Tanzania Journal of Forestry and Nature Conservation, Vol 91, No. 2 (2022) 178-192

Diet Composition and Niche Overlap of Four Sympatric Rodent Species Inhabiting Mount Rungwe Forest Nature Reserve, Tanzania

[*1,3]U. Richard, [1]R.M. Byamungu and [2]F. Magige

[1]Department of Wildlife Management,
College of Forestry, Wildlife and tourism
Sokoine University of Agriculture, Morogoro

[2]Department of Zoology and Wildlife Conservation,
University of Dar es Salaam, Dar es Salaam

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

[*]Corresponding author: richardupe@gmail.com

ABSTRACT

Understanding animal feeding behaviour is key in determining coexistence mechanisms which are vital for conservation and management. The coexistence mechanisms of sympatric species in mount Rungwe are unknown. From 2020 to 2021 a study on the dietary contribution, overlap and niche breadth of four rodents in Mount Rungwe Forest Nature Reserve was conducted. Random sampling was employed with the removal method, whereby captured rodents' stomachs were removed and their contents analyzed. Dietary contribution, overlap and niche breadth were calculated. All species consume diverse food resources and categories where *Beamys hindei* had a significantly high number of seeds/grains while *Grammomys dolichurus* and *Lophuromys machangui* contained a significantly higher number of invertebrates. Narrow niche breadth was observed for *G. dolichurus* while *Praomys delectorum, L. machangui*, and *B. hindei* had a moderate niche breadth but the dietary overlap was high in all four species. Our results conclude that *L. machangui, P. delectorum*, and *B. hindei* can coexist without competition as they have >0.5 niche breadth and high overlap, while *G. dolichurus* might experience competition because of low niche breadth and food diversity. Further investigation regarding seasonal diet partitioning and micro identification of food items is recommended.

Keywords: diet partitioning - dietary niche breadth - coexistence.

INTRODUCTION

Species coexistence depends largely on how species utilize their environment, and how they utilized resources are distributed to serve different species in an area. Several theories are involved in understanding the determinant of species coexistence in a particular community, which have been suggested in several ecological studies (Dakota *et al.* 2020, Espinelli *et al.* 2017, Kotler and Brown 1999, Pinotti, *et al.* 2011). Ecologists have proposed some theories underlying species coexistence, such as the Niche partitioning and Niche Overlap theory (Pianka 1974). The niche partitioning theory suggests that the coexistence of ecologically similar species in the same area requires some forms of resource partitioning to reduce or avoid interspecific competition (Villanueva-Bonilla *et al.* 2019). In resource partitioning, some of the resources are shared by ecologically similar species resulting in resource overlap or niche overlap. The niche overlap theory states that 'within an ecological community species partition available resource among themselves (Pianka 1974). Thus, a community with greater niche overlap is more likely to support more species than a community with less niche overlap or with less resource sharing. Resource partitioning and niche overlap help related species to coexist in an area and develop a specialization in resource utilization thus reducing interspecific competition (Delaval and Henry 2005). Thus, this might be the case for small mammals, with high metabolic rates and low energy storage capacity, hence required to consume large amounts of food relative to their body weight (Hudson and White 1985). Studying resource use and factors underlying co-existence highly depends on the organisms under study as different organisms utilize different resources differently. Coexisting species generally compete for resources e.g food, space, etc (Nie *et al.* 2019). Thus, understanding the factors behind species co-existence is fundamental, especially for communities occupying harsh environments such as mountainous areas.

On the other hand, coexistence results when each species by itself lives sufficiently in a profitable condition. Community structure can then be studied by testing for the existence of necessary conditions under various alternative scenarios of coexistence (Brown 1989, Leibold and McPeek 2006, Siepielski and McPeek 2010). Here we follow the niche partitioning and niche overlap theories to evaluate the co-existence of rodent species at Mount Rungwe Forest Nature Reserve (MRFNR). According to the competitive exclusion principle, more than one species occupying the same habitat with limited resources would exclude each other unless there are niche partitioning mechanisms among them (Hardin 1960). Thus, niche partitioning is virtual in achieving greater biodiversity and adequate resource use (Finke and Snyder 2008). However, competition occurs when the resource is limited but it is less important when resources are not a limiting factor (Mwasi *et al*. 2013).

