



Dietary patterns of a crop pest mammal species (*Mastomys natalensis*) inhabiting Agrofield-protected area interface in Western Serengeti, Tanzania

Egidius J. Rwebuga^{1, 2, 3*}, Shombe N. Hassan¹, Loth S. Mulungu¹, Alfian A. Rija¹

¹Department of Wildlife Management, Sokoine University of Agriculture, Morogoro, Tanzania. P.O.Box 3001, Morogoro, Tanzania

²The African Centre of Excellence for Innovative Rodent Pest Management and Biosensor Technology Development (ACE IRPM & BTD)

³Pest Management Centre, Sokoine University of Agriculture, Morogoro, Tanzania.

*Email: jegidius@yahoo.com

Received: 26 June 2023 / Revised: 18 August 2023/ Accepted: 01 September 2023/ Published online: 01 September 2023.

How to cite: Rwebuga, J.E., Hassan, S.N., Mulungu, L.S., Rija, A.A. (2023). Dietary patterns of a crop pest mammal species (*Mastomys natalensis*) inhabiting Agrofield-protected area interface in Western Serengeti, Tanzania, Sustainability and Biodiversity Conservation, 2(1), 32-52. DOI: <https://doi.org/10.5281/zenodo.8352346>

Abstract

Rodent pest control is challenging because of the complex dynamics of their populations. We investigated the influence of seasons and habitats on food categories and diet breadth of *Mastomys natalensis* (Smith, 1834) by analysing 107 stomachs collected in Kijereshi Game Reserve and Nyamikoma village in western Serengeti-Tanzania, using kill traps. Plant materials (41%) and invertebrates (39.1%) dominated the animal's diet in different seasons and habitats. Numerically, during the wet season, invertebrates dominated the fallow land (90.0%) followed by the wooded grassland (83.3%) and maize crop fields (76.2). Plant materials were in large quantity in maize crop fields (27.6%) and least in the wooded grassland (16.7%). Furthermore, seeds/grains were eaten more in maize crop fields (20.7%) as compared to fallow land (19.3%) and wooded grassland (6.9%). In contrast, in the dry season, plant materials occurred at a higher frequency in maize crop fields (85.7%) followed by fallow land (60%) and lastly the wooded grassland (50%). Seed/grain featured more in the diet in maize crop fields (75%) followed by fallow land (44.4%) and lastly by the wooded grassland (36.4%). Invertebrates occurred with higher frequency in the wooded grassland (72.7%) followed by fallow land (66.7%) and lastly by maize crop fields (58.3%). Statistical tests on the effects of habitats and seasonality on the dietary patterns of *M. natalensis*, revealed a non-significant effect of each individual variable respectively ($p = 0.43$) and ($p = 0.81$) respectively. Effect of seasonality and habitats on *M. natalensis* food categories were observed on plant materials but not in seeds/grains and invertebrates. The animal ate plant materials and seeds/grains substantially in the maize crop fields, suggesting that it is a potential pest. Therefore, combined management actions are needed which include clearance of bushy fallow lands and rodenticide application but preventively and remedially when there is a need.

Keywords: Dietary breadth, selectivity index, feeding, habitat heterogeneity, rodents, seasonality, Western Serengeti

Introduction

The multimammate mouse, *Mastomys natalensis* (Smith, 1834), is an important pest across southern and eastern Africa that causes substantial crop losses (Makundi et al., 1999; Wondifraw B.T, 2021). In Tanzania for example, *M. natalensis* has been considered as the most important rodent pest (Leirs & Verheyen, 1995; Mdangi, 2009) that can damage up to 48% of farmer's field crops at a density as low as 18 individual animals per hectare of crop farm (Mdangi, 2009). Further, the rodent species is a carrier of plague (Dippenaar & Gordon, 1993; Monath, 1975) that also poses considerable health risks to humans. Despite this, rodent species including *M. natalensis* provide major benefits to the environment as bio-engineers (Wright et al., 2002), play a great role in the energy trophic levels, and disperse seeds (Krebs, 2001). Also, some rodent species are a source of proteins for humans (Kilwanila et al., 2021). Management of rodents' pest impacts is challenging. Several control methods currently in use concentrate on reducing rodent population size. For example, trapping, bounty system, repelling, rodent proofing, and poisoning with rodenticides (i.e. strychnine) methods have been used (Capizzi et al., 2014). Recent research has advanced the control methods thereby targeting fertility control (Ajayi & Akhigbe, 2020; Imakando et al., 2022; Massawe et al., 2018; Selemani et al., 2022) although the efficacy of these methods on the population size of rodents in the wild is still unknown. These control methods have evolved over time suggesting the challenge the world currently faces in managing the rodent population. Such management challenges are partly caused by the complexity of the population dynamics of rodents that vary across local and spatial scales and also due to the high ability of most rodent species in utilizing subtle resources even in seemingly difficult environments to survive (Makundi et al., 2007).

Here, we study the dietary habits of rodents to assess how various land-use activities and seasonality interact to explain rodent dietary patterns and to inform the potential management strategies of the rodent population in the human-dominated landscapes of western Serengeti. *Mastomys natalensis* is an opportunistic feeder consuming various food resources based on availability (Odhiambo et al., 2008a). Existing studies indicate the species feeds more on seeds, arthropods, and grasses during the wet season and on other plant material during the dry season in the south-west (Monadjem & Perrin, 2003) and central regions of Tanzania (Mlyashimbi et al., 2018). On the other hand, grains have been found to predominate the diet of *M. natalensis* in

Botswana and Tanzania regardless of the season and habitat types assessed (Mulungu et al., 2011). These studies, although most were conducted in Tanzania, have reported different dietary patterns and their variability seems to be modulated by local-scale factors which, further add to the complexity of the rodent biology. This suggests that results from such studies cannot be representative of all other areas and that site-specific information may be more useful when planning rodent population management strategies. This is because such strategies may vary based on local ecological conditions (e.g. habitat structure, local season and length, etc.), human culture (e.g. acceptability of a control method, rodent consumption, etc.), and land use activities (e.g. available farms, protected area, etc.) (Mwasapi & Rija, 2022).

