Relationships between seasonal changes in diet of Multimammate rat (*Mastomys natalensis*) and its breeding patterns in semi-arid areas in Tanzania

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Abstract: The diet and breeding patterns of *Mastomys natalensis* in semi-arid areas of Isimani division, Iringa region, Tanzania were investigated in maize fields and fallow land. The aim was to investigate the influence of diet on breeding patterns of *M. natalensis*. Removal trapping was used to capture rodents and analyse diet categories while Capture-mark-release trapping was used to investigate breeding patterns of female *M. natalensis*. *Mastomys natalensis* comprised 94% of the total capture, and the remaining 6% comprised of six other species. Statistical analysis of food preferences indicated that both vegetative materials and seeds were significantly higher in the overall diet of *M. natalensis* compared with other food materials. Significant differences in the proportions of vegetative materials and seeds were found between seasons (dry, wet), but not between habitats (fallow, maize). There was a clear seasonal pattern in the proportion of reproductively active females with peaks in April and troughs in October. The proportion of vegetative materials was highest during the wet season and correlated positively with reproductive activity, suggesting that vegetative materials contain certain compounds (e.g. 6-MBOA) that trigger reproductive activity in *M. natalensis*. The breeding activity of *M. natalensis* in semi-arid areas might, thus, be reduced by limiting access to fresh vegetative food (e.g. young sprouting grass).

Subjects: Environment & Agriculture; Plant & Animal Ecology; Zoology; Environmental Studies & Management
1. Introduction

Rodents are a long-standing pest problem throughout the world, which disproportionately affects rural farmers through damage and loss of field and stored crops (Mdangi et al., 2013; Mulungu, 2003), transmission of diseases (Katakweba et al., 2012) and degrading building structures (Belmain et al. 2002). In many countries in Africa, agricultural fields are surrounded by fallow field margins consisting of shrubs and wild grasses, which can provide suitable sites for shelter and food for rodents (Mulungu, Makundi, Massawe, Machangu, & Mbije, 2008; Mulungu et al., 2011a). In Tanzania, rodents were estimated to reduce the total harvest output of farmers by 5–15% each year, resulting in a financial loss of about $45 million (Leirs, Verhagen, Verhagen, Mwanjabe, & Mbise, 1996; Makundi, Mbise, & Kilonzo, 1991). Fallow land can serve as a refuge for rodents, particularly outside of the cropping season, which enables them to quickly infest crop fields. Mulungu (2017) and Makundi et al. (1991) reported over 20 rodent species from seven genera to be involved in crop damage in different parts of Tanzania, with Mastomys natalensis considered the most abundant and destructive rodent pest.

Previous studies have linked breeding patterns of M. natalensis with climate (Leirs, Verhagen, & Verheyen, 1994). Annual breeding patterns of M. natalensis are linked to rainfall patterns (Leirs, Verheyen, Michaels, Verheyen, & Stuyck, 2004). Seasonal variation in the onset of rains is associated with vegetative productivity, which has been shown to trigger M. natalensis breeding (Leirs et al., 1994). Taylor and Green (1976) reported that the food supply of granivorous species is dependent on rainfall and that prolongation of the normal rainy season may generate excess food and cover, resulting in an extended breeding season and unusually large numbers of rodents. Mulungu et al. (2011a) and Odhiambo, Makundi, Leirs, and Verhagen (2008) have shown that M. natalensis is an opportunistic feeder consuming a variety of food types (invertebrates, wild grass seeds, vegetative plant material, fruits, cereal grain crops) dependent upon availability, habitat and season.

In semi-arid natural habitats, seasonality in food availability appears to drive reproductive cycles for many sylvatic rodent species (Leirs et al., 1996). Similarly, the seasonality of crop production can drive rodent breeding. For example, Duque, Joshi, Martin, Marquez, and Sebastian (2005) observed that the onset of breeding in Rattus tanezumi is linked to specific developmental stages of the rice crop. It has been reported that dietary information is essential for understanding breeding activities of rodents (Field, 1975; Leirs & Verhagen, 1995; Monadjem, 1998; Mulungu et al., 2014). According to Mulungu et al. (2014), seeds are an important food category during the breeding season and are required to meet the high energy needs of a reproducing organism. For example, it was reported that M. natalensis breeds when seeds and cereals are plentiful (Mulungu et al., 2014). Similarly, unseasonal reproduction in M. natalensis has been observed during an unseasonal wheat crop (Taylor & Green, 1976) and rice crop (Mulungu et al., 2013, 2014).