In East Africa, few studies have analyzed the diet composition of forest rodents (Clausnitzer *et al.* 2013, Schuchmann 2003). Most of the knowledge about rodent diets is based on crop fields and pestiferous rodents (Mlyashimbi *et al.* 2018, Mulungu *et al.* 2011, Odhiambo *et al.* 2008). Diet partitioning and overlap in mountainous forest rodents of MRFNR is lacking and thus their coexistence knowledge is not known. This study will help to understand if the coexistence of these rodent species in MRFNR is aided by diet partitioning and niche overlap, thus adding knowledge of the ecological requirement for the studied species in the area. Commonly, rodents are opportunistic feeders consuming a variety of food types including seeds, fruits, grains, vegetative plant materials, invertebrates, and small animals depending on the availability, habitat, and season (Arregoitia and D'eli 2021). In areas of abundant resources, they will adopt preferable food but if food is scarce, they have to adapt by either food partitioning and specialization (Arregoitia and D'eli 2021) or having different forage behavior to reduce competition. At MRFNR the vegetation is typically a montane afro-alpine that supports a thriving community of small mammals including rodents. Vertical stratification of the forest is considered an important factor allowing resource partition (Sushma and Singh 2006) among forested small mammals.

The objective of this study was to determine dietary composition as a mechanism for the coexistence of sympatric rodent species at MRFNR. Specifically, (i) to determine the percentage occurrence, percentage contribution, and relative importance of the dietary items between the sympatric species; (ii) to determine diet diversity and niche breadth of the sympatric species; (iii) to determine niche overlap among the species; and (iv) to assess the relationship between percentage food categories, percentage food categories and rodent species at MRFNR. The results will have conservation management implications as they will serve in understanding species' relationships in their sympatric existence.

MATERIALS AND METHODS

Study area

The study was carried out at Mount Rungwe Forest Nature Reserve in Rungwe District, Mbeya Region in Southern Tanzania (Fig 1). The study site lies between 9^0 03′ - 9^0 12′S and 33^0 35′ - 33^0 45′E with an elevation peak of 2981m a.s.l. The reserve experience two major seasons; a Wet season from November to May with short and heavy rains and a dry season from June to October). The mean annual rainfall ranges from 700 mm to 2,700 mm in low and higher elevations respectively Exceptionally, the southeastern part of the mountain receives rainfall of up to 3000 mm per year. The temperature varies between − 6^0 C in the highlands and 29^0 C in the lowlands (Williamson *et al.* 2014). The area is dominated by sub-mountainous and mountainous forests with some shrubs and grasses in the higher elevation.

The study was conducted in three elevations; low-elevation, mid-elevation and higher-elevation as previously described in the MRFNR management plan (URT-MRNRMP 2017). The three elevations vary in habitats, climate and vegetation composition. Lower elevation ranges from 1700-2000 m a.s.l with low montane forests habitat; mid-elevation ranges from 2000-2400 m a.s.l with montane forest habitat, and high-elevation ranges from 2400-2900 m a.s.l with bushland habitat.

