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Spatial-Temporal Variations in Dietary Consumption of Two Dominant Rodent Species (*Rhabdomys dilectus* and *Lophuromys acquilus*) on Mount Kilimanjaro, Tanzania

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Abstract: Understanding the resource partitioning and diet of sympatric species is vital for conservation and management. From April 2020 to March 2021, a study on the dietary consumption of *Rhabdomys dilectus* and *Lophuromys acquilus* was conducted on Mount Kilimanjaro. Rodent trapping was conducted in agricultural fields, fallow land, and moorland habitats during dry and wet seasons. Sherman live traps and snap traps were alternately placed in transect lines for three consecutive nights. We calculated the percentage occurrence and contribution of dietary items, niche breadth, and niche overlap of the two species across habitats and seasons. Both species consumed all the examined food items. The most abundant components were vegetative materials and seeds/starch, followed by invertebrates. *R. dilectus* and *L. acquilus* preferably consumed seeds and invertebrates, respectively, as their primary food source. Niche breadth differed significantly between species ($W = 650$, $p = 0.002$), habitat (Kruskal–Wallis chi-squared = 6.82, df = 2, $p = 0.03$), and season ($W = 700$, $p = 0.000$). There was a considerable niche overlap in diet (ranging from 0.84 to 0.98) between the species and was relatively higher in the dry season compared with wet season. Despite the observed niche overlap, spatial-temporal variations in dietary consumption between the two species can serve as a mechanism of resource portioning enabling their coexistence.

Keywords: coexistence; *Lophuromys*; *Rhabdomys*; diet; niche breadth; niche overlap; spatial; temporal

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1. Introduction

Diet is a crucial dimension for determining the evolutionary and ecological roles of an organism in its community [1]. Resource partitioning refers to differences in use of food resources by different organisms [2]. The resource partitioning ecological theory explains that sympatric species are more likely to overlap in their niches at spatial-temporal scales [3]. Resource partitioning results in niche overlap and species coexistence through spatial-temporal specialization and the successful use of different food resources [4].

Rodents have dietary preferences that vary over space and time [5–8]. Variations in dietary preference affects diet diversity, niche breadth, and overlap which may result in species coexistence [9,10]. It is anticipated that, rodent's diets are influenced by the spatial-temporal distribution and availability of food resources in their vicinity [7,9–12] which in turn affects rodent reproduction and population fluctuations [13–16]. When resources are abundant rodents become selective and specialize on the most valuable foods which is crucial for reproduction, and consume varieties when food is limited [10–12].

Studies on population ecology and diets of rodents in montane forests and agroecosystems in Australia [13–15] and Philippines [16], have been focused on the major rodent pests such as the house mice of genus *Mus* and the black rats of genus *Rattus*. The studies indicated that, food quality and quantity is a major factor influencing the diets and reproduction of the rodent species [13,14,16].

In Sub-Saharan Africa, research on the population ecology and diets of rodents in agricultural fields and fallow lands have been focused on the most prevalent rodent pests and reservoirs of zoonotic diseases. The multimammate rat (*Mastomys natalensis*) [17–21], the African giant rat (*Cricetomys ansorgei*), gerbils (*Gerbilliscus* spp.), mole rats (*Tachyoryctes* spp.), cane rat (*Thryonomys* spp.), and the striped grass mouse (*Lemniscomys* spp.) have been the subjects of extensive research on the ecology and dietary behavior of rodents [7,11]. These species are of high socio-economic importance to humans because they cause significant damage to crops and property, and transmission of zoonotic diseases [22–25]. Research on the feeding ecology of non-pest rodents including species of genus *Lophuromys* and *Rhabdomys* are scarce despite their important role in ecosystems [5,9].

The harsh-furred rat of the genus *Lophuromys*, is widely distributed across a range of habitats with moist and dense vegetation cover in West, South, and East Africa [26–29]. The African striped mouse of the genus *Rhabdomys*, family Muridae, is likewise a generalist and the most diverse group inhabiting a variety of habitats in both tropical/wet and semi-arid regions [5,27–29].

Species of genus *Rhabdomys* (*Rhabdomys dilectus*) and *Lophuromys* (*Lophuromys acquilus*) are among the most abundant small mammals in rodent populations [27,28] of Mount Kilimanjaro. The two species are sympatric in distribution with overlap in habitat occurrence [27–29]. *Lophuromys acquilus* is endemic to Mount Kilimanjaro and occurs in all habitats along the altitudinal gradient [26]. In contrast, *Rhabdomys dilectus* inhabits predominantly grasslands, agricultural fields, fallow lands, and alpine heath/moorland with the exception of montane forests [27–29]. Clausnitzer et al. [9] and Hanney [30] reported that species of the genus *Lophuromys* are omnivorous, preferentially consuming vegetative materials and insects (especially ants) that are abundant in the rainy season, but other plant parts such as roots and stems are important diets in the dry season [31,32]. Because of this, *Lophuromys* continuously breed throughout the year. On the other hand, *R. dilectus* is an omnivorous species; however, it prefers seeds and grasses/herbs [33–35]. Despite the available knowledge, the feeding habits of *Rabdomys* and *Lophuromys* on Mount Kilimanjaro have not been documented. The mechanisms that influence how the species partition for their resources and coexist together is poorly known. Such knowledge is crucial for understanding the natural history, ecological interactions of rodents (coexistence or competition) in a community as well as their impacts on the environment for management and conservation [7,36]. It aids in understanding breeding patterns of the species due to spatial-temporal food availability for population management and control [23,33,37–40]. In addition, the findings and data of this study can serve as baseline information to ecologists and park managers for decision making on management and conservation practices.

The objective of this study was to determine spatial-temporal variations in dietary consumption of the species. Specifically, (i) to determine percentage occurrence, percentage contribution and relative importance of the dietary items between the species across habitats and seasons; (ii) to determine diet diversity and niche breadth of the species across habitats and seasons; (iii) and to evaluate niche overlap as a proxy to competition or resource partitioning among the two species as a mechanism of coexistence.