Studies on the influence of diet on breeding of M. natalensis in semi-arid areas where food is limited can increase an understanding of food preferences and what potentially triggers breeding in this species. This could also serve as a tool for planning and development of management strategies for rodent pest species (Singleton, 2002). Therefore, the aim of this study was to investigate the influence of food type on breeding of M. natalensis in different seasons in semi-arid areas where maize is grown as a major food crop.

2. Materials and method

2.1. Location of the study

This study was conducted in Isimani division in Iringa region, Tanzania. The area is located between 7° 13’ 55.2” and 7° 13’ 40.8” m S, 35° 15’ 50.4” and 35° 56’ 31.2” m E and, Zone 36 M
covering at an elevation ranging from 1355 to 1396 m above sea level (Figure 1). The study area has a unimodal rainfall pattern with distinct dry and wet seasons. The mean annual precipitation ranges from 200 to 750 mm/year. It is characterised by low erratic rainfall and periodic droughts giving it a characteristic of a semi-arid nature where precipitation is below potential evapotranspiration. To capture the influence of seasonal variation on diet preference, the seasons were subdivided on the basis of rainfall and evapotranspiration relationship into three sub-seasons (Figure 2).

The year can be clearly divided into dry and wet seasons. For the purposes of our study, we have further divided the dry season into three periods, namely, start-dry mid-dry and end-dry. The start-dry period is from May to July, mid-dry from August to September and end-dry from October to November. The wet season can also be further divided into three periods: start-wet (December to January), mid-wet (February) and end-wet (March to April). Land use consists of maize fields interspersed with fallow land. Maize is the primary crop grown which reaches physiological maturity in May to June and is harvested in July to August.

2.2. Removal trapping
Removal trapping was conducted monthly from June 2015 to July 2017. Two 60 m × 60 m trapping grids (one grid was in maize and the second grid was in fallow land) were set. Each grid consisted of seven parallel lines, 10 m apart, seven trapping stations per line and spaced at 10 m apart making a total of 49 trapping stations per grid. Sherman traps (H.B. Sherman Traps, Inc., Tallahassee, FL, USA) and snap (kill) traps (1.0 × 8.5 × 16.5 cm) were used and placed at an alternating manner along a trap line at a distance of 10 m apart, and all were set for three consecutive nights at intervals of four weeks and for the duration of 2 years trapping sessions.
The traps were baited with a mixture of peanut butter and maize flour, placed in the afternoon and inspected early in the morning. Captured animals were identified to species level following the established taxonomic nomenclature (Kingdon, 1997). The weights, sex and reproductive status, either perforated or closed vagina in females and scrotal or non-scrotal testes in males, were recorded. In both fields, the stomach of each animal captured in a snap trap was removed, placed in a labelled small bottle and preserved in 70% alcohol for stomach content analysis.

In the laboratory, the preserved stomach contents were spread out in a petri dish and sorted under a binocular stereoscope, using 25x and/or 50x magnification as described by Smith, Avenant, and Chown (2002), and identified as vegetative materials (roots, stems and leaves), seeds (grains), fruits, invertebrates, animal hairs and unidentified matter. If necessary, a lugol solution was used to determine the presence of starch for maize seeds (Smith et al., 2002). The methods used to quantify diet were as described by Smith et al. (2002), where the percentage contribution of each food category to the volume of a particular stomach's contents (PV) was estimated to the nearest 10%.

2.3. Capture-mark-release trapping

Capture-mark-release trapping was carried out using two 60 × 60 m grids (one in maize field and the second in fallow land) and was set on land belonging to Uyole Agricultural Institution. Trapping was done using Sherman live traps (Sherman LFA live trap 8 × 9 × 23 cm, H.B. Sherman Traps, Inc., Tallahassee, FL, USA). Each grid consisted of seven parallel lines, 10 m apart, and seven trapping stations per line which was set at 10 m apart making a total of 49 trapping stations per grid. The traps were baited with a mixture of peanut butter mixed with maize bran/flour, placed in the afternoon and inspected early in the morning, and were set for three consecutive nights at intervals of four weeks and for the duration of 2 years trapping sessions.