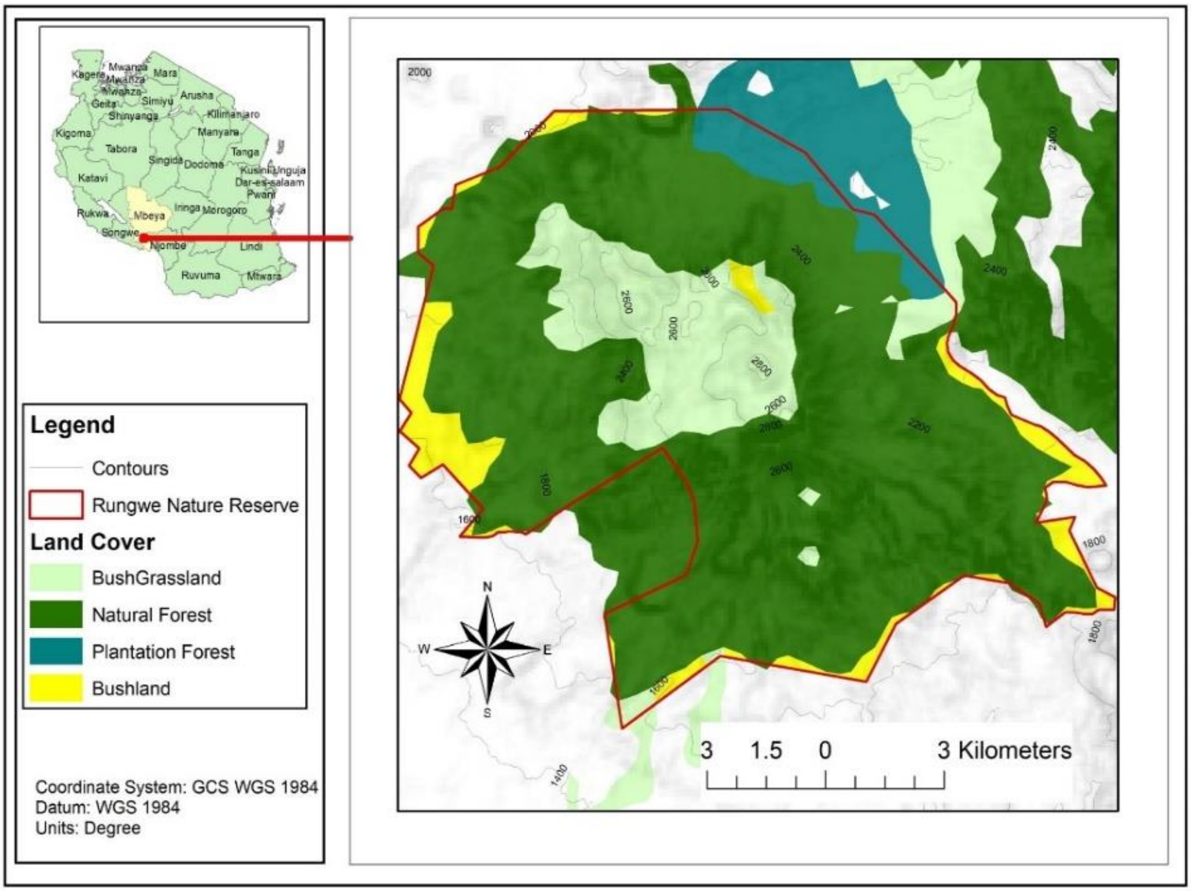

Figure 1: Map of Rungwe Forest Nature Reserve. ***Source:*** Richard *et al.* (2022)

Sampling design, rodent trapping and data collection

Sampling points were selected along the elevational gradient between 1700 to 2900 m a.s.l. covering low (1700-2000m a.s.l), mid (2000-2400m a.s.l), and high (2400-2900m a.s.l) elevations (URT-MRNRMP 2017). Data were collected between March 2020 and September 2021. The removal method using snap traps (1.0 × 8.5 × 16.5 cm), was employed with 4 transect lines of 100 m in each sampling point making a total of 12 transect lines. One hundred and thirty-two traps were set for six nights, during wet and dry seasons, with 11 traps in each transect at a 10 m distance. Snap traps were used as they kill the animal instantly before ingesting the bait and the digestion process ceases instantly. The traps were baited with a mixture of roasted coconut and peanut butter and they were checked early in the morning between 0600-0900 hrs. Trapped animals were collected and identified based on morphometric measurements and recent distribution (Bryja *et al.* 2014; Fitzgibb *et al.* 1995, Happold 2013, Walter *et al.* 2007). Collected individuals were dissected, stomach (Pylorus and Cardium) removed and fixed in 70% ethanol for food analysis based on micro-histological examination of undigested fragments.

The collected stomachs were opened and the contents were spread out in a Petri dish and sorted under X25 or X50 magnifications using a binocular microscope CX41RF, Olympus. All fragments in the stomach were examined viz. seed/grain, roots, stem, leaves, invertebrates, hairs, and other unidentified materials. When needed, a Lugol solution was used to determine the presence of starch to indicate the presence of seeds/grain in a diet.

Data analysis

Diet composition

Diet was statistically compared among the captured species of which five or more stomach samples were collected (Balˇciauskas *et al.* 2021) as these were considered the most abundant rodent species in the study area. The diet partitioning was analyzed for four species *Beamys hindei*, *Lophuromys machangui*, *Praomys delectorum* and *Grammomys dolichurus*. Analysis for seasonal and elevation differences in diet also depends on the number of stomachs collected in each season and elevation. Species whose stomachs were not analyzed due to a small number of captured individuals were *Graphiurus murinus* (n=1), *Mus spp* (n=1), *Dendromus insignis* (n=1), and *Crocidura* sp. (n=2). Percentage contribution of each diet category to the volume of the particular stomach contents (PV) was estimated to be the nearest 10% (crude), with an additional category of 5% where an item was present but contributed <10% to stomach content by volume (Smith *et al.* 2002). Percentage occurrence (PC) of a particular food item in a sampling period was calculated from the number of stomachs it was found, divided by the number of stomachs examined.

Niche breadth and dietary overlap

Niche Breadth was calculated using diet diversity which is the number of dietary items recorded per individual per species during the sampling period. Diet diversity was calculated following Ebersole and Wilson (1980) using Levins' index (Levins 1968) as:

$$\text{Diet diversity}(B) = 1/\sum Pi^2 \quad \ldots\ldots\ldots \text{ Eq. 1}$$

Where P = (PV/100) i.e., the mean proportion in the volume of each of the dietary items. Levins' index ranges from 1 to n (n = total number of food item categories).

Diversity was standardized to scale 0.0 to 1.0 by using Hurlbert's method (Krebs 1989) to obtain niche breadth:

$$B_s = (B-1)/(n-1) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{ Eq. 2}$$

Where B_s = Levins' standardized niche breadth, B = Levins' measure of niche breadth, and n = the number of possible resource states.