2. Materials and Methods

2.1. Study Area

This study is part of an on-going research project on the western slopes of Mount Kilimanjaro, located in northeastern Tanzania in Siha District in Kilimanjaro region 39. The study site is lies between 3°07′ S and 37°35′ E. (Figure 1). The research was in conducted in the Shira route along an altitudinal gradient ranging from 1500 to 3500 a.m.s.l. Mount

Kilimanjaro is characterized by a tropical montane climate with two distinct seasons; dry and wet/rainy. The dry season is from January to February and June to September. The wet season occurs from end October to December, and March to May [41]. The mean annual rainfall in lowlands or the cultivation zone is 700–1800 mm. The mean annual rainfall in montane forest zone ranges from 1000 to 2200 mm. In the heath/moorland zone the mean annual rainfall is 530–1300 mm. In addition, daily temperature range from 21 to 29 °C in lowlands and −6 to −29 °C in highlands (mountain peak zone) [41,42].

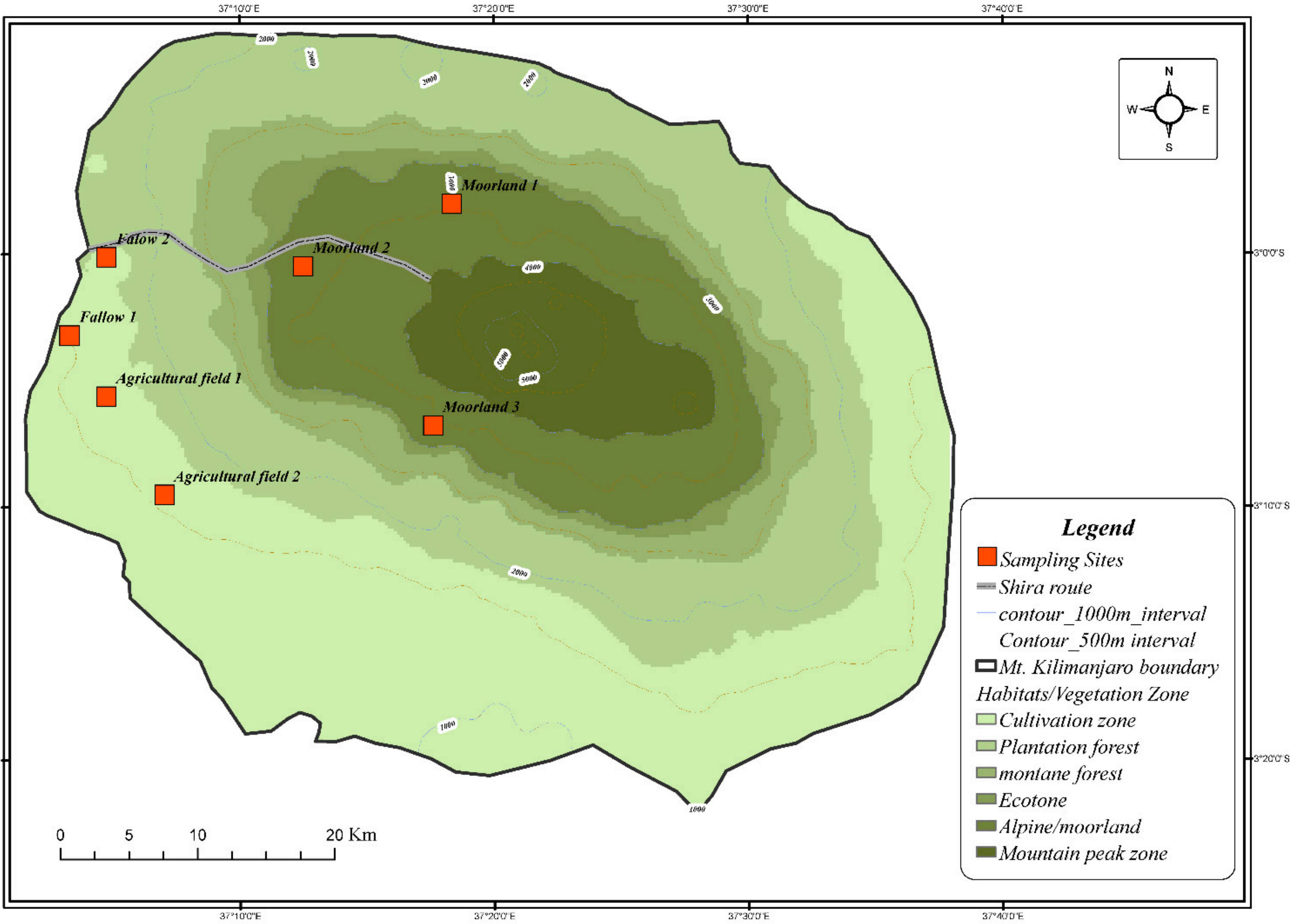


Figure 1. A map of Mount Kilimanjaro showing study sites in the selected three habitats along the Shira route.

The study was conducted in three habitats: agricultural fields, fallow land, and moorland as previously described by Mulungu et al. [27] and Stanley et al., [28]. The three habitats varied in altitude, climate, and vegetation composition and structure. The former two habitats ranged between 1500 and 2400 a.m.s.l. The majority of crops in the agricultural fields were carrots (*Daucus carota*), cabbages (*Brassera oleracea*), green peas (*Pisum sativum*), and Irish potatoes (Solanum tuberosum). Some of the crops were cultivated in a taungya system (crops being grown in between newly planted trees). Consequently, their cultivation depends on the age of the plantation forest. Fallow land is land that is uncultivated for crop rotation or other purposes. Moorland is located in the subalpine zone between 3200 and 4500 a.m.s.l. In this habitat, shrubs and herbs predominate, including *Protea kilimandscharica*, *Kniphofia thomsonii*, and *Lobelia deckenii*. It is dominated by Erica bushes, which eventually changes to *Helichrysum* spp. [42]. Moorland is characterized by extremely cold weathers in the night with temperatures ranging from −1 to 10 °C, while daily temperatures range from 10 to 21 °C.