Although seasonality and vegetation type are known to influence the dietary habits of *Mastomys natalensis* (Odhiambo et al., 2008), information on the fine-scale characteristics of vegetation (e.g. habitat heterogeneity) and anthropogenic activities (e.g. farming practices and wildfire) that modulate food abundance is less well documented (Kwok & Eldridge, 2015). Further, land use activity can also influence the dynamics of rodent dietary patterns e.g. through acting as a source or sink area of food resources acting as seasonal refugia for rodents, thereby influencing rodent population dynamics. In landscapes comprising protected areas and unprotected lands that support farming activities for example, the dietary patterns of rodents are expected to exhibit greater breadth due to the complex microhabitats available across such landscapes that are subject to varying management strategies. Such a system exists in Kijereshi Game Reserve and adjacent unprotected land interface in western Serengeti where the rodents may be able to switch habitat use based on the seasonality, land use practice, and habitat management strategies (e.g. use of prescribed early fires in the protected area). This may further impact the rodents' dietary habits, foraging patterns, and population dynamics and therefore making predictable control measures of their population challenging. Furthermore, most available studies were conducted on simple mono-crop systems, and yet the results from elsewhere are considerably variable making it difficult to apply especially in more complex systems such as the western Serengeti landscape. Hence, we hypothesized that, *M. natalensis* food categories varied between seasons and habitats.

Materials and methods

Study area

The study was conducted in Kijereshi Game Reserve and surrounding Nyamikoma village (between Latitude 2°1' and 2°4' S and Longitude 33° and 35° 1'E), in the western Serengeti

Ecosystem within Busega and Bariadi Districts in Simiyu Region (Fig. 1). On the northern side, Kijereshi Game Reserve shares the boundary with the Serengeti National Park (SENAPA) and is surrounded by six villages: Lukungu, Mwabayanda, Mwakiroba, Kijilishi, Nyamikoma, and Senta. Kijereshi Game Reserve and the fallow land–cultivated mosaic is characterized by grassland with the commonly occurring species as explained in (Rwebuga et al., 2023).

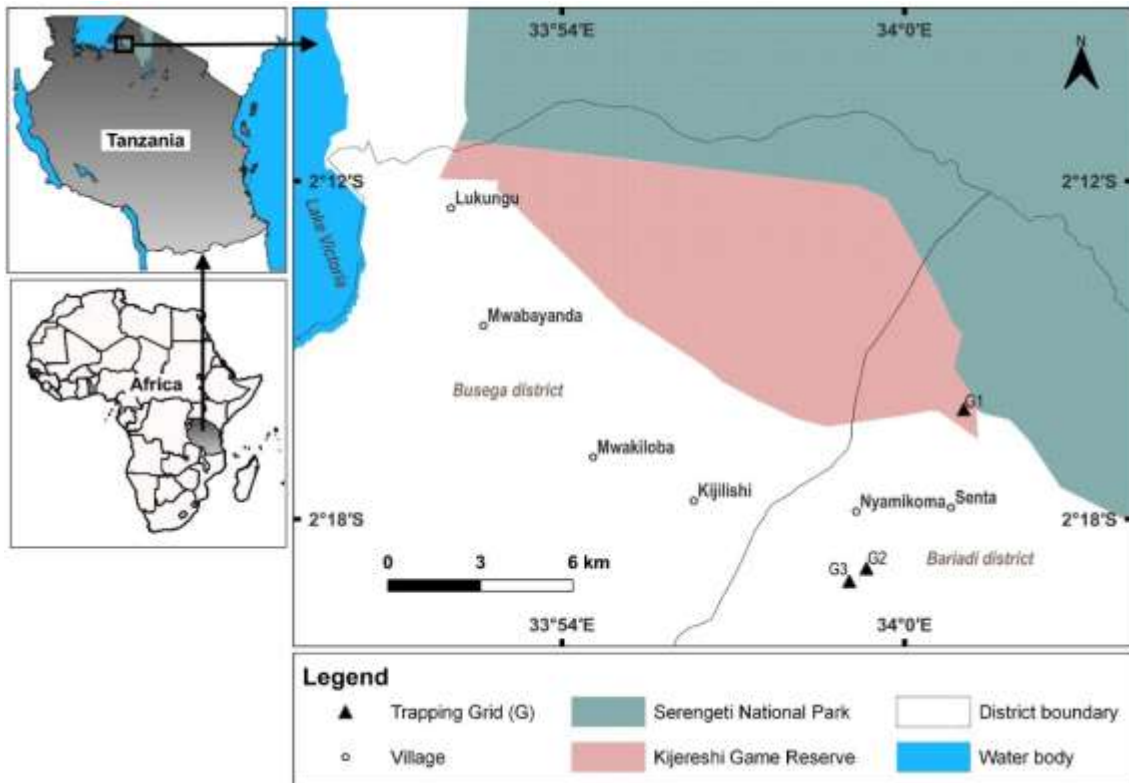


Figure 1. Location of study sites in Kijereshi Game Reserve and Nyamikoma Village

Trapping of rodents

Rodent trapping was conducted from April 2020 to March 2021 in three 70m x 70 m permanent trapping grids in each habitat; wooded grassland (WG) within Kijereshi Game Reserve and fallow land (Fallow) and maize crop fields (Maize) within Nyamikoma village which were replicated three times. Each grid consisted of seven parallel lines, 10 m apart, with seven trapping stations per line spaced 10 m apart, making a total of 49 trapping stations per grid (Rwebuga et al., 2023). One Victor kill trap (1.0 x 20.3 x 30.1 cm, Animal Trap Co., Lititz Pennal) was used per station and an amount of 1764 trapping nights were obtained.

Processing of captured animals

Captured animals were sexed and identified to species level in the field using field guides and technical experts. We collected the stomachs of each trapped individual and preserved them in a 20 ml glass bottle (HiSupplier.com) containing 70% ethanol. The stomach contents were examined in the laboratory on a Petri dish (65 mm in size, Tools and Carbide Plastics (Pty) Ltd.) and categorized into “Seeds/grain, Invertebrates, Plant materials, Hairs, and Other unidentified materials” using a microscope (25 x and 50 x magnification) as described by (Smith et al., 2002). Examined stomachs totalled 107 comprising 40 samples from WG (18 in wet season and 22 in dry season), 24 samples from maize field (12 in wet season and 12 in dry season) and 43 from Fallow crop fields (25 in wet season and 18 in dry season). The contents were sorted into the following categories: seeds/grains, vegetative plant materials (roots, stems and leaves), invertebrates, animal hairs and other unidentified matter. Lugol’s iodine solution was used to confirm the presence of seed starch (Smith et al., 2002).

Statistical analysis

To understand the importance of each food item in the stomach samples, food categories were quantified as described by (Smith et al., 2002). These are average percentage volume (PV), defined as the contribution of each item to the volume of the particular stomach content, which was estimated as the proportion of each food item over the total of all volume proportions times 100. Percentage occurrence (PO) of a particular food item in a sampling period was calculated from the number of stomachs it was found in and the number of stomachs examined times 100. Diet diversity was calculated according to (Ebersole & Wilson, 1980) as Levins’ index (Levins, 1968) which ranges from 1 to n (= total number of food item categories) as follows:

$$\frac{1}{\sum P_i^2}$$

where, P (= PV) is the percentage value of each of the diet category. Then diversity was standardised to a scale of 0–1 using Hurlbert’s method (Krebs, 1989) :

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

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 percentage volume- (PV) and percentage occurrence (PO) was used to calculate an importance value ($IV = PV \times PO/100$) for each dietary item (Cooper, 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 ($100 \times IV/PIV$) (Smith *et al.* (2002). Further, to understand dietary overlaps, we calculated the seasonal dietary overlap as per (Schoener, 1968) by using the following mathematical expression:-

$$O_{ij} = \frac{\sum p_{ij} p_{ik}}{\sqrt{(\sum p_{ij}^2 \sum p_{ik}^2)}}$$

Where p_{ij} is the contribution proportion food items in the wet season in different habitats p_{ik} is the contribution proportion of food items in the dry season in different habitats O ranges from 0 (no overlap) to 1 (total overlap).