Niche breadth here means diversity of food items used by an animal and it ranges from 0 meaning the species has limited food choices, narrow niche (<0.4) and is more specialist taxa and favour specific environment and 0.75-1 indicates broad niche, generalist taxa that are equally abundant across the environment, while 0.4-0.75 indicate the species had a moderate niche breadth.

Importance value (IV) is the values of resources understudy when compared with other resources in which if resources contribute a high percentage and had a high frequency then their importance is high than the resource which contributes less percentage with low frequency. Thus, important food value (IV) is the food item with a high contribution and frequency percentage in the diet compared to other food items consumed. An importance value for each diet item from each species was calculated following Cooper and Skinner (1978):

$$IV = PV \times PC/100 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad Eq.\ 3$$

Where IV = Important value, PV= % contribution to volume of a stomach content and PC = percentage occurrence/frequency.

The relative importance (RI) value of a particular food item was then taken as the importance value of that item expressed as the average percentage of the importance values for all food items

$$RI = 100 \times IV/\sum IV \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad Eq.\ 4$$

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

$$O_{jk} = \frac{\sum_{i}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^2 \sum_{i}^{n} p_{ik}^2}} \quad \ldots\ldots\ldots\ldots\ldots \quad Eq.\ 5$$

Where, O_{jk} = Pianka's measure of niche overlap between species $_j$ and $_k$, P_{ij} and P_{ik} = are proportions of the ith resource used by the jth and kth species, respectively. Overlap values vary from zero (no overlap) to one (total overlap).

Moreover, a general linear model was performed to determine the relationship in percent food categories consumed by rodents at MRFNR and to see if there was variation in the percentage contribution of food categories within and between rodent species.

$$Percent \sim FG + RS + FG{*}RS \quad \ldots\ldots \quad Eq.\ 6$$

Where; Percent = percent in food categories, FG = food categories, RS = rodent species, FG*RS = interaction between food categories and rodent species

Finally, pairwise comparison was done by Tukey Honest Significant Difference (Tukey HSD) with 95% confidence limits and results presented in Compact Letter Display (CLD) whereby groups with the same letters are not detectably different and groups that are detectably different get a different letter. Groups can have more than one letter to reflect overlap between sets of groups. Statistical analysis was performed using R version 4.0.3 (R Core Team 2020).

RESULTS

A total of 171 individual stomachs belonging to Muridae (*Praomys delectorum; Lophuromys machangui; Grammomys dolichurus; Mus* sp), Gliriidae (*Graphiurus murinus*), Nesomyidae (*Beamys hindei; Dendromus insignis*) and Soricidae (*Crocidura* sp) were collected. However, 166 stomach contents from *Grammomys dolichurus* n=12, *Lophuromys machangui* n=22, Praomys *delectorum* n=119, and *Beamys hindei* n=13 was analyzed for diet composition. This was due to the fact that, gut contents were analyzed for species with more than five collected stomachs.

Food items and fragments identified in stomach analysis included seeds/grains, stems, leaves, roots, invertebrates and hairs. (Plate 1).

Variation of food categories contributing to the diet of rodents

Invertebrates contributed high in the mean percent of diet categories (19%) followed by seeds/grain (10%) which was not different from leaves and stems. The least mean percentage contribution in the diet of rodents at MNFRN was roots (5%). A significant difference was observed in percent diet contribution among diet categories ($F_{5,966}$ =

34.25, $p < 0.001$) in the diet of rodents (Fig. 2). Invertebrates (a) shows significant different with seeds/grains (b), leaves (bc), stem (bc), roots (c) and hairs (c). Seeds/grains (b) were insignificant when compared to leaves (bc) and stem (bc) but significant when compared with roots (c) and hairs (c). While leaves (bc), stems (bc), roots (c), and hairs (c) contributions to the diet were insignificant