2.2. Rodent Trapping

Rodent trapping was conducted in three habitats; agricultural fields, fallow land, and moorland using a removal technique with a combination of Sherman live traps (8 × 9 × 23 cm, H.B. Sherman Traps Inc., Tallahassee, FL, USA) and snap traps (1.0 × 8.5 × 16.5 cm). Two sites were randomly selected at a minimum distance of 500 min each of the agricultural fields and fallow land and three sites in moorland.. In each site, five transect lines,50 m long and 10 m apart, were established. A total of 50 traps (25 Sherman live and 25 snap traps) were alternately placed in 5 m trap stations [12,43,44]. Sherman traps were baited with peanut butter mixed with maize flour. Snap traps were baited with coconut smeared with peanut butter. Traps were inspected every morning before 10:00 am for three consecutive nights. All trapped animals were identified to species level following [45]. Animals were weighed and sexed, and reproductive conditions were examined. Head–body length, tail, and hind leg lengths were also recorded. Guidelines were followed on proper methods of researching wild animals of the American Society of Mammologists (ASM) [46]. Animals trapped from Sherman live traps were released, and some were euthanized/killed humanly using Halothene solution soaked in cotton wool and their tissue organs (kidneys and liver) were taken for further research.. Animals killed by snap traps were dissected, their stomachs were removed and preserved in 70% ethanol for diet processing in the laboratory and their carcasses were deposited at the Institute of Pest Management of Sokoine University of Agriculture SUA in Morogoro, Tanzania.

2.3. Assessment of Food Availability

Food availability was assessed by measuring vegetation ground cover, also through assessment of food items such as fruits and seeds from plants, as well as through presence and distribution of ant mounds as indication of invertebrates (mainly ants). Ground cover was measured using 1.0 m × 1.0 m nested quadrants established in same sites use for rodent trapping as conducted by Thomas et al., [39]. Ground cover was estimated as total percentage cover of grasses and herbs in proportion to bare soil from 0 to 100%. Heterogeneous habitats with high ground cover indicated high food availability and vice versa for less ground cover.

2.4. Stomach Dissection and Data Processing

The following methods have been successfully applied in similar studies by [1,7,10,47]; a total of 286 stomachs were dissected, and their contents were spread in a petri dish and cleaned with distilled water. Washing and diluting the contents with distilled water help remove fine particles and improve identification. Each sample was divided into four Petri dishes. The macro food items were identified and grouped using identification keys prepared from natural food items. The keys were compared with observed items (sparts of plants such as leaf epidermis, seed coats/fruits, and invertebrate body parts) under examination microscope at 10× and 40× magnification. Food items were quantified into six major groups/categories namely seeds/fruits, invertebrates, roots, hairs, vegetative materials, and others (items we could not identify). Vegetative materials included but were not limited to plant leaves (monocots/dicots), grasses, stems, and barks. The presence of starch in seeds/grains and fruits was confirmed using Lugol's iodine solution [48]. The observed Seeds were mainly of monocotyledonous and few were of dicotyledonous plants. The majority of the observed invertebrates were insects and termites, along with a few earthworms. However, we did not conduct sampling and identification of plants and animals to species level.

2.5. Data Analysis

Out of the 286 dissected stomachs; only 175 stomachs of the most dominant sympatric species *Rhabdomys dilectus* (n = 103) and *Lophuromys acquilus* (n = 72) were considered for statistical analysis of dietary consumption across habitats and seasons. Stomachs of other species were not considered for analysis due to small sample size and representation across the three habitats

Prior to statistical analysis, the proportion of food items was estimated from counted fragments expressed in percentages as frequency of occurrence and contribution in Excel.

Percentage volume (PV) refers to the ratio of the number of fragments of a particular food item to the total number of identifiable fragments, estimated to nearest 10%. With an extra 5% where the item present contributed less than 10% to total volume (PV). Percentage frequency of occurrence (PC) refers to the number of stomachs containing a certain food category out of the total stomachs.

The percentage frequency of occurrence (PC) was determined as the proportion of the number of stomachs containing a certain food category in relation to all stomachs.

Importance value of each item was calculated as a product of percentage volume and frequency of occurrence of the item (IV = PV × PC/100) [49].

IV is the importance value;

PV is the percentage contribution;

PC is the percentage/frequency of occurrence.

Relative importance/contribution of each food item in the diet was expressed as proportion of importance value of each diet to the importance value of all items multiplied by 100 (IV/∑IV × 100) [7,10,11].

Niche breadth/breadth of utilization was expressed as diet diversity in terms of Levin's index [50]. Estimated by formula:

$$\text{Levins diet diversity index or niche breadth} = 1/\sum \mathrm{Pi}^2$$

where Pi = PV/100 (mean proportion in volume of diet). Levin's index ranges from 1 to n which is the total number of diet items.

Niche breadth or breadth of utilization by:

$$B = 1/\sum_i^n \mathrm{Pi}\hat{}2 = 1/\sum_i^n \mathrm{Ni}\hat{}2/\mathrm{Nt}\hat{}2$$

where B = niche breadth, Pi = proportional of individuals using resource i, Ni = the number of individuals of the species in question in the ith resources state, and Nt = the total number of individuals in all the resources state (n).

Diet diversity was then used to calculate standardized niche breadth at a scale of 0 to 1 following Hurlbert's method [50] with the formula:

$$B_s = (B - 1/n - 1).$$

where B_s = Levin's standardized niche breadth, B = Levin's measure of niche breadth, and n = number of food item categories.

Diet diversity of food items was determined by using Shannon–Weiner diversity index $H' = -\sum pilnpi$. Where H′ = Shannon diversity index and Pi = the proportion of individuals using i food resource (Shannon and Weiner, 1949).

The level of niche overlap was also estimated as a proxy of species co-existence or competition for the resources using Pianka's formula [51,52]

$$\mathrm{Ojk} \; = \sum_i^n \mathrm{Pij} * \mathrm{Pik} \,/ \sqrt{\left(\sum_i^n \mathrm{Pij}^2 * \sum_j^n \mathrm{Pik}^2\right)}$$

where O_{jk} = Pianka's measure of niche overlap between species j (*L. acquilus*) and species k (*R. dilectus*), P_{ij} and P_{ik} = are proportions of the ith resource used by the jth and kth species respectively.