After checking normality in our data (Shapiro-Wilks test, $p < 0.05$), we used Kruskal-Wallis and Wilcoxon rank test, which conform to non-normal data, in R-software version 4.2.1 (Team, 2021). These tests were used to compare differences in the dietary abundance between habitats and seasonality.

To understand the influence of habitats and seasons (independent variables) on *M. natalensis* various food categories (dependent variables) we used a generalized linear models (GLM) with a negative binomial error term and a log-link function implemented in the R-package MASS (Team, 2021) following presence of over dispersion in the data (Rija, 2021). For this analysis we used percentage food volumes which were discrete numbers and directly proportional to counted parts of each food category (Vezzosi *et al.*, 2014). We generated four candidate models representing hypotheses concerning the effects of habitats and seasons on each of the three food categories only: Invertebrates, plant materials and seeds/grains, because hairs were present in very small amounts and others categories represented unknown food categories (Makundi, R. H., Massawe, A. W., Mulungu, L. S. and Katakweba *et al.*, 2014). We applied the all-subset approach to model selection to obtain variables for including in the model as we had only two independent variables per model and all of them had unique biological importance (Symonds & Moussalli, 2011). The relative influence of each variable in the model was evaluated by the forward selection method of variable (Chowdhury & Turin, 2020). The best model fitting the data was chosen using the Akaike

Information Criterion corrected for small sample size (AICc) value and the models with higher weights were the ones taken to be most parsimonious (Symonds & Moussalli, 2011). We validated models through conducting deviance residuals distribution examination that expressed conformity (Rija, 2021).

Inclusion and exclusion criteria for rodents and shrew selection

The study was conducted according to the guidelines of the Declaration of Helsinki, and approved by the Institutional Review Board of the Sokoine University of Agriculture for research, regulations and guidelines-2019 through research clearance approval referenced SUA/ADM/R.1/8/561/2020 and the Tanzania Wildlife Conservation Act No. 5 of 2009.

Results

Dietary composition and variability across habitats and seasonality

Plant materials (leaves, grasses, stems and roots) (41%) and invertebrates (39.1%) dominated the dietary habits of the *M. natalensis*. During the wet season invertebrates were more prevalent in WG (39.2 %) followed by Fallow (31.3 %) and Maize (21.2%). Plant material was more prevalent in Maize (27.6%) followed by those in Fallow (25.3%) and WG (16.7%). Seeds/grains were eaten more in Maize (20.71%) followed by Fallow (19.25%) and lastly in WG (6.94 %). In the Dry season stomach contents were dominated by plant materials in Maize (41.67%) followed by Fallow (39.72%) and lastly in WG (23.18%). Also seeds/grains were recorded in large quantities in stomachs of *M. natalensis* in Maize (32.5%) then in Fallow (18.06%) and were minimum in WG (9.66%). Furthermore, invertebrates were also eaten substantially in WG (27.27%) followed by Fallow (20.0%) (Fig. 2). There were also animal hairs (0% -9.3%) and other unidentified food category (11.7% – 35.9%) in all habitats and seasons (Fig. 2). There was no significant difference in food categories between habitats (Kruskal-Wallis and Wilcoxon, (Chi-squared = 1.68, df = 2, p = 0.43) and seasons (W = 55013, P= 0.81).

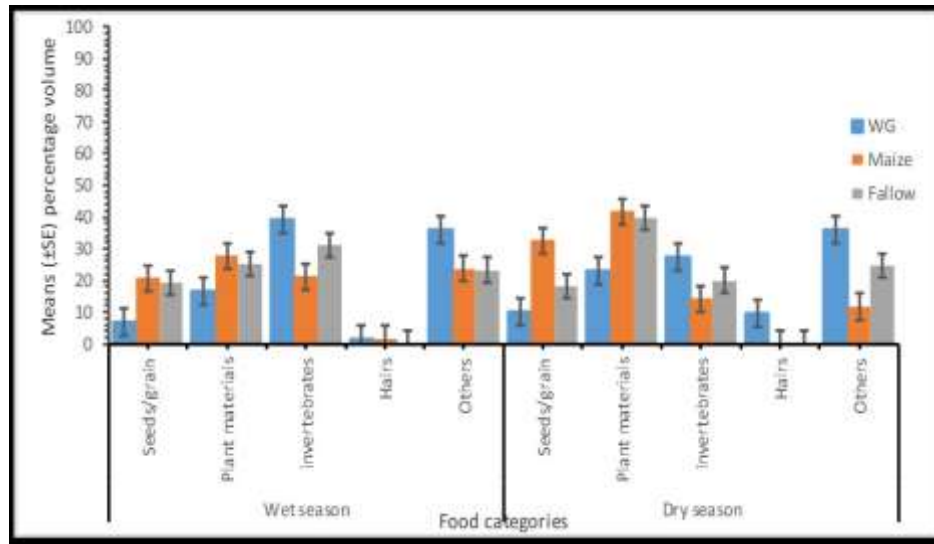


Figure 2. Mean percentage volume of various food categories in the stomachs of *Mastomys natalensis* across seasons and habitats

Percentage occurrence

During the wet season, invertebrates occurred almost equally in all three habitats WG (83.3%), Maize (76.2%) and Fallow (90.0%). Plant material occurred at a higher frequency in Maize (85.7%) followed by Fallow (60%) and then WG (50%). Seeds occurred mostly in Maize (71.4%) followed by Fallow (45%) and then WG (16.7%). Other unidentified materials also occurred in frequencies ranging from 60% to 81% and hairs from 0% to 11%. In the dry season, plant material occurred more in maize (100%), followed by Fallow (88.9%) and then WG (81.8%). Seeds/grain occurred more frequently in Maize (75%) followed by Fallow (44.4%) and lastly by WG (36.4%). Invertebrates occurred with higher frequency in WG (72.7%) followed by Fallow (66.7%) and lastly by Maize (58.3%). Other unidentified material occurred at frequencies ranging from 33.3% to 100%. Also, hairs occurred at frequencies ranging from 0% to 32% (Fig. 3).