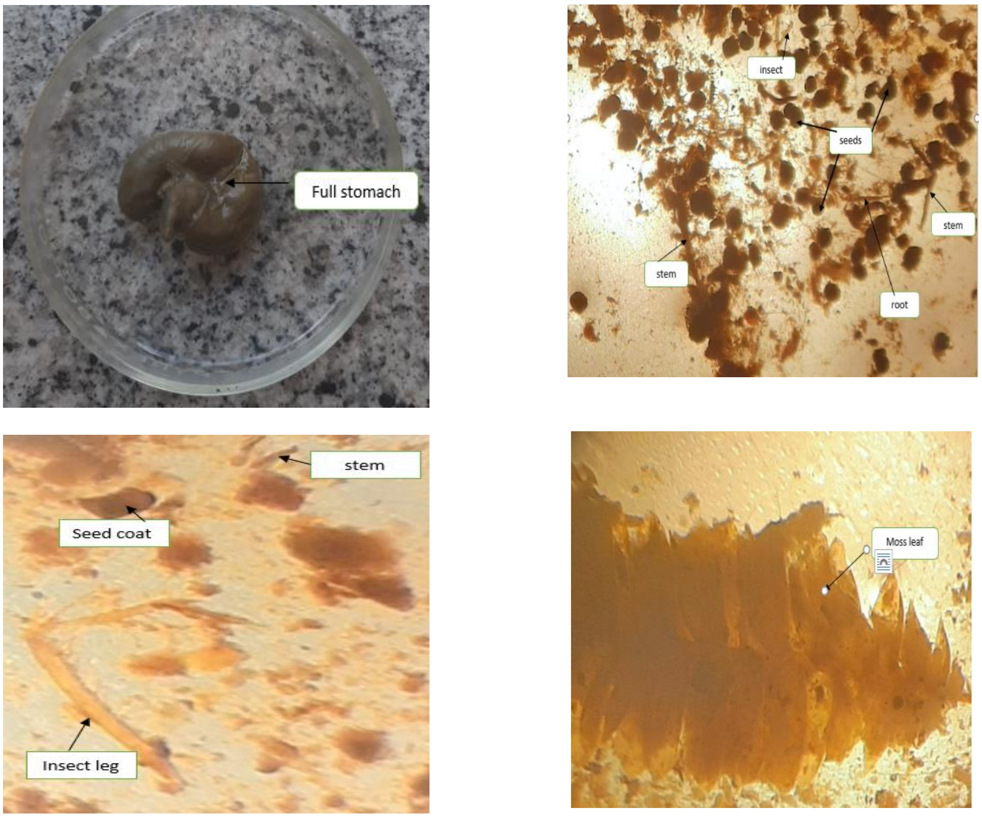

Plate 1: **Some of the food items and fragments found in MRFNR rodent stomachs.**

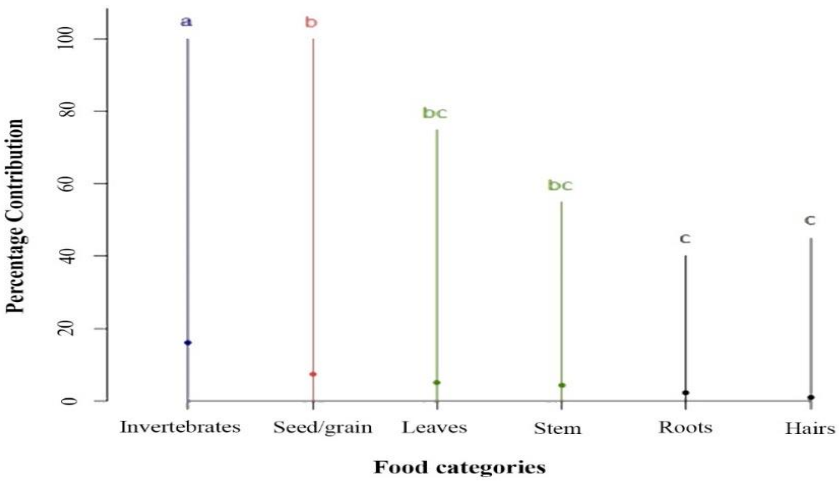

Figure. 2: Food items contribution and their difference in the diet of rodents at MRFNR. **[***Same letters indicate insignificant contribution; different letters mean significant difference between the food categories' contribution***.]**

Percentage of diet categories contribution to the diet, within and among rodents

The diets of all four rodent species comprised fragments of seeds/grain, stems, leaves, roots, invertebrates and hairs (Fig. 3). There was a significant difference in the percentage contribution of diet categories among rodent species ($F_{20,966}=19.59$, $p<0.001$). Invertebrates were highly consumed by *L. machangui* (33.9), followed by *G. dolichurus* (16.3) and *B. hindei* (15.4), but were least consumed by *P. delectorum* (13.2). Meanwhile, *B. hindei* and *L. machangui* were recorded to mostly consume seed/grain (Table 1).