Captured animals were identified to species level, weighed and toe clipped. The sex and state of maturity (perforated or closed vagina for female, and scrotal or non-scrotal for male) were recorded. Data were used to establish breeding patterns of the species.

Both trapping methods (Removal and Capture Mark Release) were conducted during the same period, site and located more than 400 m far apart from one grid to another allowing dealing with different individuals of rodents.
2.4. Data analysis

2.4.1. Small mammal species composition
The percentages of each species relative to others were calculated by dividing the number of captured individuals of each species by the total number of captured animals in a particular habitat, and multiplied by 100.

2.4.2. Diet category analysis
To investigate whether the diet of *M. natalensis* differed between seasons (dry, wet) and fields (maize, fallow), we performed a beta regression analysis with proportion of diet as response variable and field and season as explanatory variables (using the R-package “betareg”). Beta regression is often used to model percentages, as it can model continuous variables that assume values in the open standard unit interval 0–1 (Cribari-Neto & Zeileis, 2010; Ferrari & Cribari-Neto, 2004).

2.4.3. Reproductive activity
Breeding patterns were determined in CMR grids by establishing the proportion of active and non-active individuals of female *M. natalensis* in different habitats and months. Reproductive activity in females is a physiological condition and not a behaviour (Leirs & Verhagen, 1995); thus, females were considered to be reproductively active when the vagina was perforated, their nipples were swollen on account of lactation and when they were pregnant. To investigate which variables correlated with reproductive activity of females, we developed generalised additive models (GAM) with reproductive status as response variable and time (month), fields (maize, fallow) and percentage of diet (vegetative materials and seeds) as explanatory variables. A GAM approach was used because the percentage of reproductive activity animals did not follow a linear pattern over the course of 1 year. The time variable was smoothed using cyclic regression splines. Reproductive activity in individuals was analysed assuming a logit-link function with binomial distribution. Because the reproductive status could be affected by the diet consumed at previous months, we also investigated the correlations between the percentage of reproductively active females and the diet (% vegetative material or seeds) at previous months using cross-correlation functions. The R packages “betareg”, “mgcv” and “nlme” were used for these analyses (Cribari-Neto & Zeileis, 2010; Pinheiro, Bates, DebRoy, & Sarkar, 2018; R-Core Team, 2016; Wood, 2011).

3. Results

3.1. Small mammal species composition
A total of 2,307 rodents and 29 shrews were captured in 11,466 trap nights in the study area. The rodent species captured were *Mastomys natalensis*, *Lemniscomys rosalia*, *Gerbilliscus vicinus*, *Pelomys fallax*, *Arvicanthis neumani*, *Thallomys paedulcus* and *Acomys wilsoni*. *Mastomys natalensis* comprised the highest proportion (> 94%) of rodent species captured in the study area (Table 1).

3.2. Diet preferences of *M. natalensis*
The proportion of vegetative materials was significantly ($\chi^2 = 35.19$, d.f. = 1, $p$ value <0.0001) higher in the diet of *M. natalensis* during the whole wet season compared with the dry season (53% and 33% in the wet and dry seasons, respectively) (Figure 3). Seeds/grains comprised a significantly ($\chi^2 = 24.52$, d.f. = 1, $p$ = < 0.0001) higher proportion in the diet of *M. natalensis* during the dry season than in the wet season (42% and 26% in dry and wet seasons, respectively). No significant differences ($\chi^2 = 0.81$, d.f. = 1, $p$ = 0.31) were found between maize and fallow fields in the proportion of vegetative material or seeds/grains respectively ($\chi^2 = 0.81$, d.f. = 1, $p$ = 0.31 and $\chi^2 = 0.85$, d.f. = 1, $p$ = 0.62). There were also no significant differences in the diet of *M. natalensis* for fruit, animal hairs or invertebrates between seasons or fields (Figure 3).
3.3. Reproductive activities

There was a significant interaction between habitat type and time (month) on reproductive activity of *M. natalensis* ($\chi^2 = 196.56$, d.f. = 9, $p < 0.0012$) (Figure 4). However, most variation in reproductive activity was explained by the time variable ($\Delta R^2 = 0.77$), and only a little bit by the differences in habitat type ($\Delta R^2 = 0.02$). The proportion of reproductively active animals varied in a non-linear way between April (highest) and October (lowest) ($\chi^2 = 339.23$, d.f. = 8, $p < 0.0001$) (Figure 5). Differences between habitat types were only found during the wet season, when the percentage of reproductive active animals was higher in fallow than in maize fields ($\chi^2 = 4.54$, d.f. = 1, $p < 0.0005$) (Figure 5).

