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Dietary differences of the multimammate mouse, *Mastomys natalensis* (Smith, 1834), across different habitats and seasons in Tanzania and Swaziland

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Abstract

Context. The multimammate mouse, *Mastomys natalensis* (Smith, 1834), is an important agricultural pest in southern and eastern Africa where it can cause significant crop losses. *Mastomys natalensis* is known to consume a variety of food in response to the availability of food items. However, it is currently unknown whether maize crop growth stages affect the spatio-temporal diet of this species.

Aims. We examined the foods consumed by *M. natalensis* in different habitats and seasons in central Tanzania and Swaziland.

Methods. Diet was investigated in Tanzania in four different habitats (woodland, vegetable gardens, maize fields and fallow land) during different maize crop growth stages between March 2008 and February 2009. In Swaziland, this was conducted in three habitats (fallow land, cultivated fields and pristine land) during three crop growth stages (pre-planting, vegetative stage and post-harvest) between March 2008 and April 2009. Micro-histological examination of undigested fragments from the stomachs of trapped animals was made whereby the preserved stomach content was placed in a Petri dish and sorted using a 25× or 50× magnification binocular stereoscope. Stomach contents were identified as: grain and/or seeds (both grasses and maize), plant material (roots, stems and leaves), invertebrates, pods of seeds, fruits (vegetable fruit such as tomato), animal hairs and unidentified matter. If necessary, a lugol solution was used to determine the presence of starch for maize and grass seeds or grains.

Key results. In both countries, grain predominated in the diet of *M. natalensis*. Statistical analyses showed that there were no differences due to seasons or habitats. Therefore, the percentage volume and relative importance were the same across habitats and seasons in both countries.

Conclusions. Our findings highlight clearly that *M. natalensis* is a generalist species feeding on available resources depending on the season and the habitat. Its preference for grain may account for its abundance in maize plantations and confirms it as one of the major pests in crop plantations, especially grain.

Implications. This information offers a useful tool for determining the pest status in different habitats and/or seasons. The findings of this study have implications for agriculture and conservation.

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Introduction

The multimammate mouse, *Mastomys natalensis* (Smith, 1834), is an important pest in southern and eastern Africa where it can cause significant crop losses (Makundi *et al*. 1999). In addition, this species is a carrier of plague (Monath 1975; Dippenaar *et al*. 1993). In Tanzania, for example, where a diverse array of different rodent species coexist (Stanley and Hutterer 2007; Mulungu *et al*. 2008; Makundi *et al*. 2010), *M. natalensis* has been implicated as the single most important rodent pest (Leirs and Verheyen 1995; Mdangi 2009). Mdangi (2009) reported rodent damage of up to 48% caused by *M. natalensis* in farmers' fields with a rodent population density of just 18 animals per ha. It is not unusual for damage to maize to exceed 80% in certain cropping seasons and locations (Mwanjabe and Leirs 1997; Mulungu *et al*. 2003) during rodent outbreaks (Mwanjabe *et al*. 2002). *Mastomys natalensis* is also the predominant rodent in Swaziland (Monadjem 1997*a*, 1999), particularly in disturbed habitats (Monadjem and Perrin 1998), although its impact on crop production has not yet been assessed.

Odhiambo *et al*. (2008) reported that *M. natalensis* is an opportunistic feeder consuming all types of food in different frequencies reflecting the availability of food items in its habitat. Variation in food supply of small mammals in different habitats has been reported (Bomford 1987). Odhiambo *et al*. (2008) reported that, although *M. natalensis* had a wide range of food items in its diet, there was a clear seasonal effect on the consumption of different food categories. They fed more on seeds, arthropods and grasses during the wet season and on other plant materials during the dry season in the south-west of Tanzania. Similar findings have been reported elsewhere in the species' range (Monadjem and Perrin 2003).

It is currently not known whether the diet of this species differs across Africa in relation to habitat, season and/or the maize cropping cycle. Determining the food habits of a particular rodent species is a fundamental issue in understanding its ecology (Litvaitis 2000). On the basis of dietary information, we can understand the relationship between prey and predator and the feeding niche of a species within an ecosystem. Dietary information is essential for understanding foraging behaviour (Lind and Welsh 1994), habitat use (Reinert 1993) and migration activities (Forsman and Lindell 1997). The present study is therefore aimed at determining whether the diet of this rodent changes in response to seasonal food availability. This information is useful for developing strategies for reducing damage to maize crops caused by this rodent pest.