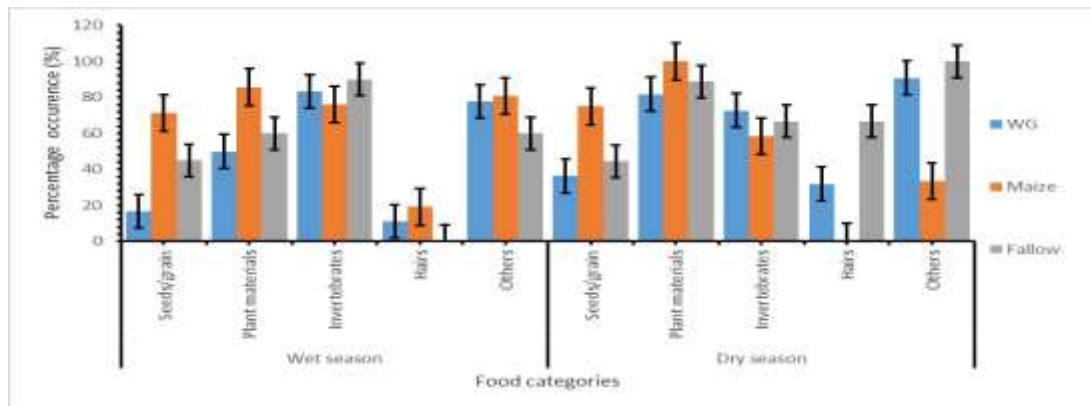


Figure 3. Variations in the percentage occurrence of food types in the diet of *Mastomys natalensi* in the three habitats and two seasons

Relative importance of dietary categories

Importance of different food categories to the *M. natalensi* diet either varied between seasons and habitats or was represented equally in some cases. During the wet season invertebrates were equally important in both WG (43.1%) and Fallow (42.3%) but less in Maize (20.7%). Plant materials were more important in Maize (30.3%) followed by Fallow (22.3%) then WG (11%). Also seeds /grains were more important in Maize (18.94%) followed by Fallow (13.0%) and then WG (9.2%). Other unidentified materials ranged from 20% to 36.8%. Hairs ranged from 0% to 4.0%. During dry season importance of food categories to the rodent diet varied between habitats and seasons. Seeds/grains were more in Maize (31.2%) followed by Fallow (20.2%) and then by WG (5.0%). Plant materials were more important in Maize (53.3%) followed by Fallow (39.6%) and lastly by WG (25.7%). Importance of the invertebrates food item to the animal food diet was expressed more in WG (26.9%) followed by Fallow (15.0%) and then by Maize (10.6%). Whereas other unidentified materials ranged from 0% to 44% in all habitats and seasons hairs had negligible importance (0.0%) (Fig. 4)

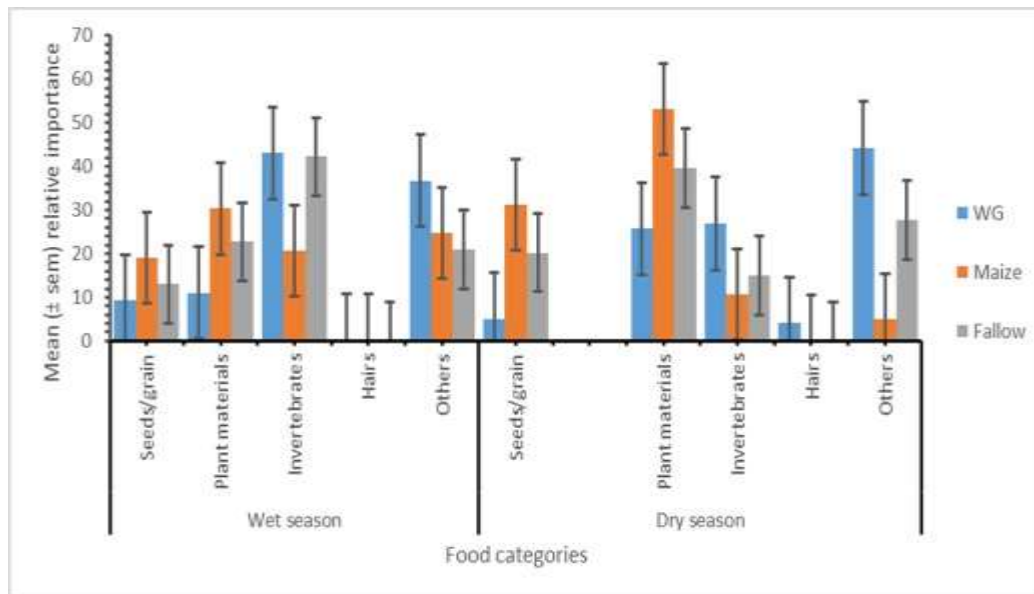


Figure 4. The mean relative importance (RI) values for each food category in different habitats and seasons

Niche breadth

Food diversity was high during dry season (0.8 ± 0.18) but low during wet (0.5 ± 0.15) season in the WG. In Maize food diversity was high during wet season (0.8 ± 0.06) but low during dry season (0.5 ± 0.17). In Fallow there were no difference in food diversities in both wet season (0.7 ± 0.04) and dry season (0.7 ± 0.12).

Seasonal dietary overlap The dietary composition of *M. natalensis* showed a large degree of seasonal overlap ($O_{ij} = 0.987$).

The effect of seasonality and habitats on *Mastomys natalensis* food categories

Effect of seasonality and habitats on *M.natalensis* food categories were observed in plant materials food categories where they had both significant and non-significant influences. Whereas, wet season and the wooded grassland habitat had negative influences on seed/grains, maize crop fields revealed a positive effect on the food category. Wet season and maize crop fields had positive but non-significant effect on plant materials whereas the wooded grassland exhibited a negative effect on the food category. On the other hand, wet season and the wooded grassland habitats revealed positive significant influence on the invertebrates food category whereas maize crop fields exhibited negative influence on the food category (Table 1). Further, the *M.natalensis* food categories associated differently with different variables. Whereas, seed/grains and plant materials associated more with dry season, invertebrates associated with wet season (Fig. 2 (A,C &E)) . On the other hand, seeds/grains and plant materials associated more with maize crop fields while invertebrates were more positively predicted by the wooded grassland habitats (Fig. 2 (B,D &F)).

Table 1. Effect of habitat and seasonality on *Mastomys natalensis* food categories volumes as estimated by GLM showing a significant effect on the final best fitting models.