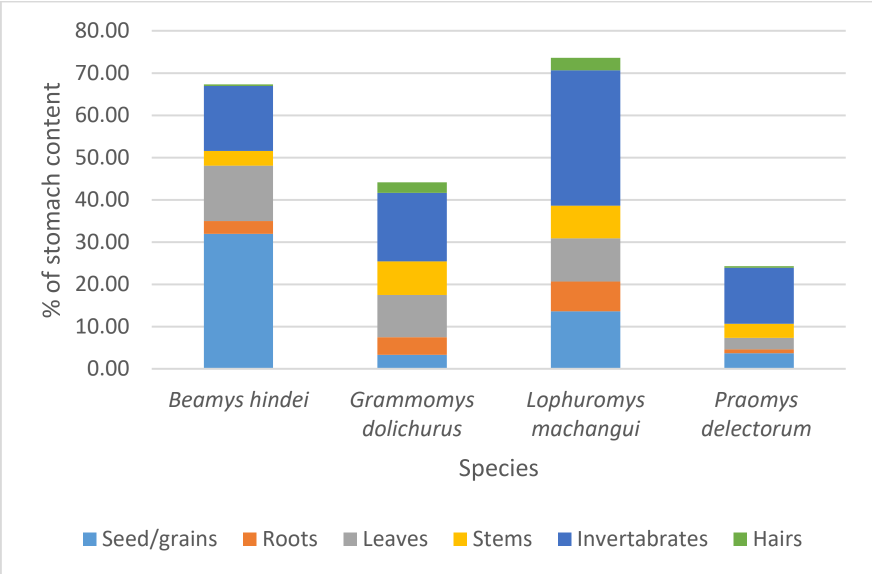

Figure 3: Mean Relative Abundance (%) diet contribution of major food categories found in stomachs of *B. hindei, G. dolichurus, L. machangui,* and *P. delectorum*.

Table 1: Variation in Percentage of diet categories contribution within and between rodent species in MRFNR

Food categories	Species	Percent Contribution
Seed/grains	*B. hindei*	31.9^{ab}
Roots	*B. hindei*	3.1^{c}
Leaves	*B. hindei*	13.1^{c}
Stems	*B. hindei*	3.5^{c}
Invertebrates	*B. hindei*	15.4^{bc}
Hairs	*B. hindei*	0.4^{c}
Seed/grains	*G. dolichurus*	3.3^{c}
Roots	*G. dolichurus*	4.2^{c}
Leaves	*G. dolichurus*	10^{c}
Stems	*G. dolichurus*	7.9^{c}
Invertebrates	*G. dolichurus*	16.3^{abc}
Hairs	*G. dolichurus*	2.5^{c}
Seed/grains	*L. machangui*	15.56^{bc}
Roots	*L. machangui*	8.6^{c}
Leaves	*L. machangui*	11.9^{c}
Stems	*L. machangui*	9.4^{c}
Invertebrates	*L. machangui*	33.9^{a}
Hairs	*L. machangui*	5^{c}
Seed/grains	*P. delectorum*	3.7^{c}
Roots	*P. delectorum*	0.9^{c}
Leaves	*P. delectorum*	2.7^{c}

Food categories	Species	Percent Contribution
Stems	*P. delectorum*	3.3[c]
Invertebrates	*P. delectorum*	13.2[c]
Hairs	*P. delectorum*	0.4[c]

(Superscript letters indicate significance level by CLD using Tukey HSD method; the same letter means the percent of food categories contribution was insignificant and different letters mean the percent of food categories contribution was significant within and/or between the rodent).

Relative food importance, niche breadth, and overlap

Important food items in the diet of *Lophuromys machangui*, *P. delectorum*, and *G. dolichurus* were invertebrates while *B. hindei* the important foods item in the diet were seeds/grains. Standardized diet diversity (niche breadth) for rodents at MRFNR ranged from 0.28 for *G. dolichurus* to 0.59 for *L. machangui* (Table 2).

The niche overlap of rodents in MRFNR ranged from 0.75 to 0.99. *Praomys delectorum* and *G. dolichurus* had the highest overlap of 0.99 which means they share almost all of the available resources and the least were *P. delectorum* and *B. hindei* (Table 3). Overlap ranges from 0 means the species do not share any resource to 1 when more than one species shares all the resources.

Table 2: Relative importance of food types in the diet and niche breadth of rodents in MRFNR (n=sampled stomach).

	B. hindei (n=13) %	*G. dolichurus* (n=12) %	*L. machangui* (n=22) %	*P. delectorum* (n=119) %
Seed/grains	33.43	1.05	7.05	1.00
Roots	1.29	1.74	5.72	0.18
Leaves	10.95	6.27	10.57	1.52
Stems	2.17	4.97	6.27	2.00
Invertebrates	11.28	13.59	33.12	17.94
Hairs	0.04	0.26	0.44	0.03
Others	40.84	72.13	36.84	77.33
Niche Breadth	0.54	0.28	0.59	0.53

Table 3: Niche overlap for dietary partitioning between four rodent species in MRFNR.

	B. hindei	*G. dolichurus*	*L. machangui*	*P. delectorum*
B. hindei	1	0.76	0.85	0.75
G. dolichurus		1	0.82	0.99
L. machangui			1	0.8
P. delectorum				1

DISCUSSION

In general, it is seemingly that MRFNR rodent species consume a greater proportion of available resources in their environment. *Beamys hindei*, *L. machangui*, *G. dolichurus*, and *P. delectorum* each consume a variety of plants (stem, seeds, leaves, roots) and animals (invertebrates, hairs) where they coexist in this tropical mountainous forest. The consumed food categories vary in their diet with a significant-high percentage contribution of invertebrates followed by seeds/grain, leaves, stem, and least roots and hairs (Fig. 2). Although most rodents are generalist and have opportunistic feeding habits, there are some differences in their diet that are determined by food availability and rodent species as also reported in other studies (Monadjem 1996, Samaniego-Herrera *et al.* 2017). As predicted, all four rodent species were omnivorous; however, the percentage contribution of food items (fruit, seed, leaves, stem, roots, and invertebrates) in the diet differed among rodents.