Materials and methods

Study sites and trapping

The study was carried out in eastern and southern Africa. The eastern African study site was in Berega village (06°10′S; 37°5′E, 840 m above sea level, a.s.l.), Kilosa District, Morogoro Region, Tanzania and fieldwork was conducted from March 2008 to February 2009. The southern African study site was in Lobamba (26°27′S; 31°12′E, 690 m a.s.l.), Hhohho Region, Swaziland and the study was conducted from March 2008 to April 2009. In Tanzania, we conducted monthly trapping of rodents in four habitats (namely, vegetable gardens, maize fields, fallow land and woodland) using Sherman LFA live traps (7.5 × 9.0 × 23.0 cm; HB Sherman Traps, Tallahassee, FL, USA) and snap (kill) traps (1.0 × 8.5 × 16.5 cm). These sample habitats were small and surrounded by maize crops on either one or two sides. 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 habitat per month. Traps were baited daily using a mixture of peanut butter and maize bran. In Swaziland, rodents were also trapped monthly in fallow land (area where maize was previously cultivated but left uncultivated for two or more years), maize field and grazing land (for cattle and goats) using 100 Sherman live traps in each habitat. The traps were set 5 m apart along a line transect and were baited with a mixture of peanut butter and maize bran; they were set in the afternoon and checked early in the morning for three consecutive nights per month. The major food crop cultivated in the Tanzanian study area was maize, and trapping sessions were categorised based on cropping (December–May), harvesting (June–July) and non-cropping (August–November) seasons. In Swaziland, the cultivated fields were categorised as pre-planting (October–November), vegetative stage (December–February) and post-harvest (March), while the fallow and 'pristine' lands remained as such for the duration of the study. In both sites, the stomachs of trapped individuals were removed, placed in labelled small bottles and preserved in 70% alcohol for food category analyses (micro-histological examination of undigested fragments).

Stomach content analysis

In the laboratory, the preserved stomach contents were spread out in a Petri dish and sorted under a binocular stereoscope, using 25× and/or 50× magnification as described by Smith *et al*. (2002). In the Tanzanian study, stomach contents were identified as grain (seeds), pods, fruits, other plant material (roots, stems and leaves), invertebrates, animal hairs and unidentified matter. In the Swaziland study, stomach contents were identified as grain, other plant material (including fruits and pods), invertebrates and unidentified matter. If necessary, a lugol solution was used to determine the presence of starch for maize seeds or grains (Smith *et al*. 2002).

Data analysis

In both studies, the method used was as described by Smith *et al*. (2002) where average percentage volume (PV; the contribution of each item to the volume of the particular stomach's content) was estimated to the nearest 10%, with an additional category of 5% where an item was present but contributed <10% to stomach content volume. Diet variety was the number of dietary items recorded per individual during the sampling period and diet diversity was calculated following Ebersole and Wilson (1980) as Levins' index (Levins 1968), as:

$$1/\sum Pi^2 \tag{1}$$

where P (= PV/100) is the mean proportion in volume of each of the dietary items. Levins' index ranges from 1 to n (n = total number of food item categories) and was used to calculate seasonal diet diversity for the different habitats. Diversity was standardised to a scale of 0–1 using Hurlbert's method (Krebs 1989):

$$B_s = (B - 1)/(n - 1) \tag{2}$$

where B_s is Levins' standardised niche breadth, B is Levins' measure of niche breadth, and n is the number of possible resource states. The combination of PV and percentage contribution (PC; the percentage of the total number of stomachs in which a particular food item has been detected) was used to calculate an importance value (IV = PV × PC/100) for each dietary item (Cooper and Skinner 1978). The relative importance (RI) value of a particular item was taken as the importance value of that item expressed as an average percentage of the sum of the importance values for all items (100 × IV/$\sum$IV).

A two-way ANOVA was used to test for differences in diet across different habitats and seasons using the statistical package SPSS 12 (Polar Engineering and Consulting, Dynelytics AG, Zurich, Switzerland).