3.4. Correlation between diet preference and reproductive activity of *M. natalensis*

Results show that reproductive activity starts after one month (in January) of vegetative sprouting (in December), while it ceases when the proportion of seed/grain materials increases in August–September (Figure 6). Most animals are reproductively active at the end of the wet season, which corresponds to the period when the percentage of vegetative material in the diet is the highest.

Table 1. Small mammal species composition in maize fields and fallow land in the study area

| Rodent species          | Maize field | Habits | Fallow land |
|-------------------------|-------------|--------|-------------|
| *Mastomys natalensis*   | 895 (96.76%) | 1328 (94.12%) |
| *Lemniscomys rosalia*   | 4 (0.43%) | 12 (0.85%) |
| *Gerbilliscus vicinus*  | 7 (0.76%) | 19 (1.35%) |
| *Pelomys fallax*        | 0          | 2 (0.14%) |
| *Acomys wilsoni*        | 0          | 3 (0.21%) |
| *Thallomys paedulus*    | 0          | 1 (0.07%) |
| *Arvicanthis neumani*   | 0          | 36 (2.55%) |
| *Crocidura spp*         | 19 (2.05%) | 10 (0.71%) |
| Total                   | 925 (100%) | 1411 (100%) |

Figure 3. Mean diet preferences (%) of *M. natalensis* during the wet and dry seasons in different habitats types (fallow versus maize field). The black bars represent standard errors.
Correlations between reproductive activity and current percentage of diet in the stomach were not significant for vegetative materials ($\chi^2 = 1.51, df = 1, p = 0.21$) or seeds/grains ($\chi^2 = 1.48, df = 1, p = 0.22$). However, correlations between reproductive activity and vegetative materials were significantly positive at earlier time lags (months 1 to 4), while correlations with seeds/grains were negative at earlier time lags (months 1 to 3) ($p < 0.01$) (Supplementary Figure 1). These results suggest that certain compounds in vegetative material might trigger reproductive activity in *M. natalensis* and that the effect is visible after a short time lag (one month).

### 4. Discussion

*Mastomys natalensis* was the dominant species in the study area. This is consistent with previous studies carried out in irrigated rice fields (Mulungu et al., 2013), fallow fields (Massawe et al., 2011) and maize farms (Sluydts, Crespin, Davids, Lima, & Leirs, 2007; Vibe-Petersen, Leirs, & Bruyn, 2006). According to Makundi, Massawe, and Mulungu (2007), the species is a pioneer in colonising disturbed habitats (e.g. by agriculture).

Most rodents inhabiting maize fields and fallow land in Tanzania are omnivorous, consuming large quantities of green vegetation, fruits, seeds and arthropods, but sometimes they are opportunistic in their selection of food items. Rodents frequently display food preferences that typically lead to a disproportionately high consumption of preferred prey species (Hope & Parmenter, 2007).
In the current study, *M. natalensis* was observed to feed largely on vegetative plant materials and seeds/grains with other categories of diet in low quantities. Similar observations were reported by Monadjem and Perrin (1998), Odhiambo et al. (2008) and Mulungu et al. (2011a). More seeds/grains in the diet of *M. natalensis* after the reproductive season were observed in the current study because this coincides with the cropping season and the harvest of the farmers, so there are more seeds on the fields. Another reason is that, new born juveniles might benefit from the protein- and starch-rich seeds on the field to grow themselves (so not reproduction). Seeds are an important food category during the breeding season and are required to meet the high energy needs of a reproducing rodent species (Mulungu et al., 2011a; Stanley & Hutterer, 2007). This feeding behaviour shows *M. natalensis*’ respond to changes in the food supply by searching for the most abundant component of its diet. Leirs et al. (1997) reported that *M. natalensis* is an opportunistic species that conforms to r-selection characteristics. Mulungu et al. (2014) reported that *M. natalensis* consumed mainly vegetative plant materials and seeds, regardless of habitat or crop growth stage in irrigated rice crop agro-ecosystem. The current study showed a relationship between diet, seasonal and habitat resources availability and suggests that *M. natalensis* is both an opportunistic and a generalist species utilising a large diversity of resources depending on the season and habitat. Similar findings by Mulungu et al. (2011b) who stated that 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 both an opportunistic and a generalist feeder.