Relative food contribution and relative food importance

The results showed variations in food categories contributing to the diet (Table 1) and differences in relative importance (Table 2) within individual species. For example, for *Beamys hindei* seeds were relatively important and contributed highly to the diet. Members of the Genus Beamys are pouched rats and thus make use of their pouches to carry food and store them for future use. Unlike other food items such as invertebrates, leaves, roots, etc seeds and grains can be stored for a long period and used during the food scarce period. *Beamys* spp are reported to store more seeds than other food items (Hanney and Morris 1962), and this suggests that seed is an important food value in the diet of *B. hindei*. To our knowledge, this is the first study describing the diet of *B. hindei*, *L. machangui*, and *G. dolichurus* at MRFNR however available information on related species to *Beamys* shows that they eat more seeds (Happold 2013). However, there are variations in the Genus Lophuromys depending on species, but they consume more invertebrates and vegetative materials (Clausnitzer *et al*. 2013; Happold 2013).

For *G. dolichurus* invertebrates scored high as an important food item (Table 2) and this can suggest that *G. dolichurus* prefers invertebrates to other food items. However, invertebrates' contribution to the stomach of *G. dolichurus* was insignificant to other food items (Table 1). This might be because, either the sample size was small to detect the differences, or the species utilized all food items in the area.

A similar study in South Africa in a temperate forest showed *G. dolichurus* preferred more fruits and plant materials than invertebrates (Wirminghaus and Perrin 1992). Another study conducted along the Riverine forest in Somalia showed that seeds were the major food item and had a high volume in the diet of *G. dolichurus* (Varty 1990). This shows that even for the same species the important food item can be different depending on geographical location and seasonality (Lunghi *et al*. 2020). *Lophuromys machangui* diet varied and had a significantly high percentage contribution of invertebrates in its diet compared to other food items (Table 1). Likewise, we found no other study on the diet of *L. machangui* but a similar study in Mount Elgon reported *L. flavopuncatus* which is a close relative of *L. machangui* to eat a diversity of invertebrates (Clausnitzer *et al*. 2013). Another study by Ademola (2022) on *Lophuromys kilonzoi*, which share the Genus with *Lophuromys machangui* found out that the species consume more plant materials 37% than invertebrates 8%.

Praomys delectorum although showed a higher amount of invertebrates in its diet but this food items contribution was not significantly different from other food categories. Also, the number of invertebrates in *P. delectorum* species was significantly less when compared with invertebrates in the diet of *L. machangui*. The contribution of seeds/grain was also insignificant compared with that of *B. hindei*. The important food for *P. delectorum* was also invertebrates. Members of the genus *Praomys* forage on the ground on leaf litter (Happold 2013) this means that they are expected to feed more on underground materials such as ground invertebrates, dropped seeds, and short leaves. Hanney (1965), in his study, found that invertebrates contributed 82% and vegetables 78% in the diet of *P. delectorum* respectively. This supports our study that *Praomys spp* is omnivorous with invertebrates contributing a higher percentage to their diet. In all four studied species, hairs had a low percent contribution to the diet (1.56 mean) and also less important food categories for all rodents species. Hairs found in the stomach are not a precise indication of the use of mammals as food since some hairs maybe probably as a result of grooming (Samaniego-Herrera *et al*. 2017).

Niche breadth

Niche breadth for the studied species ranged from narrowest niche breadth which was 0.28 for *G. dolichurus* to moderate niche breadth of 0.53, 0.54, and 0.56 for *P. delectorum*, *B. hindei*, and *L. machangui* respectively. The narrow niche breadth for *G. dolichurus* indicates that it uses relatively few food items resources and might be a specialist. A similar study by (Pereira *et al.* 2012) on carnivores reports that the niche breadth with high specialization was a result of low population density which diminishes the need of the species to exploit the unfavourable habitats and makes the species more specialized in the suitable one. This might also be true for *G. dolichurus* as it was the least in density among the captured species. Other species *P. delectorum*, *B. hindei*, and *L. machangui* had moderate niche breadth and this indicated that they considerably proportionally consume several food items. For example, in the case of *L. machangui* invertebrates contributed significantly high to the diet (33.9%) but also other food items substantially contributed such as seeds (15.6%) and leaves (11.9%). This indicates that diet diversity consumed by *P. delectorum*, *B. hindei*, and *L. machangui* is higher than that of *G. dolichurus* which had a narrow niche breadth.