Results

Habitat and seasonal effect

In Tanzania, in total, 96 *M. natalensis* individuals were trapped: 44 in maize fields, 21 in fallow land, 15 in woodland and 16 in vegetable gardens. In general, grain predominated in the diet of individuals in all habitats, followed by invertebrates (Table 1). Other food categories were less prevalent in all habitats, except plant material and fruit, which were second to grain in the woodland and vegetable garden habitats, respectively (Table 1). A fairly large percentage of material (10.6–15.9% volume) could not be identified.

In Swaziland, in total, 52 *M. natalensis* individuals were trapped (Table 2). Grain was present in 100% of the stomachs, plant material in 98.9% and invertebrates in 66.4%. Unidentified matter was found in 17.7% of stomachs. Generally, grain predominated in the diet of individuals in all habitats (mean PV > 35%), followed by plant materials (PV > 27%) (Table 2).

Seasonal variation in diet in different habitats

Percentage contribution

Invertebrates also contributed markedly to the diet of *M. natalensis* in fallow land during the cropping and harvesting sampling periods; in maize fields during the cropping period, in woodland during the non-cropping period and in vegetable gardens during the harvesting period. Plant material contributed most (>18%) to the diet of *M. natalensis* in the woodland during the non-cropping period, and in the vegetable gardens during the maize harvesting period. Fruit contributed most (>20%) to the diet in vegetable gardens during the maize harvesting and non-cropping periods (Fig. 1).

In Swaziland, the proportional contribution (PC) of the four food items was similar across the three habitats (i.e. fallow, cultivated and pristine). Grain dominated the stomach contents in all habitats (Fig. 2), closely followed by plant material. Invertebrates contributed less than 15% in all habitats, while unidentified material contributed between 14 and 22%. The relative importance of these food categories closely followed the relative pattern observed for PV (Fig. 2*b*).

Relative importance

Seeds and grain were more important in the diet of *M. natalensis* in fallow land during the cropping and non-cropping sampling periods, in maize fields during the harvesting period, in the woodland during the cropping and harvesting periods and in the vegetable gardens during all cropping periods. Plant materials were more important (>25%) in the diet of *M. natalensis* in the woodland during the non-cropping period. Fruit was more important (>20%) in the diet of *M. natalensis* in the fallow land during the maize harvesting and non-cropping periods. Invertebrates were more important (>30%) in the diet of *M. natalensis* in the vegetable garden during the cropping and harvesting period (Fig. 3).

Niche breadth

In Tanzania, food diversity was lowest in the maize fields and woodland during the harvesting period, the period when maize completely dominated as food sources (Table 3). In vegetable gardens, the opposite was found, with diversity of food taken being highest in the maize harvesting period. Food diversity remained similar in fallow land throughout the study period.

In the Swaziland study, food diversity was generally high in all habitats in all seasons (Table 4). This observation excludes pristine land in the non-cropping season, as calculation of Levins' index could not be done given that only one specimen was caught. *Mastomys* utilises the highest diversity of food items in maize fields during the cropping season. The lowest diversity was observed in fallow land during the non-cropping season. Food diversity was generally high in the cropping season and low in the non-cropping season.

Table 1. Average percentage volume of food items (±s.e.) in stomachs of *Mastomys natalensis* across all samples in different habitats in Tanzania

Food categories	Maize fields (*n* = 44)	Fallow land (*n* = 21)	Woodland (*n* = 15)	Vegetable gardens (*n* = 16)
Grain	59.20 ± 4.76	55.23 ± 6.32	55.33 ± 7.68	46.56 ± 8.49
Plant material	5.34 ± 0.84	5.24 ± 0.64	15.33 ± 5.99	7.50 ± 2.42
Pods of seed	1.93 ± 0.69	1.67 ± 0.63	3.33 ± 0.80	0.94 ± 0.50
Invertebrates	12.16 ± 2.59	18.10 ± 4.53	12.00 ± 3.96	10.31 ± 3.34
Animal hairs	3.86 ± 0.58	4.29 ± 0.99	3.33 ± 0.80	2.50 ± 0.65
Fruits	3.41 ± 1.99	0.00 ± 0.00	0.00 ± 0.00	15.00 ± 5.63
Unidentified	13.75 ± 2.53	14.76 ± 3.19	10.67 ± 2.71	15.94 ± 3.42