Model type	Parameters	Estimates \pm SE	Z-value	P (Z)
Seeds/grains	Wet season	-0.24229 \pm 0.04657	-5.203	< 0.001
	Maize crop field	0.31826 \pm 0.05146	6.185	<0.001
	Wooded grassland	-0.77697 \pm 0.06540	-11.880	< 0.001
Plant materials	Wet season	0.01919 \pm 0.04178	0.459	0.459
	Maize crop field	0.06493 \pm 0.04198	0.155	0.8771
	Wooded grassland	-0.46087 \pm 0.04533	-10.168	< 0.001
Invertebrates	Wet season	0.30155 \pm 0.03833	7.867	< 0.001
	Maize crop field	-0.32064 \pm 0.05196	-6.171	< 0.001
	Wooded grassland	0.29440 \pm 0.04281	6.876	< 0.001

, **, and * Indicate significant at $p < 0.05$, 0.01 , and 0.001 respectively*

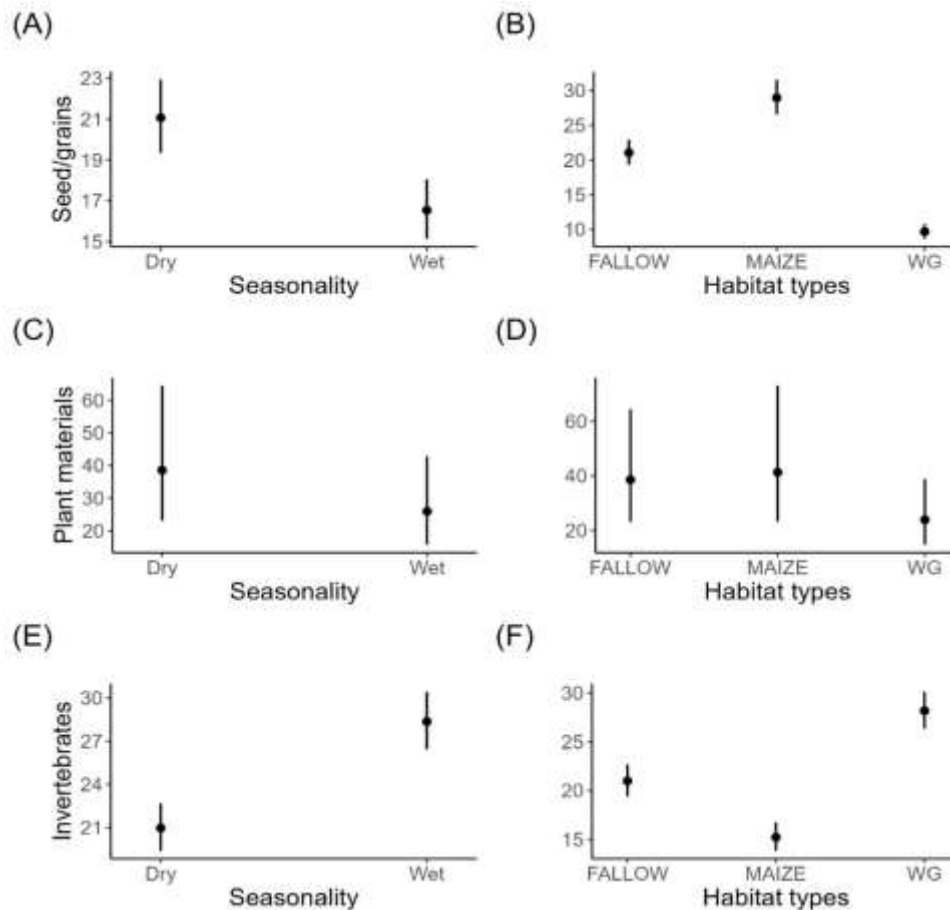


Figure 5. Effects of seasonality (A, C & E) and habitat types (B, D & F) on volumes of various food categories: seeds/grains, plant materials and invertebrates,- found in *M. natalensis* stomachs in different seasons and habitats within Kijereshi Game Reserve Nyamikoma village- landscape

Discussion

Our results showed that, predominantly, the rodent food categories' volumes and diversity varied between seasons and habitats. This suggests that *Mastomys natalensis* in the Kijeshi-Game Reserve –Nyamikoma landscape is a generalist feeder which mostly consumes invertebrates, plant materials and seed/grains dietary categories at deferring or equal rates in different habitats and seasons, hence partially conforming to our hypothesis. Our results are similar to findings by various other investigators. Delany (1964) found invertebrates remains in 23 out of 25 stomachs from Uganda. Probably this is because during the wet season invertebrates are present in abundance as it was declared by Lack (1986) that in the tropics, invertebrates are much more abundant in the wet season than in the dry season as was found out in this study (Fig. 5E). Another reason could be

that, either, some portion of the invertebrates found in the *M. natalensis* stomachs were incidental ectoparasites ingested during grooming and sedentary invertebrates ingested on plant parts or just the rodent's endoparasites which reside in stomachs (Mohtasebi et al., 2021).

During the dry season plant materials were numerically more eaten in the maize crop fields and fallow land, followed by seed/grains in maize crop fields and lastly by invertebrates in wooded grassland. To the large extent this was contrary to findings from other studies. For example, (Mulungu et al., 2011) found seeds/grains to be dominating the *M. natalensis* food categories in Tanzania and Botswana during the dry season. Although Lack (1986) reported that when seeds and invertebrates become scarce, particularly during the dry season this species turns to less nutritious vegetative plant materials, such as leaves and stems. However, in the study area during the months of June, July, August, there are still harvestable maize cobs in the farms. By October, according to farmers cropping calendar, it is maize main season sowing time. Hence, we expect to have large seed resource base in maize crop farms during these months (Fig 5A). In addition to availability of maize grains, there are also some other mature crops like legumes (*Leguminosae*), millet (*Sorghum sp*), sweet potatoes (*Ipomea sp*) and cotton (*Gossypium sp*) seeds which are either inter-cropped with maize or are in close small farms. But yet plant materials were still most important food category in the stomachs of *M. natalensis*. This could be explained by the fact that Kijereshi Game Reserve and most of its surroundings are wet in the most part of the year (Norton-Griffiths, 1975; Thirgood et al., 2004) hence there are fresh grasses resulting from germinating monocotyledonous seeds which attract *M. natalensis* (Randolph & Cameron, 2001). Another reason could be that, because this species is r-selected (Leirs, 1995), hence they ingest fresh grass leaves that contain 6-Methoxy-2-benzoxazolinone (6-MBOA) compound which acts as a predictor for the onset of reproduction in most mammals including rodents (Neal, 1996).