Prior to statistical analysis, percentage occurrence data were arcsine transformed for normal distribution [12]. We used Two-way Analysis of Variance (ANOVA) in R program version 3.6.2 (https://cran.r-project.org/bin/windows/base/old/3.6.2/ [53], accessed on

19 March 2022) to evaluate the percentage occurrence of food items in stomachs of the two species across habitats and seasons. We determined the correlation of body size of individuals with percentage occurrence of food items. Compared body size between the species, sex and sex conditions. Finally, we conducted Mann–Whitney (Wilcoxon rank sum) and Kruskal–Wallis tests to compare mean percentage contributions, diet diversity (Shannon Index) and niche breadth between species across habitats and seasons.

3. Results

3.1. Species Composition

A total of 286 individuals were captured from snap traps. Of the captured individuals, there were 11 species of rodents and 1 (*Crocidura* spp). *Rhabdomys dilectus* was the most abundant species with 36.1% (n = 103) of the total captures across the habitats. *Lophuromys acquilus* was the second most abundant species which comprised 25.17% (n = 72) of the total captures, followed by *Mastomys natalensis* with 24.48% (n = 70) of the total captures across the habitats (Table 1). *M. natalensis* predominantly occurred in agricultural fields and fallow land whereas *R. dilectus* predominated in the moorland.

Table 1. Sample size and percentage % composition (number in parentheses) of rodent species across habitats.

Species	Agricultural Field	Fallow Land	Moorland	Grand Total
Arvicanths niloticus	0(0)	1(0.93)	0(0)	1(0.35)
Crocidura spp.	1(1.1)	2(1.85)	2(2.3)	5(1.75)
Dendromus spp.	0(0)	1(0.93)	3(3.45)	4(1.4)
Aethomys kaiseri	0(0)	2(1.85)	0(0)	2(0.7)
Gramomys dolichurus	0(0)	4(3.7)	0(0)	4(1.4)
Lemniscomys striatus	0(0)	16(14.81)	0(0)	16(5.59)
Lophuromysacquilus	19(20.88)	25(23.15)	28(32.18)	72(25.17)
Mastomys natalensis	41(45.05)	29(26.85)	0(0)	70(24.48)
Otomys spp.	0(0)	1(0.93)	1(1.15)	2(0.7)
Pelomys falax	0(0)	1(0.93)	0(0)	1(0.35)
Praomys delectroum	1(1.1)	4(3.7)	1(1.15)	6(2.1)
Rhabdomys dilectus	29(31.87)	22(20.37)	52(59.77)	103(36.01)
Grand Total	91(100)	108(100)	87(100)	286(100)

3.2. Percentage Occurrence

In general, the overall percentage occurrence of food items did not significantly differ between the two species (W = 13, *p*-value = 1); however, *L. acquilus* had a comparatively higher percentage occurrence of all food items than R. *dilectus*. Diet differed between seasons (W = 611.5, $p = 0.017$) but no differences were observed between habitats (Kruskal–Wallis value = 0.275, df = 2, $p = 0.871$).

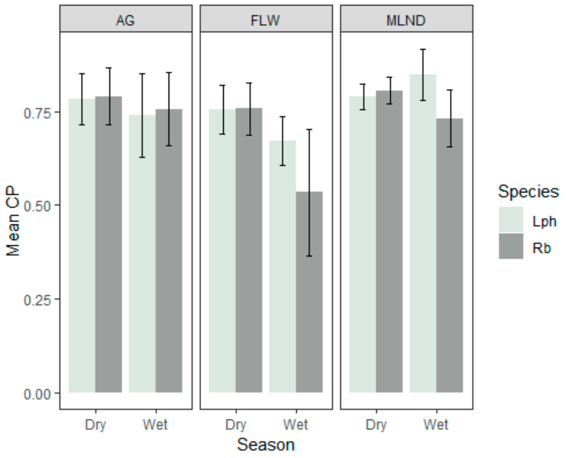
Among the food categories, vegetative materials and seeds/starch predominated in the diets of both species. The percentage occurrence of vegetative materials did not significantly differ between the two species ($F_{1,172} = 0.025$, $p = 0.87$). However, *R. dilectus* had a relatively higher proportion of vegetative materials (>65%). In addition, no significant differences were observed across seasons ($F_{1,172} = 1.256$, $p = 0.26$) and habitats ($F_{2,170} = 1.98$, $p = 0.142$).

Percentage occurrence of seeds/starch significantly differed between seasons ($F_{1,171} = 4.23$, $p = 0.04$), but not between species ($F_{1,171} = 0.94$, $p = 0.33$) and habitats ($F_{2,169} = 2.15$, $p = 0.12$). However, seeds constituted a considerably greater proportion of *R. dilectus*' diet (>58%).

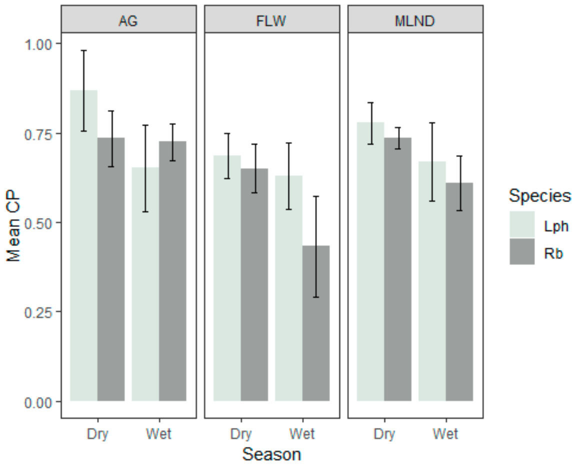
The Percentage occurrence of invertebrates was significantly different between species ($F_{1,171}$ = 32.38, p = 0.000). In addition, it significantly differed across seasons ($F_{1,171}$ = 5.79, p = 0.02) and the interaction between species and seasons ($F_{1,171}$ = 10.04, p = 0.001). Invertebrates occurred in higher frequencies in the stomachs of *L. acquilus*, during wet season (>14%), but no difference was observed across habitats ($F_{2,169}$ = 0.02, p = 0.98).