Table 2. Average percentage volume of food items (±s.e.) in stomachs of *Mastomys natalensis* across all samples in different habitats in Swaziland

Food categories	Maize fields (*n* = 31)	Fallow land (*n* = 11)	Pristine land (*n* = 10)
Plant material	27.80 ± 4.30	30.61 ± 4.33	31.10 ± 4.45
Grain	35.15 ± 3.37	42.73 ± 2.01	41.62 ± 3.45
Invertebrates	15.02 ± 3.02	11.70 ± 5.15	9.00 ± 3.92
Unidentified	22.05 ± 3.09	14.95 ± 2.10	18.28 ± 3.35

Discussion

Grain was the dominant food type for *M. natalensis* in the study area. This agrees with the findings reported by Odhiambo *et al.* (2008). Other food types, including plant material and invertebrates, occurred in relatively smaller quantities. Leirs and Verheyen (1995) and Field (1975) reported that seeds are an important food category during the breeding season, which is required to meet the high energy needs of a reproducing organism. Furthermore, proteins are very important during pregnancy (Field 1975), an observation supported by the findings of Monadjem (1998) who showed that both seeds and invertebrates increased in the diet of *M. natalensis* in Swaziland during the breeding season. This is consistent with the large proportion of invertebrates in the diet of *M. natalensis* during some seasons of this study. It has been reported that the presence of secondary plant compounds may

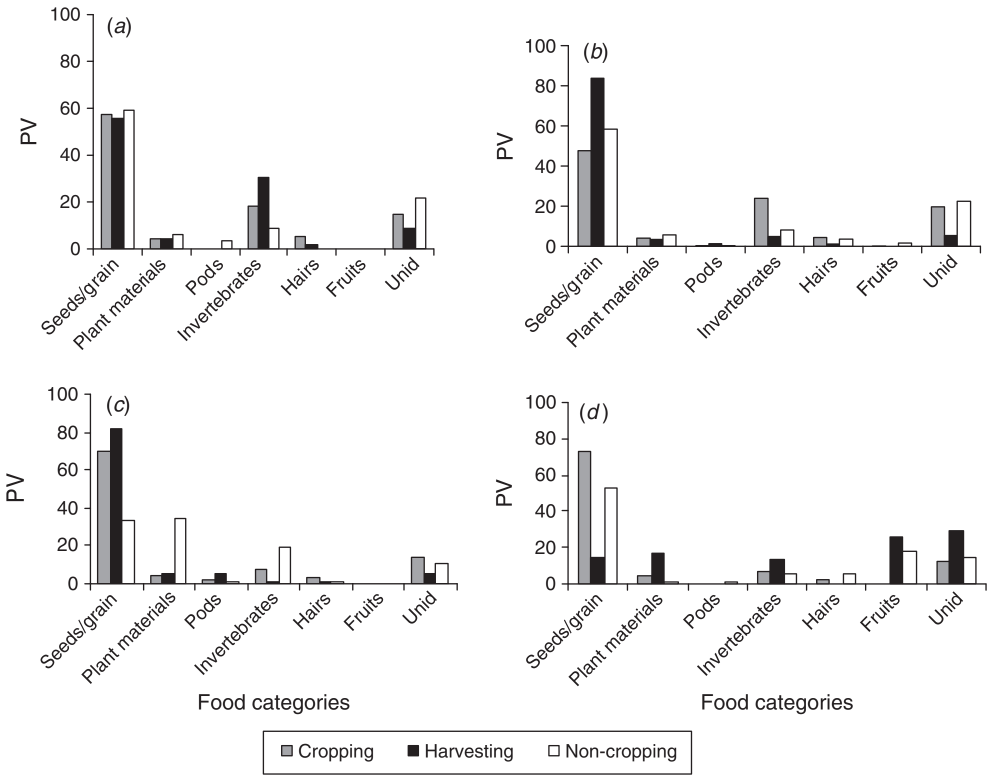

Fig. 1. Mean percentage volume of different food categories to the diet of *Mastomys natalensis* in different habitats and seasons in Tanzania: (*a*) fallow fields, (*b*) maize fields, (*c*) woodland and (*d*) vegetable gardens.