There was no significant difference among *M. natalensis* food categories within habitat and season factors. These findings are similar to many from other studies (Leirs & Verheyen, 1995; Odhiambo et al., 2008). Mulungu et al. (2014) when investigating food preferences of *M. natalensis*, within irrigated rice and fallow field habitats found no significant differences in the proportion of the different stomach components of rodents captured across the two habitats and seasons. This suggests equal availability of food resources and states across both seasons and habitats. During wet season invertebrates in the stomachs of *M. natalensis* were equally important in wooded grassland and fallow land but generally more important than plant materials and seeds/grains in all habitats. But in the dry season the contents of the stomachs from maize crop fields and fallow land

were equally important but more important than invertebrates and seeds/grains in all three habitats. The same results were obtained by Rowsey et al. (2020), who recorded varied proportions and frequencies of rodent food categories spatially and temporally. This probably might be due to some food items being rapidly digested and hence underestimated (Kronfeld and Dayan, 1998) or others over estimated when consumption is measured in terms of frequency of occurrence (Reynolds & Aebischer, 1991) . Although it has been noted that more frequent consumption of a particular food does not necessarily reflect the importance of that food to the animal in terms of nutritional benefits (Ropper & Mickevicius, 1995).

On the other hand, niche breadth variations were detected in two habitats. In the wooded grassland it was low during the wet season but increased during the dry season whereas in maize crop fields it was high during the wet season but decreased during the dry season. In fallow land there was no niche breadth variation across both seasons. Niche breadth variations of *M. natalensis* was also reported by (Mulungu et al., 2011). The concept of niche breadth underlies many hypotheses (Feinsinger et al., 1981). For example, the physical environment, resources availability, and competition are thought to affect the breadth of a population's niche, including diet over ecological or evolutionary time spans (Sih, 1977). A number of theoretical models of optimal foraging strategy have been proposed (Pyke, 1976; Emlen, 1968; MacArthur & Pianka, 1966; Pulliam, 1974). For example, optimization of foraging model, is generally based on maximizing energy gained per unit time spent during foraging. Approaches to the problem of diet selection have assumed that different kinds of food can be ranked by desirability, with those requiring the least amount of processing time (capturing, subduing, and consumption of the food) per nutritional gain being the most desirable (Ebersole & Wilson, 1980). This theory seems to concur with variation in niche breadth in the wooded grassland where it was low during the wet season but increased during the dry season meaning that some more food items were taken in. Ebersole (1977) studied the foraging of captive *Peromyscus crinitus* and *Peromyscus eremicus* feeding on seeds. Both of the *Peromyscus* species responded to changes in food density as predicted by optimal foraging models, becoming less selective under lower food densities which in the field is expected to be during the dry season. This hypothesis antagonizes our observations in the maize crops fields where more food items were selected during the wet season than the dry season which is expected to have scarce resources. This is in line with Ebersole & Wilson (1980) who observed a negative correlation between food density and diet diversity in *P. eremicus*. Hence, suggesting presence of a number of various food items but which are lower in densities during the wet season than the dry season.

Optimal foraging theorists agree that as overall food density decreases, the diet of an optimally foraging animal should become more diverse through the inclusion of food items of lower desirability (Ebersole & Wilson, 1980). This phenomenon can further be explained by the fact that during the dry season there is a lot of produce harvests including maize crops according to the farmers' crop calendar in the study area. Despite this, there was no variation in niche breadths in fallow land, suggesting a stable food resource supply during both wet season and dry season as was observed by Mulungu et al. (2014), and supported by a strong index of seasonal dietary overlap. Further, seasons and habitats had varied influences but on plant materials food category only. The wooded grassland had a significant positive influence while maize crop fields' habitat had a non-significant positive influence; the wet season had a significant negative effect. Our results concur with Mulungu et al. (2011) who contended that *M. natalensis* is a generalist feeder that feeds on available resources depending on availability. We would have expected seasonality and habitats to have significant effect on the seeds/grains and invertebrates categories of *M. natalensis*. Skoglund (1992) when working in the Serengeti ecosystem reported the presence of an abundant seed bank, reaching up to 21 000 seeds m² which rodents in the area can easily get access to especially during the dry season (Belsky A. J., 1986; Gómez, 2004). Elsewhere, Oliveira (2010) concluded that rainfall and humidity were the best predictors of insect abundance. Hence, it is still little known as to why habitat and seasonality are not influential covariates on seed/grains and invertebrates food categories of *M. natalensis* in our study area.

Studying the influence of seasons and habitats on diet categories of the dominant rodent species (*Mastomys natalensis*) in the Western Serengeti ecosystem Tanzania offers a useful tool for determining its feeding strategy in the study locality. The animal seems to be an omnivore that selects more invertebrates and plant materials during different seasons of the year or depending on their availability. Hence, it can pose some competition with both herbivorous and insectivorous animals. Therefore, this work will set a benchmark from where to start re-designing new management strategies of *M. natalensis* in the area. These rodents were found to eat plant materials and seeds/grains to a substantial extent in the maize crop fields habitat hence it could be a potential pest in the agricultural area. Therefore, combined management actions should be taken. Cover materials should be removed from crop farms and neighbouring fallow areas. Also rodenticides should be used preventively and remedially when there is a need.

Acknowledgement

We are grateful to African Centre of Excellence for Innovative rodent pest Management and Biosensor Technology Development-ACE II for sponsoring my PhD project. We are also grateful to Prof. Fortunatus Makonda for doing the vegetation sampling and analysis and Mr. Khalidi Kibwana from SPMC for actively assisting in the process of data collection in the field.

Authors contribution

All authors conceived the study and designed methodology. EJR collected data, conducted analysis and wrote original drafts of the manuscripts. AAR analysed and reviewed original draft manuscripts, SNH reviewed the manuscripts. SNH, LM and AAR supervised the research. All authors read and approved final version of the manuscript for publication.

References

- Ajayi, A. F., & Akhigbe, R. E. (2020). Staging of the estrous cycle and induction of estrus in experimental rodents: an update. *Fertility Research and Practice*, 6(1), 1–15.
<https://doi.org/10.1186/s40738-020-00074-3>
- Belsky A. J. (1986). Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania. 1. Colonization of grazed and ungrazed plots. In *J. Ecol.* (Vol. 74).
- Capizzi, D., Bertolino, S., & Mortelliti, A. (2014). Rating the rat: Global patterns and research priorities in impacts and management of rodent pests. *Mammal Review*, 44(2), 148–162.
<https://doi.org/10.1111/mam.12019>
- Chowdhury, M. Z. I., & Turin, T. C. (2020). Variable selection strategies and its importance in clinical prediction modelling. *Family Medicine and Community Health*, 8(1).
<https://doi.org/10.1136/fmch-2019-000262>
- Cooper, R. L. and J. D. S. (1978). Importance of termites in the diet of the aardwolf *Proteles cristatus* in South Africa. *South Africa Journal of Zoology*, 14, 5–8.
- Delany, M. J. (1964). A study of the ecology and breeding of small mammals in Uganda. *Proceedings of the Zoological Society of London*, 142, 347–370.
- Dippenaar, N. J., Swanepoel, P. and Gordon, D. H. . (1993). Diagnostic morphometrics of two medically important southern African rodents, *Mastomys natalensis* and *M. coucha* (Rodentia: Muridae). *South African Journal of Science*, 89, 300–303.
- Ebersole, J. P. (1977). *Experiments of optimal foraging in Peromyscus*. In: Crowder L ed, *Ecology Lab Experiences, An Ideas Forum*.
- Ebersole, J. P., & Wilson, J. C. (1980). Optimal Foraging: The Responses of *Peromyscus leucopus* to Experimental Changes in Processing Time and Hunger. In *Oecologia (Berl.)* (Vol. 46).
- Emlen, J. M. . (1968). Optimal choice in animals. *Am. Natur.*, 102, 385–390.
- Feinsinger, P., Spears, E. E., & Poole, R. W. (1981). A Simple Measure of Niche Breadth. In *Source: Ecology* (Vol. 62, Issue 1).
- Gómez, J. M. (2004). Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex*. *Evolution*, 58(1). <https://doi.org/10.1554/02-617>