The percentage occurrence of roots significantly differed between species ($F_{1,\,171}$ = 4.04, p = 0.05). Roots occurred in higher frequencies in the diet of *L. acquilus* (>10%), but no differences were observed between seasons ($F_{1,\,171}$ = 1.51, p = 0.22) and habitats ($F_{2,169}$ = 0.07, p = 0.93).

The percentage occurrence of hairs differed between seasons ($F_{1,169}$ = 8.01, df = 1, p = 0.005). There was higher frequency of occurrence of hairs in dry season. However, there were no difference between species ($F_{1,169}$ = 0.61, p = 0.44) and habitats ($F_{2,169}$ = 1.29, p = 0.28). However, frequency of occurrence of hairs was relatively higher in the stomachs of *L. acquilus*. (Figure 2a–e).

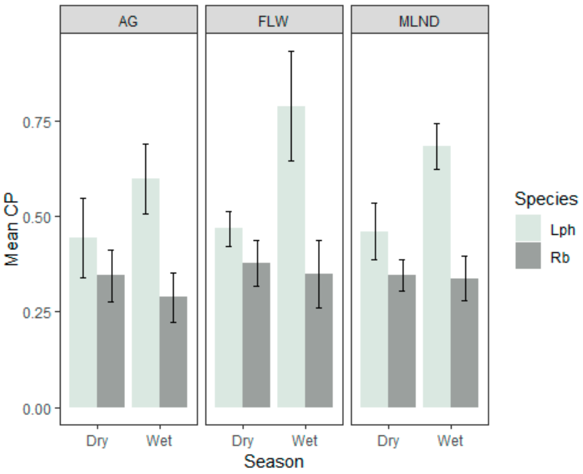


(**a**)



(**b**)

Figure 2. *Cont.*



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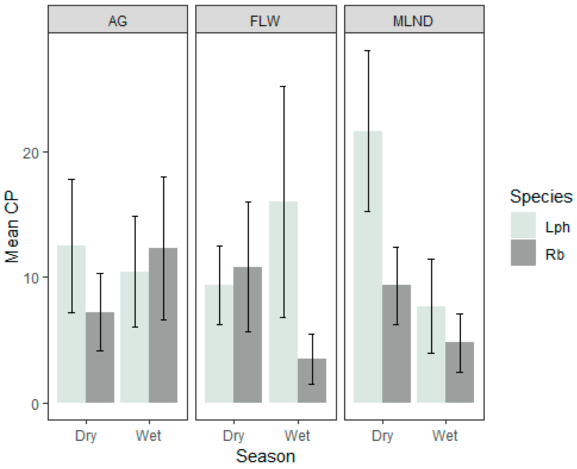

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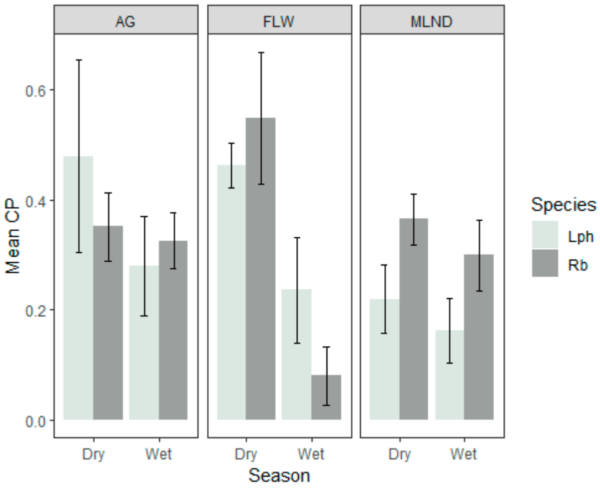


(**e**)

Figure 2. Mean percentage occurrences (CP) for vegetative materials (**a**), seeds/starch (**b**), invertebrates (**c**), roots (**d**), and hair (**e**) of the two rodent species across habitats and seasons. Abreviations: AGR: agricultural fields; FLW: fallow land; MLD: moorland; Lph: *Lophuromys acquilus*; Rb: *Rhabdomys dilectus*.

3.3. Body Size

There was a significant positive correlation between the overall percentage occurrence of food items and body size/weight of the two species; Estimate ± SE, *p*-value (0.003 ± 0.0008, $p < 0.001$) (Figure 3). Moreover, there was a significant difference in body size between the two species ($F_{1,874} = 232.6$, $p < 0.001$), sex ($F_{1,874} = 8.0$, $p = 0.005$), and sex condition ($F_{1,874} = 32.97$, $p < 0.001$). Whereby, *L. acquilus* was significantly larger than *R. dilectus*, males were significantly larger than females, and animals with sexually active conditions were significantly larger than non-active individuals (Figure 4a–c).