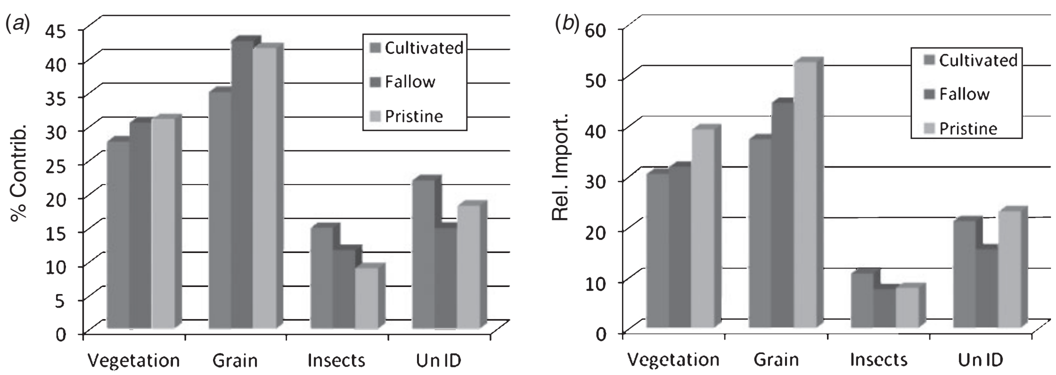

Fig. 2. (*a*) Mean percentage volume and (*b*) relative importance of different food categories in the diet of *Mastomys natalensis* in Swaziland between March 2008 and April 2009.

trigger reproduction and influence growth of rodents (Jung and Batzli 1981; Linn 1991; Neal 1996; White and Bernard 1996). This could be argued as the reason *M. natalensis* consumed plant material in limited amounts in this study.

Despite some spatial variation, the results of this study agree with earlier studies from across the species distribution range (Delany 1964; Swanepoel 1980; Leirs and Verheyen 1995; Monadjem 1997*b*, 1998; Odhiambo *et al*. 2008), suggesting that *M. natalensis* is primarily granivorous, but may take other foods opportunistically or as they become available. Alternatively, when seeds and invertebrates become scarce, particularly during the dry season (Lack 1986), this species turns to less nutritious vegetative plant material, such as leaves and stems or may disappear from the habitat, as observed in Swaziland in the non-cropping season on pristine land.

Other studies of the diet of *M. natalensis* also suggest feeding habits with some spatio-temporal variation (Oguge 1995; Odhiambo *et al*. 2008). Oguge (1995) reported that *M. natalensis* was omnivorous, eating mainly seeds and arthropods, with herbs forming a small but regular part of their diet. Delany (1964) found insect remains in 23 out of 25 stomachs from Uganda. In this study, grain found in all habitats and seasons is mostly likely from maize seeds planted, cobs leftover during harvesting, soil seed bank and weed seeds