- Imakando, C. I., Fernández-Grandon, G. M., Singleton, G. R., & Belmain, S. R. (2022). Impact of fertility versus mortality control on the demographics of *Mastomys natalensis* in maize fields. *Integrative Zoology*, 17(6), 1028–1040. <https://doi.org/10.1111/1749-4877.12580>
- Kilwanila, S. I., Msalya, G. M., Lyimo, C. M., & Rija, A. A. (2021). Geographic biases in cane rat (*Thryonomys*) research may impede broader wildlife utilization and conservation in Africa: A systematic review. In *Scientific African* (Vol. 12). <https://doi.org/10.1016/j.sciaf.2021.e00785>
- Krebs, C. J. (1989). *Niche Overlaps and Diet Analysis. Ecological Methodology.* (Harper and Row: New York, NY.).
- Krebs, C. J. (2001). *Ecology: The experimental analysis of distribution and abundance* (5th ed.). xBenjamin Cummings.
- Kronfeld, Noga and Dayan, T. (1998). A new method of determining diets of rodents. *Journal of Mammalogy*, 79(4), 1198–1202. <https://doi.org/10.2307/1383011>
- Kwok, A. B. C., & Eldridge, D. J. (2015). Does fire affect the ground-dwelling arthropod community through changes to fine-scale resource patches? *International Journal of Wildland Fire*, 24(4), 550–559. <https://doi.org/10.1071/WF14088>
- Lack, P. C. (1986). Diurnal and seasonal variation in biomass of arthropods in Tsavo East National Park, Kenya. *African Journal of Ecology*, 24, 47–51.
- Leirs, H., Verheyen, W. (1995). *Population Ecology of Mastomys natalensis (Smith, 1834). Implications for Rodent Control in Africa.* 'Agricultural Editions No. 35.
- Leirs, H. (1995). *Population ecology of Mastomys natalensis (Smith 1834): implication for rodent control in East Africa.*
- Levins, R. (. (1968). *Evolution in Changing Environments.* (Princeton University Press: Princeton, NJ.
- MacArthur, R. H., & Pianka, E. R. (1966). On Optimal Use of a Patchy Environment. *The American Naturalist*, 100(916), 603–609. <https://doi.org/10.1086/282454>
- Makundi, R. H., Massawe, A. W., Mulungu, L. S. and Katakweba, A., Mlyashimbi, E. C. M., Ngowo, V., Mdangi, M., Katakweba, A. S., Tesha, P., Mrosso, F. P., Mchomvu, M., Kilonzo, B. S., & Belmain, S. R. (2014). Food preferences of the multi-mammate mouse, *Mastomys natalensis*, in irrigated rice habitats in Tanzania. *International Journal of Pest Management*, 60(1), 1–8. <https://doi.org/10.1080/09670874.2013.871759>
- Makundi, R. H., Massawe, A. W., & Mulungu, L. S. (2007). Reproduction and population dynamics of *Mastomys natalensis* Smith, 1834 in an agricultural landscape in the Western Usambara Mountains, Tanzania. *Integrative Zoology*, 2(4), 233–238. <https://doi.org/10.1111/j.1749-4877.2007.00063.x>
- Makundi, R. H., Ogege, N. O., & Mwanjabe, P. S. (1999). Rodent pest management in East Africa - an ecological approach. *Ecologically-Based Rodent Management*, 460–476. <https://doi.org/10.2193/2005-623>
- Massawe, A. W., Makundi, R. H., Zhang, Z., Mhamphi, G., Liu, M., Li, H. J., & Belmain, S. R. (2018). Effect of synthetic hormones on reproduction in *Mastomys natalensis*. *Journal of Pest Science*, 91(1), 157–168. <https://doi.org/10.1007/s10340-017-0894-4>

- Mdangi, M. (2009). *Assessment of rodent damage to maize (Zea mays L.) in the field and stores at Berega Village, in Kilosa District Tanzania. Masters Thesis, Sokoine University of Agriculture, Morogoro, Tanzania.*
- Mlyashimbi, E. C. M., Mariën, J., Kimaro, D. N., Tarimo, A. J. P., Isabirye, M., Makundi, R. H., Massawe, A. W., Mdangi, M. E., Kifumba, D., Nakiyemba, A., Leirs, H., Belmain, S. R., & Mulungu, L. S. (2018). Relationships between seasonal changes in diet of Multimammate rat (*Mastomys natalensis*) and its breeding patterns in semi-arid areas in Tanzania. *Cogent Food and Agriculture*, 4(1). <https://doi.org/10.1080/23311932.2018.1507509>
- Mohtasebi, S., Teimouri, A., Abbaszadeh Afshar, M. J., Mobedi, I., Abbasian, H., Totonchian, N., & Mowlavi, G. (2021). First report of *Spirocera lupi* larva in dung beetles (*Scarabaeus armeniacus*) in the central region of Iran: A morphological and molecular identification. *Comparative Immunology, Microbiology and Infectious Diseases*, 77, 1–16. <https://doi.org/10.1016/j.cimid.2021.101671>
- Monadjem, A., & Perrin, M. (2003). Population fluctuations and community structure of small mammals in a Swaziland grassland over a three-year period. *African Zoology*, 38(1), 127–137. <https://doi.org/10.1080/15627020.2003.11657200>
- Monath, T. P. (1975). Lassafever: review of epidemiology and epizootiology. *Bulletin WHO*, 52, 577–592.
- Mulungu, L. S., Mahlaba, T. A., Massawe, A. W., Kennis, J., Crauwels, D., Eiseb, S., Monadjem, A., Makundi, R. H., Katakweba, A. A. S., Leirs, H., & Belmain, S. R. (2011). Dietary differences of the multimammate mouse, *Mastomys natalensis* (Smith, 1834), across different habitats and seasons in Tanzania and Swaziland. *Wildlife Research*, 38(7), 640–646. <https://doi.org/10.1071/WR11028>
- Mulungu, L. S., Mlyashimbi, E. C. M., Ngowo, V., Mdangi, M., Katakweba, A. S., Tesha, P., Mrosso, F. P., Mchomvu, M., Kilonzo, B. S., & Belmain, S. R. (2014). Food preferences of the multi-mammate mouse, *Mastomys natalensis*, in irrigated rice habitats in Tanzania. *International Journal of Pest Management*, 60(1), 1–8. <https://doi.org/10.1080/09670874.2013.871759>
- Mwasapi, B. S., & Rija, A. A. (2022). Local habitat characteristics influence abundance and community structure of rodents in a regenerating Lulanda reserved forest, southern Tanzania. *Restoration Ecology*, 30(1), 1–10. <https://doi.org/10.1111/rec.13501>
- Neal, B. R. (1996). Reproductive response of *Tatera leucogaster* (Rodentia) to supplemental food, water, and 6-methoxybenzoxazolinone. *Mammalia*, 60, 651–666.
- Norton-Griffiths, D. H. and L. P. Ennycuik. (1975). The patterns of rainfall in the Serengeti Ecosystem, Tanzania. *E. Afr. Wildl. J.*, 13(3–34), 347–314.
- Odhiambo, R. O., Makundi, R. H., Leirs, H., & Verhagen, R. (2008a). Dietary selection in *Mastomys natalensis* (Rodentia: Muridae) in the maize agro-ecosystems of central and southwestern Tanzania. *Mammalia*, 72(3), 169–177. <https://doi.org/10.1515/MAMM.2008.007>
- Odhiambo, R. O., Makundi, R. H., Leirs, H., & Verhagen, R. (2008b). Dietary selection in *Mastomys natalensis* (Rodentia: Muridae) in the maize agro-ecosystems of central and