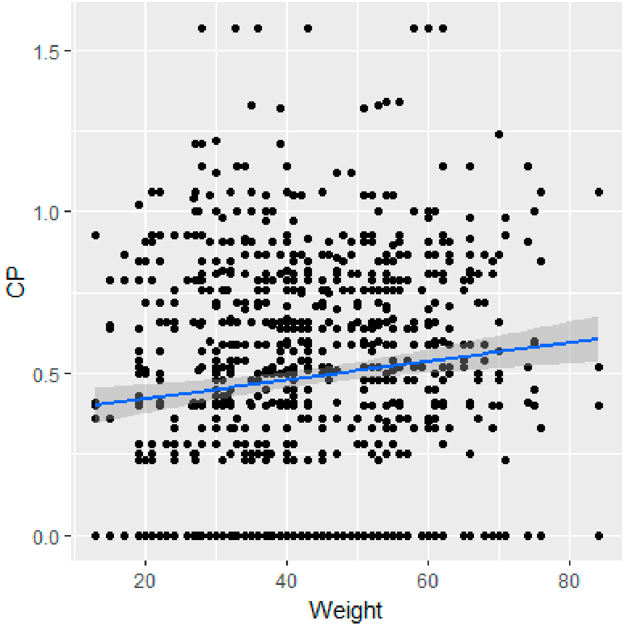
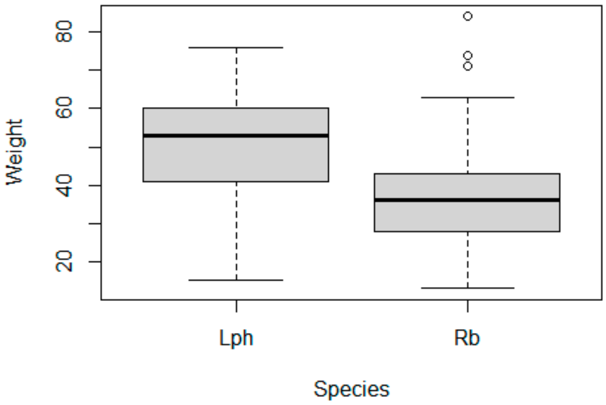
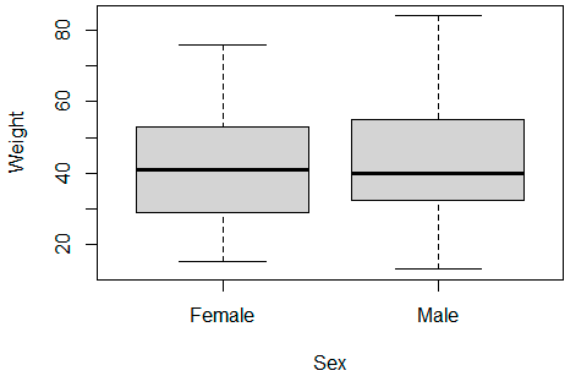


Figure 3. Relationship between the overall percentage occurrence of food items (CP) and weight of speciesPercentage occurrence was moderately positively correlated with weight of rodents as indicated by the blue line.



(**a**)

Figure 4. *Cont.*



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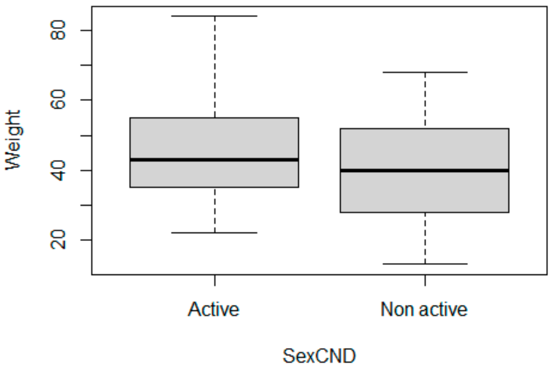

(**c**)

Figure 4. There was a significant difference in body size/weight between the two species (**a**). Moreover, body size significantly differed between sex (**b**) and sex condition (**c**). SexCND = sex condition, Lp = *Lophuromys acquilus*, Rb = *Rhabdomys dilectus*.

3.4. Percentage Contribution

The mean percentage contribution of vegetative materials did not significantly differ between species (W = 7, p = 0.09), seasons (W = 21, p = 0.7), and habitats (Kruskal–Wallis chi-squared = 2.1923, df = 2, p = 0.33).

Seeds/starch were the second most prevalent category and its mean percentage contribution between species was not statistically significant (W = 30, p = 0.06). However, the percentage contribution was relatively higher in *R. dilectus*. There was no significant difference across seasons (W = 21, p = 0.6991) and habitats (Kruskal–Wallis chi-squared = 2.1923, df = 2, p = 0.33).

The third dominant food category was invertebrates whereby percentage contribution was significantly different between species (W = 30, p = 0.05). There was higher percentage contribution of invertebrates to the diet of *L. acquilus*; however, the difference between seasons was not significant (W = 12, p = 0.39). Additionally, there was no significant difference between habitats (Kruskal–Wallis chi-squared = 3.58, df = 2, p = 0.17).

The percentage contribution of other food categories did not contribution of other food categories did not significantly differ between species, across seasons and habitats. However, *L. acquilus* had relatively higher percentage contribution of roots and hair in both habitats and seasons compared with *R. dilectus*.

3.5. Relative Importance

Vegetation materials were the most important food item to the diet of both species across habitats and seasons. It was greater than 29% in moorland, 28% in agricultural fields, and 22% in fallow land across both dry and wet seasons. In addition, seeds/starch was the second most important food category to the diet of both species across habitats and seasons. Invertebrates were remarkably important to the diet of *L. acquilus* in wet season across the three habitats compared with that of *R. dilectus* (Tables 2–4).

Table 2. Relative importance in percentage (%) and sample size (n) of *L. acquilus* and *R. dilectus* in agricultural fields across the 2 seasons.

	Species and Season			
	L. acquilus		***R. dilectus***	
	Dry (n = 8)	**Wet (n = 11)**	**Dry (n = 18)**	**Wet (11)**
Seeds/Starch	29.83	23.80	28.86	29.70
Vegetative materials	28.98	32.32	32.38	33.03
Roots	5.33	4.22	2.30	4.84
Hairs	8.31	4.41	6.40	5.81
Invertebrates	13.05	16.23	10.99	6.89
Others/Unidentified	14.49	19.03	19.07	19.73

Table 3. Relative importance in percentage (%) and sample size (n) of *Lophuromys acquilus* and *Rhabdomys dilectus* in fallow land across the 2 seasons.

	Species and Season			
	L. acquilus		***R. dilectus***	
	Dry (n = 15)	**Wet (n = 10)**	**Dry (n = 12)**	**Wet (n = 10)**
Seeds/Starch	23.46	19.52	25.15	16.44
Vegetative materials	29.04	27.71	29.66	22.31
Roots	4.18	5.29	4.73	1.37
Hairs	9.76	2.65	12.21	0.52
Invertebrates	27.64	31.57	14.72	14.40
Others/Unidentified	18.92	20.26	16.53	31.96

Table 4. Relative importance in percentage (%) and sample size (n) of *Lophuromys acquilus* and *Rhabdomys dilectus* in moorland habitat across the 2 seasons.