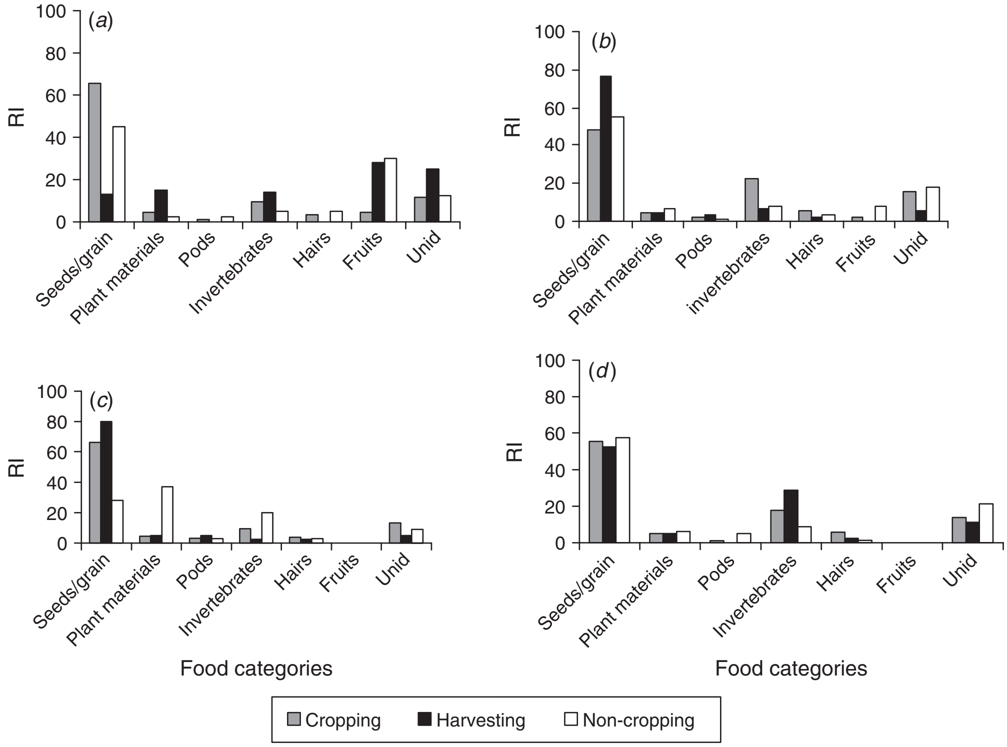

Fig. 3. Mean relative importance of different food categories in the diet of *Mastomys natalensis* in different habitats and seasons in Tanzania: (*a*) fallow fields, (*b*) maize fields, (*c*) woodland and (*d*) vegetable gardens.

Table 3. Levins' index for food diversity[1] from different habitats and seasons of the maize crop in Tanzania

Seasons	Woodland	Fallow land	Maize fields	Vegetable gardens
Cropping	0.21	0.21	0.37	0.20
Harvesting	0.09	0.27	0.10	0.67
Non-cropping	0.46	0.26	0.31	0.39

[1]Index scale ranges from 0 to 1, where 1 = highest diversity and 0 = lowest diversity.

Table 4. Levins' index for food diversity[2] from different habitats and seasons of the maize crop in Swaziland

Seasons	Maize fields	Fallow land	Pristine land
Pre-planting	0.96	0.66	0.74
Vegetative	0.65	0.65	0.68
Post-harvesting	0.57	0.44	–

[2]Index scale ranges from 0 to 1, where 1 = highest diversity and 0 = lowest diversity.

(Taylor and Green 1976; Mwanjabe 1993). Similarly, Rabiu and Rose (1997) reported that seeds constituted ~50% of the food mass consumed by *M. natalensis* during the rainy season and maintained the same levels of seed intake year-round in different habitats.

Although the results indicated that across habitats and seasons the species consumed grain more frequently, some variation existed in niche breadth, which suggests that there is some resource selectivity by individuals depending on the environment (Petraitis 1979). The peak feeding response on different food categories in some habitats and seasons supports an environmental effect on resource utilisation by *M. natalensis.* For example, the narrow niche breadth observed in woodland and maize field habitats during the harvesting season could indicate that there was plenty of grain available – a preferred food for *M. natalensis* in those habitats during those periods. In contrast, the wider niche breadth in the vegetable garden habitat during the maize harvesting season potentially indicates its opportunistic and generalist feeding habits, when grain and other seeds were not available in equally large quantities. The most abundant food categories in the *M. natalensis* diet were grain, invertebrates, fruits and plant materials.

Our findings highlight clearly that *M. natalensis* is a generalist species utilising a large diversity of resources depending on the season and habitat. In some habitats and seasons, the narrow niche breadth confirms that *M. natalensis* is a supreme opportunist. The changes in niche breadth with seasons and habitats indicate a relationship between diet and seasonal and habitat resource availability and suggest that *M. natalensis* is an opportunistic feeder. Therefore, studying the feeding habits of *M. natalensis* offers a useful tool for determining the pest status of the species in different habitats and/or seasons.

The research confirms that *M. natalensis* is largely but not exclusively granivorous; therefore, management actions may be more effective when seeds or grains are not available in the environment. Targeted management when preferred food sources are limited will have a relatively larger impact on the rodent population and reduce recruitment levels at the beginning of the cropping season.

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