Niche overlap

The diet overlap between all four species was considerably high. High overlap might probably be a result of sharing the abundant common food items in the area. The extensive niche overlap does not necessarily signify competition as two or more organisms can share abundant resources without impacting the welfare of the other (Pianka 1974). When resources are abundant, interspecific competition declines, and high trophic niche overlap is permitted (Reid *et al.* 2013). Therefore, the overlap may be directly attributed to environmental heterogeneity and resource abundance (Mulungu *et al.* 2011). Though diet overlap can also be detected when the demand for resources exceeds supply and this will lead to interspecific competition as species need to expand their trophic niche to make up for their nutritional demands (Reid *et al.* 2013). Mwakisunga (2017), Bracebridge *et al.* 2012, and Richard *et al.* 2022 report the abundance and diverse resources at MRFNR and this might be the reason for high niche overlap between rodents as the resources are abundant hence they can be shared with minimal competition.

Grammomys dolichurus

Invertebrates in the diet of *G. dolichurus* ranked high among other food items (Table 2). This is true also when comparing food resource overlap. *G. dolichurus* had a very strong overlap with *P. delectorum* (0.99), and *L. machangui* (0.82) which also feed primarily on invertebrates. The very strong overlap between *P. delectorum*, *G. Dolichurus*, and *L. machangui* may not be due to indicative of competition but rather reflective of the heterogeneous nature of their habitat and high resource abundance in the area (Mulungu *et al.* 2011). MRNFR is a tropical forest and presents a heterogeneous environment with an abundance and variety of food for rodents (Richard *et al.* 2022).

Beamys hindei

The overlap of *B. hindei* was very strong with *L. machangui (0.85)* and strong with *P. delectorum (0.75)* and *G. dolichurus (0.76).* This is because apart from seeds which were the major contributor and important food category in the diet for *B. hindei*, invertebrates were the second major contributor in its diet, so higher overlaps with *L. machangui* whose important food was also the invertebrates.

Lophuromys machangui

The niche overlap between *L. machangui* and *P. delectorum*, *B. hindei*, and *G. dolichurus* was very strong. Relatively *L. machangui* consumes a variety of food items in a considerable proportion and also it shows a moderate degree of diet specialization hence overlapping with other species in the area. Although the diet of *L. machangui* was significantly high in invertebrates also other food items like seeds (15.6%) and leaves (11.9%) contributed a considerable amount to the diet.

Praomys delectorum

Praomys delectorum had a strong overlap (0.99) with G. dolichurus and *L. machangui* (0.80) than the *B. hindei* (0.76) (Table 4). Our results suggest that *P. delectorum, L. machangui, G. dolichurus,* and *B. hindei* can coexist through high food availability and diet partitioning. A similar study attributed the coexistence of *P. californicus* and *P. boylii* which has similar diets to *P. delectorum* to feeding primarily on invertebrates but of different species (Reid et al. 2013). The coexistence of these rodents at MRFNR might be a result of food abundance or the consumed food materials e.g., invertebrates might be of different species for different rodents hence the difference in proportion and preference. The coexistence due to the abundant foods can be supported by our findings as during the rain period all four species were recorded contrary to the dry season where only *P. delectorum* and *L. machangui* were recorded. During the rainy season dietary partitioning breaks down and the diet converges due to high food abundance. Thus, the availability of food resources largely determines the niche breadth and overlap between species (Sushma and Singh 2006).

CONCLUSIONS AND RECOMMENDATIONS

From the current study, it is concluded that if more than one coexisting species has high diet overlap but also high niche breadth it means that those species have a variety of food choices. These coexisting species may reduce competition by feeding on those wide varieties of food categories and this was a case for *L. machangui* but also for *P. delectorum* and *B. hindei.* Moreover, if coexisting species have high niche overlap but narrow niche breadth then their coexistence is less likely and they will have competition for resources and this was the case for *G. dolichurus*. This might also explain their low abundance in terms of numbers compared to other species in the area (Richard *et al.* 2022). This implies that *L. machangui, B. hindei,* and *P. delectorum* can coexist in MRFNR without competition for food resources while *G. dolichurus* might face competition with other rodent species. The study has provided baseline data on dietary habit, niche breadth, and overlap for four sympatric rodents but further studies are required for microanalysis of those diet items contributed in each species. In this study, invertebrates have been shown as one of the food items that small mammals mostly depend on, and this gives an alert for the importance of these invertebrates in the ecology of MRFNR. Enhancing conservation of the area will increase food items in terms of abundance and diversity and this will contribute to the increase of small mammals' density and diversity and thus enhance the functionality of the Rungwe ecosystem. It is essential to preserve habitats such as isolated mountains e.g. the Rungwe forest that maintains rodent assemblage with diverse diets in a natural habitat. This may have important implications for the ecological functioning of the area.

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