- southwestern Tanzania. *Mammalia*, 72(3), 169–177.
<https://doi.org/10.1515/MAMM.2008.007>
- Oliveira, V. A. (2010). *Seasonality of insects in the semi-arid Caatinga of northeastern Brazil*.
- Pulliam, H. R. (1974). On the Theory of Optimal Diets. *The American Naturalist*, 108(959), 59–74. <https://doi.org/10.1086/282885>
- Pyke, G. H. . (1976). *Optimal foraging, the marginal value theorem.pdf*. 752(4), 739–752.
- Randolph, J. C., & Cameron, G. N. (2001). Consequences of diet choice by a small generalist herbivore. *Ecological Monographs*, 71(1), 117–136. [https://doi.org/10.1890/0012-9615\(2001\)071\[0117:CODCBA\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2001)071[0117:CODCBA]2.0.CO;2)
- Reynolds, J. C., & Aebischer, N. J. (1991). Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the Fox *Vulpes vulpes*. *Mammal Review*, 21(3), 97–122. <https://doi.org/10.1111/j.1365-2907.1991.tb00113.x>
- Rija, A. A. (2021). *Local Habitat Characteristics Determine Buttery Diversity and Community Structure in a Threatened Kihansi Gorge Forest, Southern Udzungwa Mountains, Tanzania*. <https://doi.org/10.21203/rs.3.rs-811050/v1>
- Ropper, T. J., & Mickevicius, E. (1995). Badger *Meles meles* diet: a review of literature from the former Soviet Union. *Mammal Review*, 25(3), 117–129. <https://doi.org/10.1111/j.1365-2907.1995.tb00451.x>
- Rowsey, D. M., Keenan, R. M., & Jansa, S. A. (2020). Dietary morphology of two island-endemic murid rodent clades is consistent with persistent, incumbent-imposed competitive interactions. *Proceedings of the Royal Society B: Biological Sciences*, 287(1921). <https://doi.org/10.1098/rspb.2019.2746>
- Rwebuga, E. J., Mulungu, L. S., Rija, A. A., Hassan, S. N., Development, T., & Centre, M. (2023). *Ecological correlates of population abundance of a pest small mammal species (Mastomys natalensis) inhabiting a protected area-farmland landscape in western*. 92(1), 159–169.
- Schoener, T. W. (1968). The Anolis Lizards of Bimini : Resource Partitioning in a Complex Fauna Author (s): Thomas W . Schoener Published by : Wiley Stable URL : <http://www.jstor.org/stable/1935534> REFERENCES Linked references are available on JSTOR for this article : You may. *Ecological Society of America*, 49(4), 704–726.
- Selemani, M., Makundi, R. H., Massawe, A. W., Mhamphi, G., Mulungu, L. S., & Belmain, S. R. (2022). Impact of contraceptive hormones on the reproductive potential of male and female commensal black rats (*Rattus rattus*). *Integrative Zoology*, 17(6), 991–1001. <https://doi.org/10.1111/1749-4877.12563>
- Sih, A. (1977). . Optimal foraging theory used to deduce the energy available in the environment. *Biotropica*, 9, 216.
- Skoglund, J. (1992). The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. *Journal of Vegetation Science*, 3(3). <https://doi.org/10.2307/3235760>
- Smith, V. R., Avenant, N. L., & Chown, S. L. (2002). The diet and impact of house mice on a sub-Antarctic island. *Polar Biology*, 25(9), 703–715. <https://doi.org/10.1007/s00300-002->

0405-8

- Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. In *Behavioral Ecology and Sociobiology* (Vol. 65, Issue 1, pp. 13–21). Springer Verlag. <https://doi.org/10.1007/s00265-010-1037-6>
- Team, R. C. (2021). *A language and environment for statistical computing*.
- Thirgood, S., Mosser, A., Tham, S., Hopcraft, G., Mwangomo, E., Mlengeya, T., Kilewo, M., Fryxell, J., Sinclair, A. R. E., & Borner, M. (2004). Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Animal Conservation*, 7(2), 113–120. <https://doi.org/10.1017/S1367943004001404>
- Vezzosi, R. I., Eberhardt, A. T., Raimondi, V. B., Gutierrez, M. F., & Pautasso, A. A. (2014). Seasonal variation in the diet of *Lontra longicaudis* in the Paraná River basin, Argentina. *Mammalia*, 78(4), 451–463. <https://doi.org/10.1515/mammalia-2013-0053>
- Wondifraw B.T, M. Y. T. and A. . S. (2021). Assessment of crop damage by rodent pests from experimental barley crop fields in Farta District, South Gondar, Ethiopia. *PLoS ONE*, 16(8), e0255372. <https://doi.org/https://doi.org/10.1371/journal.pone.0255372>
- Wright, J. P., Jones, C. G., & Flecker, A. S. (2002). *An ecosystem engineer , the beaver , increases species richness at the landscape scale*. 96–101. <https://doi.org/10.1007/s00442-002-0929-1>