.04	0.89
Maize harvesting period	0.22 \pm 0.05	0.57 \pm 0.04	0.77
Non maize cropping period	0.45 \pm 0.05	0.51 \pm 0.04	0.88
Yearly	–	–	0.94

high in all three maize cropping seasons and throughout the year (Table 3). However, relatively higher values were observed during the maize cropping and non maize cropping season (Table 3).

DISCUSSION

The two rodent species were diet generalists and opportunists, consuming almost all food types in proportion to their abundance in the environment (Odhambo *et al.* 2005, 2008). A major difference between the diets of the two species was the consumption of plant materials, ingested in abundance by *G. vicinus* while *M. natalensis* ingested only small amounts. *Gerbilliscus vicinus* consumed predominantly plant materials while *M. natalensis* ate more seeds/grain.

Gerbilliscus vicinus had a relatively larger niche breadth for all maize cropping seasons. The larger niche breadth may be attributed to its larger size; however, no data are given on size differences between the species, which determines, in many cases, the types of food categories consumed (Keeley & Grant 1997; Anderson & Mathis 1999; Karpouzi & Stergiou 2003). This could have impor-

tant consequences in the ability to consume varieties of food categories and satisfy their higher energetic needs due to their weight differences. *Mastomys natalensis* having lower niche breadth could be due to a marked dependence on seeds/grains across the seasons.

Mastomys natalensis and *G. vicinus* also overlapped considerably in their food niche. In part, the differences may be due to the differences in the proportion of plant materials they consumed. For *G. vicinus*, plant materials were the most frequently consumed items, while for *M. natalensis* seeds/grains were the important food resource. Probably seeds/grains and plant materials do have a homogeneous distribution in fallow land over time since no difference was observed between seasons.

The empirical approach to the ecological coexistence problem is embodied by resource partitioning studies; both make the assumption that communities are competitively structured (Gordon 2000). But other processes beyond interspecific competition, such as predation, parasitism, environmental variability and heterogeneity, set more

important limits to the growth of natural populations (Gordon 2000) and coexistence of species (Colli *et al.* 1992). In addition, variation in the use of time, space and food result from two or more factors, such as competition, predation, morphological and physiological constraints (Schoener 1974) and which may interact (Putman 1996). The wide niche overlap documented here does not necessarily indicate competition, because if resources are not in short supply, two organisms can share them without detriment to one another (Pianka 1974). Because of this, the overlap in the use of the resources may be directly related to the degree of environmental heterogeneity.

We conclude that the two rodent species in central Tanzania differ in the food categories preferred in fallow land, which is the most important niche dimension segregating the two species from competition. This may result from the larger food niche breadth of *G. vicinus* compared with that of *M. natalensis*, which in turn, may be due to differences in the proportion of plant materials consumed by *G. vicinus* and seeds/grain consumed by *M. natalensis*, thus permitting coexistence.

ACKNOWLEDGEMENTS

This work was supported by the ECORAT Project, financed by the European Union and the Southern African Development Community (SADC) Secretariat through the Implementation and Coordination of Agricultural Research and Training programme. The contents are the sole responsibility of the authors and can under no circumstances be regarded as reflecting the position of the SADC Secretariat or the European Union. Loth S. Mulungu acknowledges financial support received through a South–North mobility scholarship from the Flemish Interuniversity Council (VLIR-UOS). We appreciate the excellent field assistance from Khalid S. Kibwana and G. Mhamphi of Pest Management Centre, Sokoine University of Agriculture, Morogoro, Tanzania.

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