	Species and Season			
	L. acquilus		***R. dilectus***	
	Dry (n = 15)	**Wet (n = 13)**	**Dry (n = 30)**	**Wet (n = 22)**
Seeds/Starch	27.66	23.27	29.58	23.03
Vegetative materials	29.75	37.85	33.10	32.93
Roots	11.08	1.92	2.80	1.41
Hairs	2.23	1.32	6.42	5.35
Invertebrates	13.02	14.54	8.49	10.11
Others/Unidentified	16.27	21.09	19.62	27.17

3.6. Diet Diversity, Niche Breadth, and Overlap

Niche breadth of the two species was significantly different ($F_{1,9} = 18.50$, $p = 0.002$). *L. acquilus* had a significantly higher niche breadth and food diversity compared with that of *R. dilectus*. There were no statistically significant variations in niche breadth between seasons ($F_{1,9}$ = 1.066, p = 0.329) and habitats ($F_{2,8}$ = 0.92, p = 0.437) (Table 5).

Table 5. Niche breadth, diet diversity (in parentheses), and niche overlap (O_{jk}) between species j (*L. acquilus*) and species k (*R. dilectus*) across the habitats (AG: agricultural field; FLW: fallow land; and MLND: moorland) and seasons. Niche breadth or Levin's Index of food diversity ranges from 0 to 1, where 1 = highest diversity and 0 = lowest diversity, also niche overlap ranges from 0 (no overlap) to 1 (total overlap).

Species	**AG**		**FLW**		**MLND**	
	Dry	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**
L. acquilus	0.83 (1.7)	0.87 (1.72)	0.83 (1.7)	0.95 (1.77)	0.9 (1.75)	0.86 (1.70)
R.dilectus	0.78 (1.66)	0.78 (1.67)	0.80 (1.69)	0.81 (1.67)	0.79 (1.67)	0.78 (1.66)
Niche overlap (O jk)	**0.94**	**0.84**	**0.98**	**0.86**	**0.88**	**0.84**

Moreover, diet diversity (Shannon Index) significantly differed between species ($F_{1,9}$ = 15.06, p = 0.004) but not between seasons ($F_{1,9}$ = 0.06, p = 0.814) and habitats ($F_{2,8}$ = 0.76, p = 0.5). In addition, there was a considerable niche overlap in the diets of *L. acquilus* and *R. dilectus* across habitats and seasons, ranging from 0.84 to 0.98. However, niche overlap in the diets of both *L. acquilus* and *R. dilectus* was much greater during the dry season than the rainy season (Table 5).

4. Discussion

In the current study, *Lophuromys acquilus* and *Rhabdomys dilectus* consumed all the examined food items across habitats and seasons. Our study corroborates with previous studies in eastern Africa, which indicated that most rodents (including the two species) are diet generalists or omnivorous [7,10,11,54–56]. Omnivory may account for a successful wide distribution range of *L. acquilus* and *R. dilectus* on Mount Kilimanjaro and elsewhere [27,45,57]. Generally, the percentage occurrence, percentage contribution, and relative importance of invertebrates varied between the two species. This can serve as a mechanism of resource partitioning between them enabling their coexistence in a community. On the other hand, vegetative materials and seeds predominated in the diets of both *L. acquilus* and *R. dilectus* in all habitats and seasons. However, vegetative materials were significantly important to both species whereas seeds were relatively important to *R. dilectus*. Both species consumed the highest proportions of vegetative materials compared with other food items, presumably because plants are the most abundant food supply throughout the year [5]; hence, both species rely on them as their primary food source. Moreover, during the rainy season, vegetative materials have a high primary productivity and nutritional content, serving as a significant source of energy for reproduction [58]. This corroborates with the breeding of many rodents, especially *Mastomys natalensis* which is associated with rainfall [19,36,38,59]. Rainfall influences the availability of vegetative resources [10,11]. Similarly, Mlyashimbi et al. [47] and Mulungu et al. [7,10,12] reported that the higher proportions of vegetative materials consumed by *M. natalensis* during wet season were positively correlated with its reproductive activity. It is believed that newly sprouted green plants and germinating seeds are a significant source of high-quality food. Green plants and germinating seeds are reported to be rich in plant hormones such as gibberellic acid or 6-MBOA which triggers the onset of breeding in *M. natalensis* [47] and the majority of granivorous rodents, such as the house mouse (*Mus musculus* and *Arvicanthis neumanni*) [13,14,60–62].

Invertebrates were important food items in the diet of *L. acquilus* during wet season. The higher number and nutritional content of invertebrates in wet season likely explains our observation [9,11,63]. However, we did not measure the availability of invertebrates. Our results are consistent with those of Clausnitzer et al. [9,55] on Mount Elgon in Uganda, who reported that species of the same genus (*Lophuromys flavopanctatus*) consumed more invertebrates during wet season, which corresponds with the high abundance and nutritional importance of invertebrates as a high-value protein source necessary for growth and reproduction [37]. Similarly, studies by Hanney [30] and Cole [64] in Malawi and Ghana, respectively, reported that the diet of *Lophuromys* was more than 80% invertebrates. Further, the species significantly relies on invertebrates as they could not survive for more than a week in captivity without being fed on invertebrates [30]. In addition, Monadjem [40] reported an increase in the proportion/number of invertebrates in the stomachs of *M. natalensis* during the wet season; it is during this season when most rodents breed [19,38,39,47,59].