In various studies, a positive relationship has been reported between rainfall and reproductive success in populations of *Mastomys* (Achigan, Codjia, & Bakonon-Ganta, 2003; Makundi et al., 2007; Massawwe, 2003; Workneh, 2003). The duration and quality of rainfall both influence available food (Granjon, Cosson, Quesseveur, & Sicard, 2007). Dietary information is essential for understanding breeding activities of rodents (Monadjem, 1998; Mulungu, Happy Lopa, & Mdang, 2016; Mulungu et al., 2014). Some studies indicated that African rodent species have a reproduction cycle which is related to seasonal changes in the diet (Bronson, 1989; Sicard & Fuminier, 1996). In areas where farmers produce two maize crops per year, the breeding duration of *M. natalensis* is extended (Mulungu, 2017). According to Mulungu (2017), Bekele and Leirs (1997) reported that breeding in mosaic crop-fallow fields is seasonal and related to rainfall periods, but extended rainy seasons resulted in longer periods of breeding, higher litter sizes and subsequent population increases. Also, Taylor and Green (1976) had observed a seasonal breeding in a seasonal crop in Kenya. Previous studies showed that breeding of *M. natalensis* was extended when rainfall was prolonged in wheat crop fields (Swanepoel, 1980) and in irrigated rice fields (Mulungu et al., 2013, 2014).

In irrigated cropping systems, the link with rainfall is much weaker, although breeding is still most prominent in the rainy seasons as is the case in single crop maize production areas. In the current study, vegetative materials comprised the largest proportions of the diet of *M. natalensis* during the reproductive season. Diet is likely to play a role because it influences reproductive physiology directly when food is ingested and absorbed (Glass & Swerdloff, 1980; Leirs, 1994). Surprisingly, in a semi-arid area with a short rainfall season and subsequent shorter duration for food availability like in the current study resulted in a longer period of reproductive activity of *M. natalensis* compared with other locations in Tanzania with bimodal rainfall patterns. This could be attributed by a larger amount of vegetative material found in the stomach of rodent in the study area during the wet season. It was reported that green plant food (vegetative materials) induces breeding in *M. natalensis* due to the chemical compound or a secondary plant compound called 6-methoxy-2-benzoxazolinone (6-MBOA), originating in young sprouting plant or grass with a labile precursor formed enzymatically from a glucoside when the plant tissues are crushed (Klun & Robinson, 1969; Leirs, 1994). This molecule (6-MBOA) is more likely found in vegetative materials than in seeds and could be the reason why in the current study reproductive activity is at its highest point in April after *M. natalensis* consumes mostly vegetative materials in the past months. The reproductive activity decreased rapidly and reached the lowest level around September and October. This was probably due to the influx of juveniles into the population.

Most female *M. natalensis* are reproductively active when the proportion vegetative materials are at maximum. In some desert environments, maintaining reproductive activity throughout the year can ensure quick responses to reproductive opportunities that may arise from unpredictable changes in water and/or food availability (Bronson, 2009; Schneider, 2004). The timing of reproduction is related to the timing of germination in grasses initiated by rainfall (Leirs, 1994).

5. Conclusion
*Mastomys natalensis* is the most abundant pest species in the study area and its diet varied with season and habitat type. Vegetative materials were present in high proportions of the diet of *M. natalensis* during the entire wet season, whereas seeds were present in high proportions during the entire dry season. *Mastomys natalensis* is reproductively active from January to September, although it reaches the highest level in April, which corresponds to the long rain period, suggesting that reproduction is linked to the amount of rainfall. Reproductive activity correlated positively with the past percentage of vegetative material in the diet during the wet season. Reducing breeding activity might thus be achieved by preventing access to fresh vegetative food (e.g. young sprouting grass) during the wet season.
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