Lophuromys acquilus had a considerably higher diet diversity and a broader niche breadth across habitats and seasons. The higher breadth of food spectrum indicates that *L. acquilus* unlike *R. dilectus* is a generalist species adapted to both disturbed and less favorable environments [45,55]. This is evident from a successful wider distribution range of genus *Lophuromys* across all habitats above 500 a.m.s.l., which suggests generalist behaviour [32,45]. Further, it is suggests that other food items such as roots, stems, and hair serve as important food to *L. acquilus* during the dry season when food availability appears to be limited [31,32]. However, the presence of hair in the diets of rodent species might be the result of grooming or occasional necrophagy [25,30]. Consistently, species of the same genus, *Lophuromys flavopanctatus,* was reported to feed on remains of dead rodents (including its own kind) and small vertebrates such as frogs [9,30]. On the other hand, the lower diet diversity and niche breadth of *R. dilectus* were likely attributable to less proportions of invertebrates. *R. dilectus* prefers plants specifically grasses and grass seeds as its primary food source. In accordance with the findings of Curtis and Perrin [5], *R. dilectus* preferentially selected fruits and seeds as well as leaves and other vegetative parts of shrubs in the laboratory. Furthermore, it is reported that *Rhabdomys* species are predominantly herbivorous or granivorous in their natural environment [35]. They preferentially consume grasses and seeds and are more adapted to grass lands, hence commonly known as the grass rats [9,35,45,55,57]. For that case, *R. dilectus* plays an important role in seed dispersal in tropical savanna and grassland regions [33,54].

In addition, significantly high niche breadth and diet diversity of *L. acquilus* can be attributed to morphological differences with *R. dilectus*. *L. acquilus* was significantly larger than *R. dilectus* hence the higher diet diversity and niche breadth. It has been suggested that morphological differences result into variations in niche breadth serving as a mechanism of coexistence between species [34,65]. Consistently, a study by Mulungu et al. [7] found that differences in diet diversity and niche breadth between *M. natalensis* and *Gerbilliscus Vicinus* were attributed to their differences in body size.

The overall diet diversity/niche breadth was relatively higher in fallow land, followed by agricultural fields, and lowest in moorland. This was attributed to the fact that fallow land is more heterogeneous, with high ground cover and vegetation density, which provide supplementary food to rodents inhabiting these areas. Fallow lands provide refuge during off-cropping season to rodents inhabiting agricultural fields. Moreover, high diet diversity in agricultural fields can be due to supplementary food in form of seed/grains during the cropping season [11,66]. However, increasing deforestation and use of pesticides/insecticides in agricultural fields result in habitat destruction and fragmentation, which affects food availability by reducing ground cover and the abundance of invertebrates [66]. In contrast, the lowest niche breadth in the moorland can be attributed to poor climate and harsh weather conditions which affect primary productivity of plants hence reduced food availability [55]. Furthermore, extreme cold and harsh weather conditions affect the activity patterns and foraging behaviour of rodents [55].

There was a considerable niche overlap in diet of the two species across habitats and seasons. Niche overlap was relatively greater in the dry season probably due to sharing of food sources among the species, suggesting that there would be some degree of competition for the shared foods when in limited supply [2,67]. However, the smaller niche overlap during wet season was probably due to high consumption of invertebrates by *L. acquilus*. This observation supports the Optimal Foraging Theory (OFT) which suggests that species utilization of food resource is contingent on its availability and spatial-temporal distribution in the environment [3,51]. When food resources are abundant, species tend to become more selective and specialized and eat varieties when food availability is limited in order to meet their nutritional needs [12,54]. Specialization enables the use and sharing of the available food resources among the species without compromising one another [2,4]. Therefore, high consumption of invertebrates by *L. acquilus* can help reduce competition among the species, allowing them to coexist in habitats of west Mount Kilimanjaro. Consistently, a study by Clausnitzer et al. [9], on Mount Elgon in Uganda reported a considerable niche overlap in the diets of *L. flavopanctatus* and *Crocidura*. However, the rodent species segregated their diets during wet season by consuming distinct invertebrate species. This reduced competition over the resources enables their coexistence in the Afro-alpine environments. However, in this study we did not identify invertebrates to the species level making it difficult to identify niches of the two species in question.

Apart from the differences in dietary consumption, variations in evolutionary traits enables coexistence of sympatric species through differential use of food resources [25,34,65]. For instance, variations in activity patterns of rodents can serve as a mechanism of coexistence through partitioning in time of use which reduces inter-specific competition [2,25,34,65]. *L. acquilus* and *R. dilectus* have differences in activity patterns and foraging behavior, which likely limit intraspecific competition among them. According to Haney [30], *L. acquilus* is a nocturnal species although it occasionally forages during the day; *R. dilectus,* in contrast, is strictly diurnal [5,57,68,69]. Consequently, despite the observed niche overlap in the consumption of food resources, the differences in activity patterns of the two species may serve as an additional mechanism for their coexistence on Mount Kilimanjaro and elsewhere.

5. Conclusions and Recommendations

The general conclusion is that, dietary consumption of *L. acquilus* and *R. dilectus* on Mount Kilimanjaro is reflective of the spatial-temporal availability of food resources and habitat heterogeneity. There were spatial-temporal variations in the dietary consumption of *L. acquilus* and *R. dilectus*. Both species consumed more of vegetative materials, seeds/starch, and invertebrates. However, invertebrates were more important to the diet of *L. acquilus* than *R. dilectus*. Moreover, *L. acquilus* had a significantly larger niche breadth and diet diversity compared with *R. dilectus.* Both *L. acquilus* and *R. dilectus* were omnivorous, they consumed most food items in same proportions across both habitats and seasons, resulting in a substantial niche overlap between them. However, the reported larger niche overlap does not suggest competition. High invertebrate consumption by *L. acquilus* during the wet season might have resulted in niche segregation and reduced interspecific competition enabling their coexistence.

To the best of our knowledge, this is the first study in Tanzania on variations in dietary consumption of *R. dilectus* and *L. acquilus*. Therefore, it contributes to general understanding of the feeding ecology of rodents and paves a way for conservation and management of the species, particularly *L. acquilus,* which is endemic to Mt Kilimanjaro.. However, the results are preliminary and lack identification of dietary items to species level. Future research should take into account the assessment of food availability including sampling of invertebrates and identification of food items using DNA metabarcoding. Such information would determine which plant and animal species are mostly preferred by rodents for effective management and conservation of the rodent community on Mount Kilimanjaro. Moreover, it is important to elucidate the question of activity patterns of the two species as a mechanism of coexistence, and the importance of diets to their survival and reproduction.

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Data Availability Statement: Authors agree to deposit the data associated with this study in an Institutional repository of Sokoine University of Agriculture and it will be publicly available once the manuscript is accepted for publication at Journal of Diversity.

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